2-12-2009

Celebrating Darwin's Legacy: Evolution in the Galapagos Islands and the Great Plains

Paul A. Johnsgard
University of Nebraska-Lincoln, pajohnsgard@gmail.com

Celebrating Darwin's Legacy

EVOLUTION IN THE GALÁPAGOS ISLANDS AND THE GREAT PLAINS

1. Lazuli Bunting *Passerina amoena*
2. Indigo Bunting *Passerina cyanea*
3. Lazuli x Indigo hybrid

FEBRUARY 12 - MARCH 29, 2009
GREAT PLAINS ART MUSEUM

Celebrating Darwin's Legacy

Evolution in the Galápagos Islands and the Great Plains

Paul A. Johnsgard

Guest Curator

An exhibition of photographs by Linda R. Brown, Josef Kren, Paul A. Johnsgard, Allison Johnson, and Stephen Johnson; paintings by Allison Johnson; drawings by Paul A. Johnsgard; and related Darwiniana. Sponsored by the Center for Great Plains Studies, James Stubbendieck, director, and the Great Plains Art Museum, Amber Mohr, curator, in honor of the bicentennial of Charles Darwin's birth (1809–2009) and the 150th anniversary of *The Origin of Species* (1859).

Great Plains Art Museum

February 12–March 29, 2009

Exhbition Catalog

GREAT PLAINS ART MUSEUM
UNIVERSITY OF NEBRASKA–LINCOLN
1155 Q STREET, HEWIT PLACE
LINCOLN, NE 68588-0250

Cover image: Allison Johnson. "Male lazuli (*Passerina amoena*, left), indigo (*Passerina cyanea*, right), and hybrid (middle) buntings," 2008, graphite and acrylic, 11 x 14 in. These two species are closely related and are mostly geographically isolated, the Lazuli in the scrub woodlands of the western Great Plains and the Indigo in the deciduous forest edge of the eastern Great Plains. They often hybridize where their ranges overlap along the Platte and Niobrara valleys, indicating their close evolutionary relationships and common ancestry.

ISBN 10: 0-938932-19-5

Acknowledgments

Costs of printing this booklet were provided by the Center for Great Plains Studies. The exhibition was made possible through the cooperation of the Great Plains Art Museum and the Center for Great Plains Studies. Dr. Stephen Johnson helped greatly with printing the photographs and collecting many of the rare items of Darwiniana that are in the exhibit. The original idea of a bicentennial Darwin exhibit was first discussed with the Great Plains Art Museum's then-curator Reece Summers, and it was enthusiastically endorsed by Amber Mohr when she began serving as museum curator in 2007. The advice and support of the Center for Great Plains Studies, and its director James Stubbendieck, made the exhibit possible. The center's editorial staff directed the editing, layout, and printing of this booklet, which is greatly appreciated.

Undertaking the Galápagos observations and selecting, assembling, and preparing the associated photographs, drawings, and paintings for our exhibit was a collaborative effort equally involving Linda Brown, Allison Johnson, Josef Kren, and myself. It could not have been done without the total effort and support of all of these people and many others. To all the people who helped with both the Galápagos and Great Plains fieldwork and research, we offer our sincere thanks.

Preface

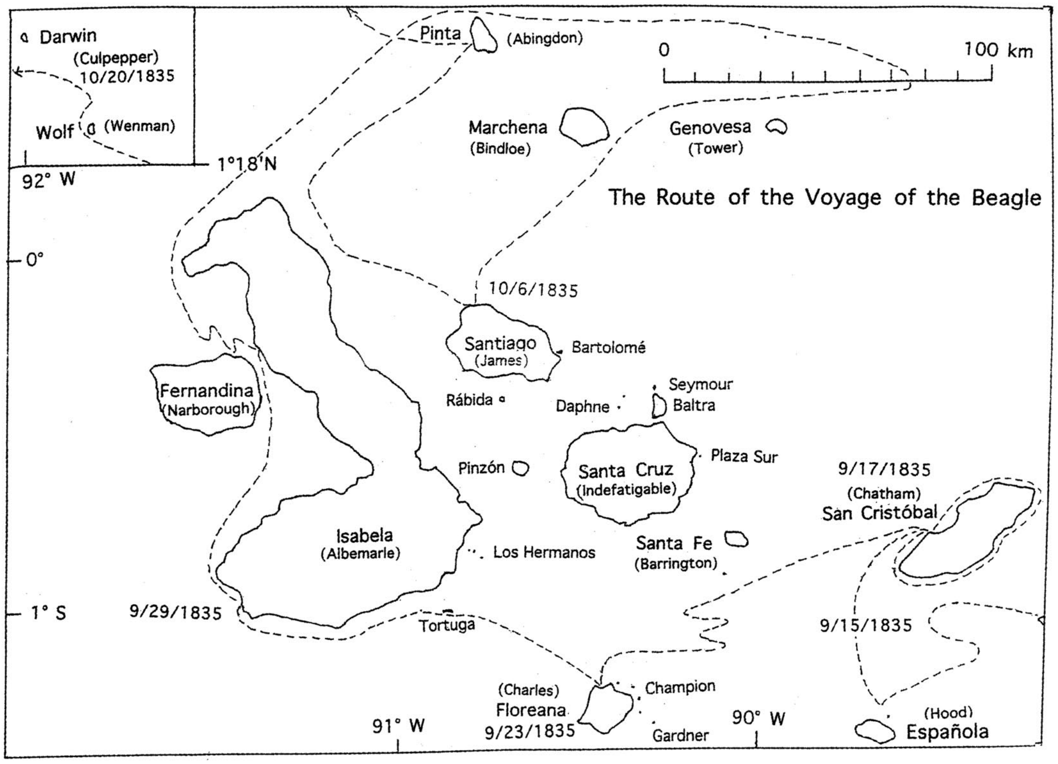
NOT LONG AGO I made a late fall visit to Indian Cave State Park, located in the southeastern corner of Nebraska along the Missouri River. Cirrus clouds warned of impending cold weather; and skeins of snow geese, refugees of the Pleistocene, were headed south toward warmer lands. I stopped at an overlook that provided a spectacular panoramic view of the entire ten-mile-wide valley, and I tried to imagine what Charles Darwin would have thought and concluded if he had been there standing alongside me. With his practiced geologist's eyes, I suspect that he would have noted that the present-day Missouri River is now too small to account for the enormously wide and deep valley it flows through. Perhaps he might have guessed that it must have once been a much more mighty river, carrying water of vast melting glaciers from the north and eroding out the present-day valley over the past ten or twenty thousand years.

From my vantage point, I could not see any of the boulders that had been carried by the southernmost glacial lobe as it reached south as far as northern Kansas. On retreating, the glacial ice randomly dumped and spread countless rocks and boulders, along with other ice-borne materials, over much of present-day easternmost Nebraska and western Iowa. The land I was standing on was a mixture of glacial till and the accumulation of wind-blown loess that had been carried in from far to the west, probably during interglacial times. Perhaps Darwin might have associated such glacial landscape features with those of Scotland and Wales, where he had taken geological field trips during his undergraduate years.

Beneath the till and loess is a thick layer of sandstone (Indian Cave Sandstone), the remnants of sediments laid down in a marine environment about 300 million years ago. It had been eroded away to form a sheer cliff at least fifty feet thick. In some areas its surface shows an irregular pattern of almost-parallel lines touching one another at shallow angles, where underwater sandbars in a wide river valley had moved the sand back and forth as a result of current variations. This cross-bedding shows that the area was once submerged, and the alternating layers of sandstone and shale reflect rising and falling periods of sea-level changes. During this time, giant dragonflies would have flitted about above the swamp surface, primitive fern-like trees and some of the earliest seed-bearing plants would have been present. Early reptiles would have strived to occupy and dominate this rich environment. Many of these swamp-living reptiles were probably amphibious fish eaters, resembling modern crocodiles; but unlike amphibians, they would have laid shelled eggs that could develop and hatch on land. Freeing themselves from water, these early reptiles began to consume land plants, insects, and other land invertebrates, starting the evolutionary diversification (i.e., adaptive radiation, in Darwin's terms) that would have eventually led to mammals and birds.

Below the sandstone is a thin layer of coal that represents a coastal swamp that was eventually drowned by the rising sea, gradually converting the dead organic materials to coal. Darwin would have certainly recognized the coal and probably associated it with the thick beds of coal present in the English Midlands, laid down during the corresponding Carboniferous period. He might also have observed some thick layers of limestone that are exposed in nearby ravines and reflect the shallow marine environment that existed a few million years later. This layer, too, has its counterpart in England, and finding it would have no doubt excited Darwin. Still farther below, and not visible anywhere in Nebraska, are the older Paleozoic (225–570 million years ago) and Precambrian (prior to 570 million years ago) layers of metamorphic and igneous rocks. During these ancient times, the earliest stages of life on Earth evolved, a period that nonetheless represents a fairly advanced time relative to Earth's total four billion–year history.

In one area, the sandstone erosion has produced a shallow cave. Engraved on the nearly vertical walls are some faint pictographs, now mostly obscured by the juvenile scribblings of modern-day tourists. The pictographs portray bison, elk, and other less recognizable figures, proving that some 1,500 years ago the surrounding land was rich with big game and supported a thriving Native American culture. That culture, along with the bison and elk, is long gone from the area. Gone, too, are the Carolina parakeet and passenger pigeon, which in Darwin's day would



The 1835 route of H.M.S. Beagle in the Galápagos Archipelago. Map by Paul A. Johnsgard.

have lived in this part of the Missouri Valley but which became rare and finally extinct as a result of uncontrolled hunting early in the twentieth century.

Darwin knew that extinction is a vital part of evolution's slow but inexorable progress, and it is now increasingly separating those species that are able to adapt to human-driven environmental change from the many that will not be able to deal with the effects of global warming and environmental degradation. Added to the extinction of these species will be the effects of natural selection on humans, too—owing to still-uncontrolled global human population increases, a fundamental component of Malthusian and Darwinian theory.

If Darwin had wandered through the nearby forest, he would have seen oaks, lindens, ashes, and hornbeams, each only slightly different from counterpart species that he would have known well from his beloved Kent countryside. The half-dozen species of oaks in the nearby forest would have given him ideas on interspecies variability within a familiar genus, but he would have been puzzled by the pawpaw and redbud trees, which are unknown in England. Both are North American specialties and are relict survivors of the great temperate hardwood forest (the Arcto-Tertiary flora) that occupied much of southeastern North America in preglacial times. Darwin certainly would have wanted to collect specimens from these unique trees for further study!

Also in the forest canopy were some busily foraging black-capped chickadees and loose flocks of migrating American robins. Darwin would have immediately recognized the chickadee as a very close relative of English titmice, and the robin as a near relative of the mistle thrush. Like the general similarities Darwin noticed between the birds of the Pacific coast of South America and those of the Galápagos Islands, these species probably would have set Darwin to thinking about possible historic geographic connections linking the bird faunas of America and Europe.

Unfortunately, my vision of visiting with Charles Darwin was only a daydream; but we have been left with a lifetime of his writings that cover large areas of geology, paleontology, botany, and zoology and that pose evolutionary questions and ideas that continue to occupy modern science. What more could a nineteenth-century scientist ask for?

Exhibitor Information

EXHIBITORS

Linda R. Brown, Lincoln, Nebraska. B.S. (Pharmacy) University of Nebraska-Lincoln, Lincoln, NE, 1965.

Paul A. Johnsgard, Lincoln, Nebraska. Foundation Professor Emeritus, University of Nebraska-Lincoln. B.S. (Zoology) North Dakota State University, Fargo, ND, 1953; M.S. (Wildlife Management) Washington State University, Pullman, WA, 1955; Ph.D. (Vertebrate Zoology), Cornell University, Ithaca, NY, 1959.

Allison Johnson, Scottsbluff, Nebraska. Undergraduate (Biology) St. Olaf College, St. Olaf, MN.

Stephen Johnson, Scottsbluff, Nebraska. B.S. University of Utah, Salt Lake City, UT, 1971; Ph.D. (Anatomy) University of Utah, Salt Lake City, UT, 1976; M.D. University of Vienna, Vienna, Austria, 1980.

Josef Kren, Lincoln, Nebraska. B.S. Jan Evangelista Purkyne University, Czech Republic, 1985; Ph.D. (Vertebrate Zoology) University of Brno, Czech Republic, 1989; Ph.D. (Ornithology) University of Nebraska-Lincoln, Lincoln, NE, 1996.

EXHIBITORS' STATEMENT

UNDERTAKING THE GALÁPAGOS OBSERVATIONS and selecting, assembling, and preparing the associated photographs, drawings, and paintings for our associated exhibit was a collaborative effort equally involving L. Brown, P. Johnsgard, A. Johnson, and J. Kren. It could not have been done without the total effort and support of many others, including Dr. Stephen Johnson, who printed nearly all the photographic images and also loaned many important items of Darwiniana. During June 2005, four of us spent eleven days travelling throughout the Galápagos Archipelago via a commercial yacht. We traveled 640 nautical miles, making landfalls at twelve islands—including all four of those visited by Darwin, sometimes landing on the same beaches he visited—and took sixteen hikes in search of plants and animals. We photographed fifty-four bird species, eleven reptiles, and five native mammals. We also photographed about fifty plant species, including many of those that were first collected by Darwin and subsequently described as new species or genera. Images were later drawn, painted, or photographed in order to illustrate comparable evolutionary phenomena and processes occurring on the Great Plains and to point out that evolution is a process that can be observed in our own back yards as well as in such exotic locations as the Galápagos Islands.

Art Checklist

GALÁPAGOS PHOTOGRAPHS

BY LINDA R. BROWN (LRB), JOSEF KREN (JK), ALLISON JOHNSON (AJ), AND PAUL A. JOHNSGARD (PAJ).

Galápagos Landscape, Bartolome Island. 13" x 19" (JK)

Galápagos Red-Footed Booby (*Sula sula websteri*). Two 13" x 19" images (AJ)

Nazca Booby (*Sula granti*). 13" x 19" (AJ)

Galápagos Flycatcher (*Myriarchus magnirostris*). 9.5" x 13" (JK)

Galápagos Blue-Footed Booby (*Sula nebouxii excisa*). 9.5" x 13" (JK)

Galápagos Blue-Footed Booby (*Sula nebouxii excisa*). 9.5" x 13" (LRB)

Galápagos Penguin (*Spheniscus mendiculus*). 13" x 19" (PAJ)

Galápagos Flightless Cormorant (*Phalacrocorax harrisi*). 9.5" x 13" (JK)

Galápagos Lava Heron (*Butorides sundevalli*). 9.5" x 13" (PAJ)

Galápagos Great Blue Heron (*Ardea herodias cognata*). 13" x 19" (AJ)

Galápagos Yellow-Crowned Night Heron (*Nyctanassa violaceus pauper*). 13" x 19" (AJ)

Magnificent Frigatebird (*Fregata magnificens*). 9.5" x 13" (PAJ)

Galápagos Great Frigate Bird (*Fregata minor ridgwayi*). 13" x 19" (PAJ)

Galápagos Great Frigate Bird (*Fregata minor ridgwayi).* 9.5" x 13" (PAJ)

Galápagos Great Frigate Bird (*Fregata minor ridgwayi*). 13" x 19" (JK)

Waved Albatross (*Diomedea irrorata*). 13" x 19" (JK)

Red-Billed Tropicbird (*Phaethon aethereus*). 13" x 19" (AJ)

Galápagos White-Cheeked Pintail (*Anas bahamensis galapagensis*). 9.5" x 13" (JK)

Galápagos Vermilion Flycatcher (*Pyrocephalus rubinus nanus*). 13" x 19" (JK)

Galápagos Flycatcher (*Myriarchus magnirostris).* 9.5" x 13" (JK)

Galápagos Hawk (*Buteo galapagoensis*). 13" x 19" (PAJ)

Galápagos Yellow Warbler (*Dendroica petchia aureola*). 9.5" x 13" (PAJ)

Lava Gull (*Larus fuliginosus*). 9.5" x 13" (PAJ)

Swallow-Tailed Gull (*Larus furcatus*). 9.5" x 13" (PAJ)

Galápagos Dove (*Zenaida galapagoensis*). 9.5" x 13" (JK)

Galápagos Mockingbird (*Mimus parvulus*) and Lava Lizard (*Microlophus albemarlensis*). 13" x 19" (PAJ)

Galápagos Mockingbird (*Mimus parvulus*). 9.5" x 13" (LRB)

Hood Island Mockingbird (*Mimus macdonaldi*). 9.5" x 13". (PAJ)

Galápagos finch nest. 9.5" x 13" (LRB)

Large Ground Finch (*Geospiza magnirostris*). 9.5" x 13" (PAJ)

Genovesa Sharp-Billed Ground Finch (*Geospiza d. difficilis*) 9.5" x 13" (LRB)

Espanola Large Cactus Finch (*Geospiza c. conirostris*). 9.5" x 13" (LRB)

Medium Ground Finch (*Geospiza fortis*). 9.5" x 13" (PAJ)

Small Ground Finch (*Geospiza fuliginosa*). 9.5" x 13" (AJ)

Woodpecker Finch (*Camarhynchus pallidus*). 9.5" x 13"(AJ)

Medium Tree Finch (*Camarhyncus pauper*). 9.5" x 13" (PAJ)

Warbler Finch (*Certhidea olivacea*). 9.5" x 13" (PAJ)

Cactus Finch (*Geospiza scandens*) and Medium Ground Finch (*Geospiza fortis*). 13" x 19" (PAJ)

Galápagos California Sea Lion (*Zalophus californicus wollebacki*). 13" x 19" (LRB)

Galápagos California Sea Lion (*Zalophus californicus wollebacki*). 9.5" x 13" (PAJ)

Galápagos California Sea Lion (*Zalophus californicus wollebacki*). 9.5" x 13" (LRB)

Fernandina Marine Iguana (*Amblyrhynchus c. cristatus*). 13" x 19" (AJ)

Fernandina Marine Iguana (*Amblyrhynchus c. cristatus*). 13" x 19" (JK)

Santa Cruz Giant Tortoise (*Geochelone elephantophus porteri*). 13" x 19"(JK)

Santa Cruz Giant Tortoise (*Geochelone elephantophus porteri*). 9.5" x 13" (LRB)

Espanola Giant Tortoise (*Geochelone elephantophus hoodensis*). 13" x 19" (PAJ)

Pinta Island Giant Tortoise (*Geochelone elephantophus abingdoni*). 9.5" x 13" (PAJ)

Santa Fe Iguana (*Conolophus pallidus*). 13" x 19" (PAJ)

Galápagos Land Iguana (*Conolophus subcristatus*). 13" x 19" (AJ)

Geographic and Sexual Variation in Lava Lizards (*Microlophis* spp.). Four 9.5" x 13" images. (AJ and PAJ)

Central Galápagos Racer (*Alophus biseralis dorsalis*). 9.5" x 13" (AJ)

Galápagos Painted Locust (*Shistocerca melanoceros*). 9.5" x 13" (AJ)

Galápagos Silver Argiope Spider (*Argiope argentata*). 9.5" x 13" (JK)

South Plaza Prickly Pear (*Opuntia e. echios*). 13" x 19" (JK)

Santa Fe Prickly Pear (*Opuntia echios barringtonensis*). 13" x 19" (LRB)

San Cristobal Candelabra Cactus (*Jasminocereus t. thouarsii*). 13" x 19" (LRB)

Tree Scalesia (*Scalesia pedunculatus*). 13" x 19" (PAJ)

Lava Cactus (*Brachicereus nesoticus*). 9.5" x 13" (LRB)

GREAT PLAINS PHOTOS

(BY PAUL A. JOHNSGARD EXCEPT AS NOTED)

Dwarf (Silver) Sagebrush (*Artemisia cana*). Great Plains Art Collection. 16" x 24"

Prickly Pear Cactus (*Opuntia* sp.) and Bison (*Bison bison*) Skull. Great Plains Art Collection. 16" x 24"

Purple Prairie-Clover (*Petalostemon purpureum*). Great Plains Art Collection. 16" x 24"

White Prairie-Clover (*Petalostemon candida*). Great Plains Art Collection. 16" x 24"

Bigroot Cactus (*Opuntia humifusia*) and Slant-Faced Grasshopper (Gomphocerinae). 13" x 19"

Soapweed (*Yucca glauca*). 13" x 19"

Yucca Moth (*Teticula yuccasella*). 13" x 19"

Coyote (*Canis latrans*). Great Plains Art Collection. 16" x 24"

Swift Fox (*Vulpes velox*). 13" x 19"

Black-Tailed Prairie Dog (*Cynomys ludovicianus*). 13" x 19" (LRB)

Richardson's Ground Squirrel (*Spermophilus richardsonii*). Great Plains Art Collection. 16" x 24"

Bison (*Bison bison*). Great Plains Art Collection. 16" x 24"

Pronghorn (*Antilocarpa americana*). 13" x 19" (LRB)

Ruby-Throated Hummingbird (*Archilochus colubris*) and Trumpet-Creeper (*Campis radicans*). 13" x 19"

Ruby-Throated Hummingbird (*Archilochus colubris*) and Bee-Balm (*Monarda didyma*). 13" x 19"

Greater Prairie Chicken (*Tympanuchus cupido*). Great Plains Art Collection. 16" x 24"

Red-Tailed Hawk (*Buteo jamaicensis*). Great Plains Art Collection. 16" x 24"

Long-Billed Curlew (*Numenius americana*). Great Plains Art Collection. 16" x 24"

Western Hognose Snake (*Heterodon nasicus*). 13" x 19"

Plains Milk Snake (*Lampropeltis triangulum*). 13" x 19"

Massasaugua Rattlesnake (*Sistrurus catenatus*). 13" x 19"

Ornate Box Turtle (*Terepena ornata*). 13" x 19"

Alligator Snapping Turtle (*Macroclemys temmincki*). Two 13" x 19" images. (LRB)

Short-Horned Lizard (*Phrynsoma douglassi*). 13" x 19"

Prairie Lizard (*Sceloperus consobrinus garmani*). 13" x 19"

Paddlefish (*Polydon spathula*). Two images. 9.5" x 13"

Spotted Gar (*Lepisteus ocellatus*). 13" x 19"

Shovelnose Sturgeon (*Scaphirhyncus platorhynchus*). 13" x 19"

Fossil *Tyrannosaurus rex*. 13" x 19"

Fossil Dragonfly (Odonata). 13" x 19"

Fossil Bird (Passeriformes). 13" x 19"

Fossil Chalcothere (*Moropus*). 13" x 19"

Landscape, Badlands National Park, South Dakota. 13" x 19" (SJ)

PAINTINGS
(BY ALLISON JOHNSON)

Galápagos Red-Billed Tropicbird (*Phaethon aethereus*). Watercolor. 16" x 21"

Galápagos Great Frigate Bird (*Frigata minor*). Watercolor. 12" x 18"

Galapagos Magnificent Frigate Bird (*Fregata magnificens*). Acrylic. 15" x 18 3/4"

Galápagos Swallow-Tailed Gull (*Creagrus furcatus*). Watercolor. 11" x 14"

Galápagos Medium Ground Finch (*Geospiza fortis*). Colored pencil. 11" x 15"

Galapagos Large Ground Finch (*Geospiza magnirostris*). Colored pencil. 9" x 11"

Galápagos Medium Ground Finch (Male) (*Geospiza fortis*). Colored pencil. 9" x 11"

Species Plasticity among Galapagos Finches (*Geospiza scandens* and *G. conirostris*). Colored pencil. 9" x 11"

Species Variation between Galápagos and Hood Island Mockingbirds (*Mimus* spp.). Watercolor. 15" x 13 1/4"

Species Variation between Charles and Chatham Island Mockingbirds (*Mimus* spp.). Watercolor. 22" x 15 1/2"

South American Long-tailed Mockingbird (*Mimus* longicauda). Watercolor. 16 3/4" x 14 3/4"

Geographic Diversity among Galápagos Lava Lizards (*Microlophus* spp.). Watercolor. 15" x 18 3/4"

Geographic Diversity in the North American Prairie and Fence Lizards (*Sceloperus* spp.). Watercolor. 15" x 18 3/4"

Great Plains (*Pyrocephalus rubinus mexicanus*) and Galápagos (*P. r. nanus*) Vermilion Flycatchers. Acrylic. 15" x 18 3/4"

Great Plains (*Dendroica petchia aestiva*) and Galápagos (*D. p. aurelia*) Yellow Warblers. Acrylic. 15" x 18 3/4"

Great Plains Indigo, Lazuli, and Hybrid Buntings (*Passerina amoena* and *Passerina cyanea*). Acrylic. 15" x 18 3/4"

DRAWINGS
(BY PAUL A. JOHNSGARD)

Postulated Phylogeny of the Species of Galápagos Finches. Print from ink drawing. 11" x 15"

Beak Variations Relative to Body Size and Foods in the Galápagos Finches. Print from ink drawing. 11" x 15"

Head and Beak Variation in Galápagos Finch Species (Geospizinae). Print from ink drawing. 11" x 15"

Wings and Heads of the Galápagos Flightless Cormorant (*Phalacrocorax harrisi*) and Double-Crested Cormorant (*P. auritus*). Print from ink drawing. 11" x 15"

Heads of Galápagos Mockingbirds (*Mimus* spp.) and South American Long-Tailed Mockingbird (*Mimus longicauda*). Print from ink drawing. 11" x 15"

Bushy-Tailed Wood Rat (*Neotoma cinerea*). Colored print. Great Plains Art Collection. 11" x 16"

Passenger Pigeon (*Ectopistes migratorius*). Colored print. Great Plains Art Collection. 11" x 16"

Carolina Parakeet (*Conuropsis carolinensis*). Colored print. Great Plains Art Collection. 11" x 16"

Mountain Lion (*Felis concolor*). Colored print. Great Plains Art Collection. 11" x 16"

Grizzly Bear (*Ursus horribilis*). Colored print. Great Plains Art Collection. 11" x 16"

Whip-poor-will (*Caprimulgus vociferus*). Colored print. Great Plains Art Collection. 11" x 16"

Lewis's Woodpecker (*Melanerpes lewis*). Colored print. Great Plains Art Collection. 11" x 16"

Mountain Plover (*Charadrius montana*) and Merlin (*Falco columbarius*). Ink drawing. 15" x 24"

Sandhill Cranes (*Grus canadensis*). Print from ink drawing. 21" x 27"

Burrowing Owl (*Athene cunicularia*) and Blue Grama Grass (*Bouteloua gracilis*). Print from ink drawing. 12" x 21"

MAPS
(BY PAUL A. JOHNSGARD)

Route of HMS Beagle through the Galápagos Archipelago. 11" x 15"

Geographic Ranges of the Galápagos Finches (Geospizinae). 11" x 15"

Geographic Ranges of Lava Lizards (*Microlophus* spp.) and Land Iguanas (*Conolophus* spp.). 11" x 15"

Geographic Ranges of Marine Iguana Subspecies (*Amblyrhynchus cristatus*). 11" x 15"

Geographic Ranges of Giant Tortoise Subspecies (*Geochelone elephantophus*). 11" x 15"

Geographic Relation of Giant Tortoise (*Geochelone elephantophus*) Carapace Shapes to Galápagos Prickly Pear Cacti Life-Forms (*Opuntia* spp.). 11" x 15"

DARWINIANA
(ON LOAN FROM DR. STEPHEN JOHNSON EXCEPT AS NOTED)

Origin of Species, *The Descent of Man*, and *Voyage of the Beagle*. Three volume reprint set. London: John Murray, 1901.

Origin of Species. Third edition, seventh thousand. London: John Murray, 1861.

The Decent of Man. Reprinted from the second English edition. New York: A. L. Burt, [1874?].

The Voyage of the Beagle and *Origin of Species*. London: Collins' Clear-Type Press, [1860?].

Voyage of a Naturalist ("*The Voyage of the Beagle*"). New edition. London: John Murray, 1890.

The Power of Movements of Plants. First edition, second thousand. London: John Murray, 1880.

Coral Reefs. Second revised edition. London: Smith, Elder, and Company, 1874.

The Zoology of the Voyage of the HMS Beagle. Facsimile edition, bound in four volumes, with wooden storage case. London: Royal Geographical Society, 1994.

Charles Darwin signature in pencil (not authenticated). In *Anecdotes for the Fireside; or, A Manual for Home*, by Rev. Daniel Smith.

Charles Darwin autograph in ink, "Charles Darwin, Down, Kent, April 11, 1880."

Carte de vista of Charles Darwin, with reproduced signature, "C. Darwin." N.d.

Carte de vista of Charles Darwin, with reproduced signature, "C. Darwin." [1880?]

Carte de vista of Charles Darwin, labeled, "Darwin." N.d.

Carte de vista of Charles Darwin. 1865.

Cabinet card portrait of Charles Darwin. N.d.

Full-page magazine engraving from *Illustrated London News*, March 11, 1871.

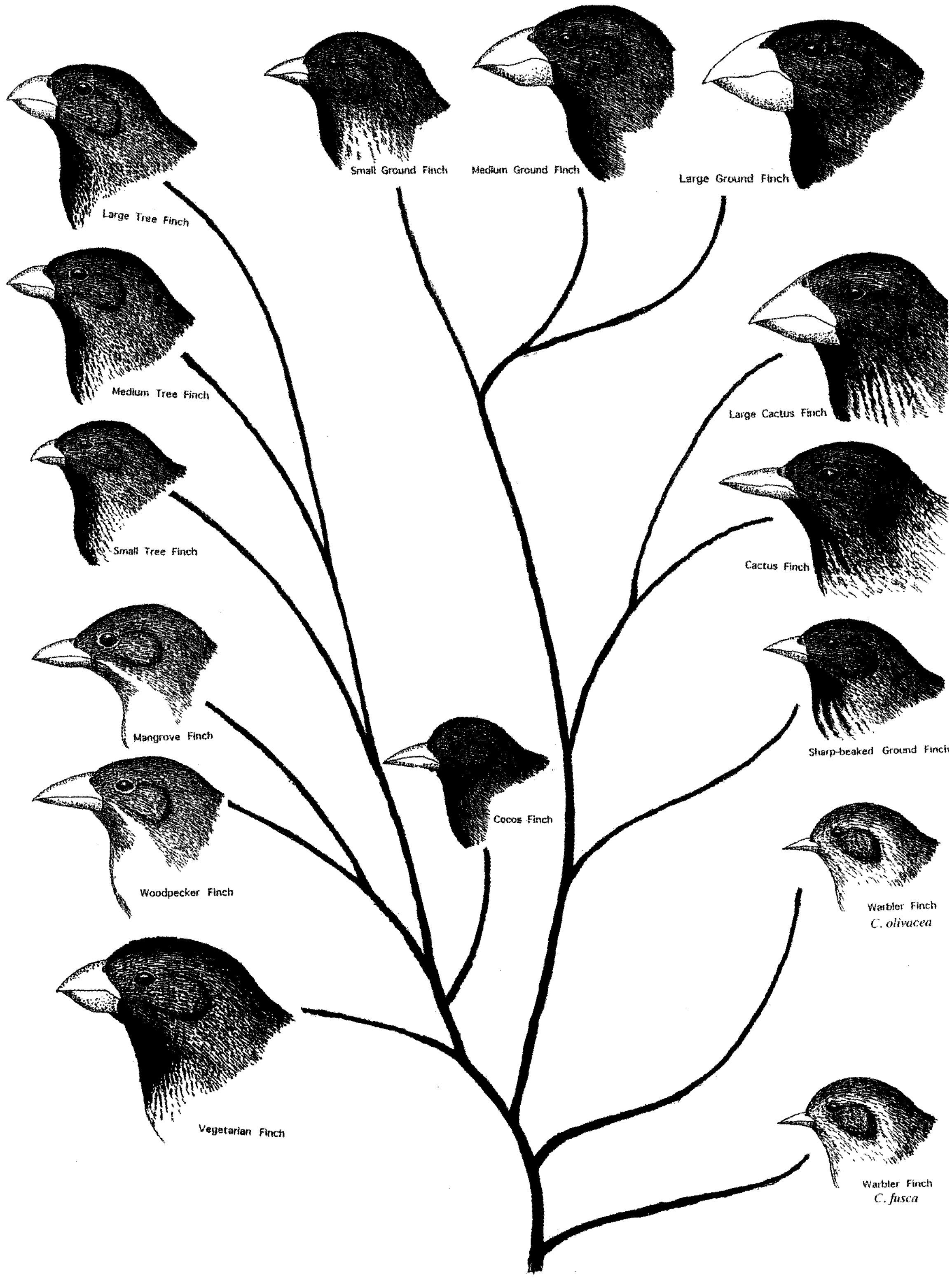
Full-page magazine engraving of Charles Darwin, in five-page article entitled, "Reminiscence of Charles Darwin," *New Monthly Magazine*, 1874.

Half-page magazine engraving, "The Origin of Species, Dedicated by Natural Selection to Dr. Charles Darwin. As Thirsty as a Fish," caricature by C. H. Bennett, *Illustrated Times*, October 10, 1863.

Copies of three papers on animal behavior and natural selection by Charles Darwin and copies of two papers by Alfred Russell Wallace in *Nature*, November 1872–April 1873.

Color lithograph caricature of Charles Darwin, *Vanity Fair*, September 30, 1871.

Fifteen-volume, half-leather set of Darwin's books, including autobiography and letters. New York: D. Appletons, 1897. On loan from Paul A. Johnsgard.



Postulated phylogeny of the species of Galápagos finches (Geospizinae). Drawn to scale. Print from pen drawing by Paul A. Johnsgard. Recent genetic information indicates that the seemingly singular Warbler Finch actually consists of two nearly identical "sibling" species that split off the rest of the finch radiation very early in the group's evolution from Central American ancestors. The surviving members of the earlier of the two warbler finch lineages are now confined to a few peripheral islands, while the other is widespread in the archipelago.

Introduction

CHARLES DARWIN VISITED the Galápagos Islands for thirty-five days during 1835, as a naturalist during a five-year hydrographic and shoreline-mapping expedition of the British brig HMS Beagle (Darwin 1845). This voyage ultimately led to his discovery of the significance of local geographic variations among related but isolated animal populations in influencing evolutionary changes and facilitating species proliferation. Twenty-four years after these seminal Galápagos observations, Darwin's observations would become crystallized in his theory of natural selection, as outlined in his epochal 1859 book, *The Origin of Species.*

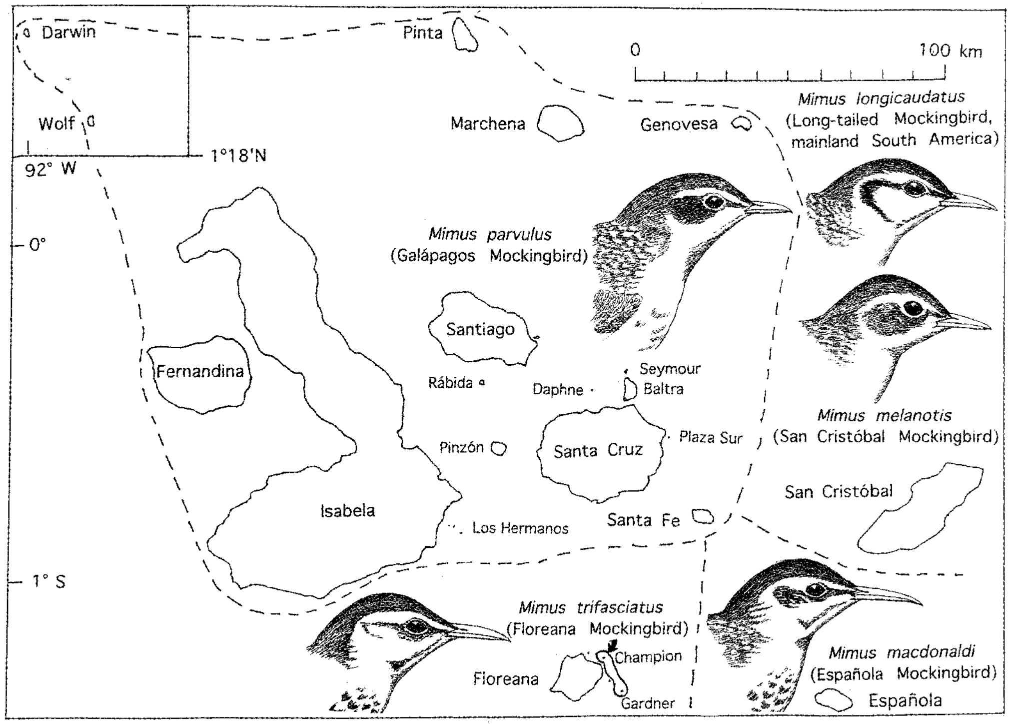
Any biologist is likely to dream of someday visiting the Galápagos, not only because it is the birthplace of modern evolutionary biology. It is also one of the few places in the world that has been only slightly changed since Charles Darwin set foot on these islands almost two centuries ago, with 95 percent of its flora and fauna still surviving. Marine iguanas still cluster in seemingly countless droves on the lava shores of Fernandina Island, mockingbirds still fearlessly approach tourists, and a few giant land tortoises can still be seen wandering freely on the highlands of Santa Cruz Island.

Nearly all the major animal species that Darwin encountered are still there, although a few populations of giant tortoises have become extinct from hunting, and all are quite rare. A chance comment to Darwin by Nicholas Lawson, who was then the acting English vice-governor of the islands, to the effect that it is possible to deduce from what island a tortoise had originated by its dorsal shell shape, scale pattern, and overall size, had a lasting effect. It was this singular observation, and the fact that Darwin had already noted minor plumage and beak variations among the three types of mockingbirds he had collected on the four islands he had visited, that evidently triggered Darwin's speculations as to the possible significance of such seemingly inexplicable biological variability.

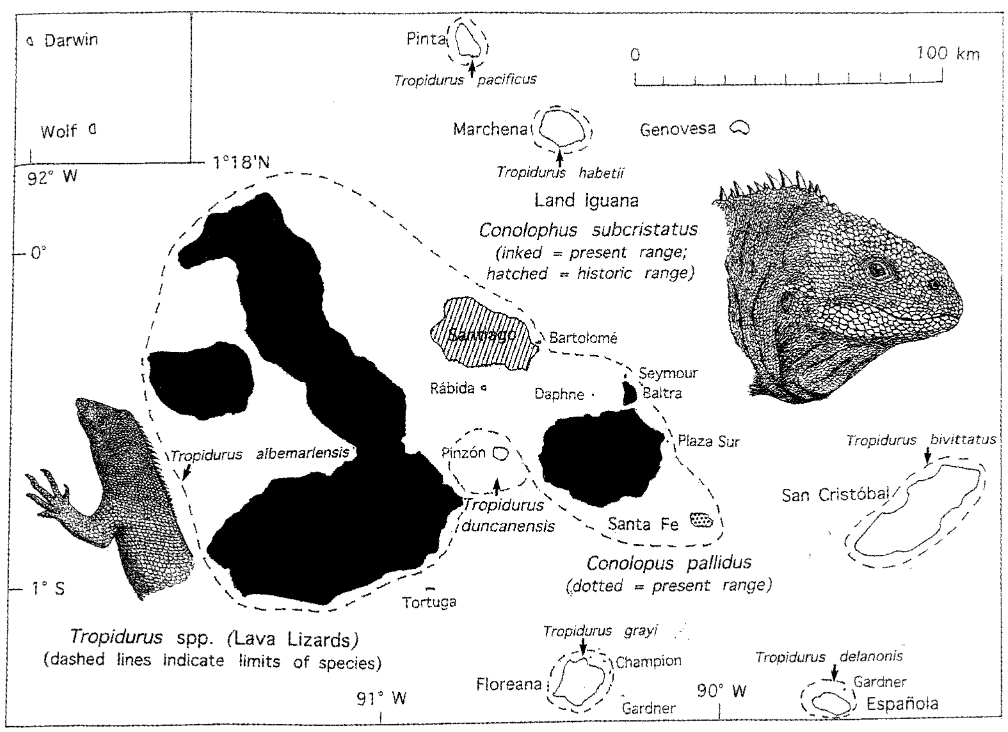
Darwin observed in his notes taken during the Galápagos visit that the small, finch-like birds that he and other Beagle crew members had collected exhibited a "perfectly graduated series in the size of their beaks." In retrospective notes made during the long voyage home, Darwin noted that such facts as the interisland tortoise variations and the remarkable interisland variations existing among Galápagos mockingbirds raised questions as to the biological significance of such local structural differences. More importantly, he realized that the very existence of such intraspecies variations in nature might undermine long-held concepts of species immutability and special creation.

The concept of special creation had been a central tenant of Christianity from time immemorial, and challenging the idea that species have remained constant ever since their initial creation was not a prospect to be taken lightly. However, it was not until his return to England when the Zoological Society's ornithologist John Gould had studied his collection of thirty-seven Galápagos birds that the real significance of the Galápagos collections became apparent. Of twenty-six land bird specimens, Gould determined that twenty-five belonged to new species unique (endemic) to the Galápagos and that three of eleven seabird specimens were similarly of previously unknown species. Of the sparrow-like specimens brought back from the Galápagos, Gould recognized that the sample consisted of a unique group of eleven to thirteen related finch species. Gould and Darwin also recognized that many of the Galápagos birds showed strong taxonomic similarities to those found on the South American mainland.

The biological importance of the Galápagos finches would become fully apparent years later. Darwin first commented in detail on these dull-looking birds (later to be named "Darwin's finches") in the second (1845) edition of his journal documenting the voyage of the Beagle. Darwin then sagely noted that, from their diverse beak structures, one might imagine that, "from an original paucity of birds in this archipelago, one species had been taken and modified for different ends." This basic evolutionary (and revolutionary) idea was to be gradually expanded and its theoretical



Comparisons of the Galápagos mockingbirds (Mimus spp.) and the South American Long-tailed Mockingbird (Mimus longicauda). Drawn to scale. Print from ink drawing by Paul A. Johnsgard. Evidence suggests that the four Galápagos mockingbirds originated from early colonizations of the islands by a South American ancestral Long-tailed Mockingbird.



Map of the distribution of the Galápagos Land Iguana Conolophus, showing the ranges of the two species (inked, hatched and dotted), and of the Galápagos Lava Lizards, with seven species, showing the limits of their ranges (dashed lines). Print from ink drawing by Paul A. Johnsgard .

basis explained over the next fourteen years by Darwin's theory of species modification through the mechanism of natural selection (Darwin 1859).

During Darwin's twenty days spent on the islands, he not only studied their geology and animal life but also collected several hundred plant specimens (every plant that he had been able to find in flower) from all four islands that he visited. These totaled 209 numbered specimen records and nearly 200 species. Joseph Hooker (1847) later described nearly 80 percent of these specimens as representing new taxonomic discoveries. A high proportion of these plants also proved to be endemic to the Galápagos Archipelago, although Hooker realized that many also had their nearest relatives on the western coast of South America.

Darwin was especially impressed by the endemic sunflower-like genus *Scalesia*, of which he collected six species. Based on his observations, not one of these evidently occurred on more than one island. It is now known that some of the approximately dozen recognized species of *Scalesia* do have extensive interisland ranges, but this group of plants nevertheless provides an evolutionary botanical counterpart to Darwin's finches. It provides a case of extreme interisland variability, the species exhibiting remarkable radiation in leaf shapes, and in life forms ranging from small shrubs to trees that are among the tallest of any on the islands.

Likewise, the widespread prickly pear cactus genus *Opuntia* shows marked life-form variations on different islands in the Galápagos Archipelago, ranging from sprawling, sometimes almost vine-like, shrubs to tree-like giants. The tree-like species have their trunks covered by a thick layer of bark, perhaps as an adaptation to avoid excessive browsing by giant tortoises. And the cactus-eating giant tortoises have in turn locally modified the shape of their upper shells (carapace) in such a way to evidently allow them to reach up with their long necks and browse ever higher to reach *Opuntia* leaf pads, gradually producing the remarkable carapace variations noted by Darwin. On islands where tortoises apparently never colonized, the cacti are more shrub like and may even exhibit shorter and much softer spines.

A COMPARISON OF THE GALÁPAGOS AND GREAT PLAINS PHYSICAL ENVIRONMENTS

The Galápagos Islands are located about six hundred miles west of the Ecuadoran coast, straddling the equator. They were formed by volcanic action over a period of at least the past 5 million years. The land area of the Galápagos Archipelago totals 3,042 square miles, representing barely half the area of Nebraska's Cherry County and about 0.5 percent of the land area of the Great Plains south of Canada, roughly 600,000 square miles. The archipelago consists of thirteen major islands plus more than one hundred islets. Its maximum elevation (1,700 meters, or 5,100 feet) is located on Isabela Island, where five volcanic cones rise. A single active volcanic peak on Fernandina Island, the second-largest island, reaches about 1,500 meters (4,800 feet).

Geological data suggest that the archipelago is no more than 5 million years old, with the easternmost islands being the oldest (some have now eroded below ocean level) and the westernmost islands of Fernandina and Isabela being the youngest (at less than 1 million years). The islands are entirely volcanic in origin and have never had any direct connection to the mainland of South America. The central and eastern islands also have hundreds of inactive and eroded volcanic cones that are no higher than about 900 meters. All the higher elevations intercept moisture-laden air to some degree, and the resulting localized precipitation patterns strongly influence the local distributions of both plants and animals.

Although the archipelago's average annual precipitation roughly corresponds to that of Nebraska's tallgrass prairie region, its volcanic substrate doesn't retain moisture and its predominant vegetation is desert like. The southeast trade winds and the associated cold-water Humboldt Current flow in a general northwesterly direction out of the coastlines of Ecuador and Peru, striking the southern coasts of the Galápagos Islands. This current and its associated cool trade winds out of the southeast have their most obvious climatic effects during the cool and dry months of June to December.

Warm waters coming out of the Panamanian Basin from the northeast via the northern trade winds also seasonally affect the Galápagos Islands. This relatively weak current (the Panama flow) brings associated warm, moisture-laden clouds from the Panama Basin to the northeastern islands and is most influential during the warm and wet months of January to June. Unusually warm and wet El Niño periods lasting well beyond the usual warm and wet months occur in some years, when the trade winds fail and equatorial west winds bring warm surface waters east toward the Galápagos Islands. Such events often have devastating effects on animals that depend on the presence of fish and other foods associated with the nutrient-rich waters of the Humboldt Current coming northwest from the Pacific coast of South America.

The seasonal trade winds and their related currents are also probably responsible for bringing in wind-carried seeds, spores, and various living organisms from the western coasts of Central and South America. At the peak of Pleistocene glaciations, ocean levels would have lowered as much as 120 meters, causing some of the central islands to be nearly connected (Jackson 1985). Such ocean-level reductions may have helped terrestrial species colonize some islands that are now rather distantly separated by water barriers.

Like other archipelagos, the Galápagos Islands have facilitated opportunities for speciation and endemism for land animals and plants by providing variously isolated sites that offer new habitats and differing species compositions. These varied physical and biological conditions allow for local evolutionary adaptations to different but similar environments and offer unique niche opportunities in association with different biotic assemblages. Additionally, the arid coastline of Peru presents a rich source of potential colonizing species for the arid thorn forest and desert scrub environments of the Galápagos. Such organisms must be able to reach the islands by flying or swimming, exploiting water currents or favorable winds. Surface water and streams are absent from most islands, which largely restricts colonizing animal life to those species who are able to produce metabolic water from their foods or who can tolerate the salinity of sea water.

In contrast, for tens of millions of years, the Great Plains has consisted of one of the most uniform and biologically productive major North American habitats. It has formed within the last 70 million years, as the vast, Mesozoic intracontinental sea, which covered the interior of North America, was gradually filled by erosion from the then-rising Rocky Mountains to the west. Except for a few ancient and island-like metamorphic or igneous intrusions such as the Black Hills, the Great Plains has historically consisted of vast areas of almost continuous grasslands, developed over wind- and water-carried substrates with only slight topographical diversity. The regions surrounding the Great Plains consist largely of temperate forests and deserts, which are not likely to provide a source of species preadapted to survival in a grassland-dominated environment. And, because of the plains' relatively uniform topography and climate, few opportunities have existed for isolated populations to develop unique local adaptations and associated genetic diversity. As a result, overall biological diversity is low, and there is little evidence of regional speciation in the Great Plains.

Unlike with the Galápagos Islands, volcanism has played only a minor role in shaping the topography and biological history of the Great Plains. In fact there are only two major volcanic landmarks: Devils Tower in Wyoming (formed about 40 million years ago) and Capulin Volcano in New Mexico, which last erupted 56,000–62,000 years ago. Devils Tower is an iconic Great Plains landmark of columnar basalt that has gradually become exposed by erosion of its surrounding sediments. Capulin Volcano is a cinder cone peak rising from the Raton-Clayton volcanic field, which has been periodically active for the past 9 million years. Periodic ashfalls drifting east from volcanoes in western North America have also sometimes produced Pompeii-like effects in killing and entombing large numbers of animals that happened to be trapped by their fallout, such as at Ashfall Fossil Beds Geologic Park in northeastern Nebraska. Erosion in western parts of the region has produced areas of "badlands" in several states, of which the South Dakota Badlands are best known. There, wind and water erosion has produced moonlike landscapes of mostly Oligocene (23.3–35 million years old) exposures and a rich array of fossil life. In Nebraska, sediments from the Miocene age (5–23.3 million years ago) at Agate Fossil Beds (ca. 23 million years old) and at Ashfall Fossil Beds (ca.

10 million years old) have revealed progressively more recent samples of animal and plant evolution on the Great Plains.

In contrast, because of the independent volcanic origin and great distance of the Galápagos Islands from the South American mainland, the plants and animals tend to exhibit a very high level of endemicity, both among individual islands and collectively relative to continental America. The six hundred–mile ocean gap from the South American mainland and the difficult environmental conditions existing on the islands have both served as effective barriers to colonization. As a result, there is a relatively low incidence of major American mammalian groups (no primates, cats, dogs, deer, etc.). Some otherwise widely distributed continental plant taxa are also rare or absent as native Galápagos species.

ENDEMICITY AND DIVERSITY OF GALÁPAGOS AND GREAT PLAINS INSECTS

The Galápagos Islands support relatively few terrestrial invertebrates, the majority of which consist of snails and such arthropods as insects. Most of these clearly originate in Central and South America, especially the drier coastal regions. There are more than three hundred species of butterflies and moths known from the islands, the great majority of which are moths; many of these are smaller than their mainland counterparts. Among the larger moths, an estimated 30 percent represent endemic species, and another 18 percent represent endemic subspecies. Of the twenty known Galápagos butterflies, several are strong flyers, with ranges extending to the southern United States. Some of these are also found on the Great Plains, such as the monarch (*Danaus plexippis*), queen (*Danaus gilippus*), painted lady (*Vanessa cardui*), and cloudless sulfur (*Phoebis sennae*). There are eight dragonflies and damselflies (Odonata), only one of which is endemic. One species, the spot-winged glider (*Pantala hymenea*), is also widespread on the Great Plains, where over three hundred species of Odonata may be present, nearly one hundred of which occur in Nebraska.

At least two hundred species of Galápagos beetles (Coleoptera) are known, as well as eighty true bugs (Hemiptera) and twenty grasshoppers, crickets, and katydids (Orthoptera) (Fitter, Fitter, and Hosking 2000). By comparison, North America has at least 24,000 known species of coleoptera, about 4,000 species of hemipterans, and 1,800 species of orthopterans. In common with other island fauna, many Galápagos insects have reduced flying abilities. There are three wholly flightless cockroaches (*Ischnoptera* spp.) as well as four flightless grasshoppers (*Halemus* spp.). These grasshoppers rather closely resemble the flightless lubber grasshopper (*Brachystola magna*), one of a very few flightless grasshoppers of the Great Plains. The Great Plains region is unusually rich in grasshoppers; as many as 60 species may be found in a single grassland (Arenz and Joern 1996) and at least 130 species occur in Nebraska.

In common with the Great Plains, and mostly because of human activities, there have been many recent colonizations of alien insects on the Galápagos Islands. These include several undesirable insects, such as eleven cockroaches, three ants (*Wasmannia*, *Solenopsis*, and *Monomorium*), two wasps (*Polistes* and *Brachygastra*), a blackfly (*Tabanus*), and a cottony cushion scale insect (*Icerya*).

ENDEMICITY AND DIVERSITY IN GALÁPAGOS AND GREAT PLAINS VERTEBRATES

Compared with the Galápagos, the Great Plains has relatively few endemic land vertebrates. As a geographic entity it is far larger and has existed for a much longer period than the Galápagos, namely since the gradual rise of the Rocky Mountains over the past 40–60 million years. The subsequent development of a rain shadow to the eastward lee of the mountains eventually transformed the western parts of the Great Plains into arid grasslands and semidesert scrub, whereas the eastern portions received enough Gulf Coast moisture to develop into prairie and localized woodland or riverine forest.

Approximately fifty Great Plains vertebrate species may be classified as quasi endemics in that they are mostly limited to the Great Plains region. Very few of these are endemics in the strict sense of being wholly unique to the Great Plains, especially the birds, many of which migrate seasonally or often stray beyond their usual breeding limits. Among the most characteristic avian endemics of the Great Plains are two nonmigratory species of prairie chickens (*Tympanuchus cupido* and *T. pallidicinctus*) as well as such migratory species as the mountain plover (*Charadrius montanus*), marbled godwit (*Limosa fedoa*), Sprague's pipit (*Anthus spragueii*), Baird's sparrow (*Ammodramus bairdii*), and two longspurs (*Calcarius mccownii* and *C. ornatus*) (Johnsgard 1979, 2002).

Typical mammalian endemics of the Great Plains include the black-footed ferret (*Mustela nigripes),* swift fox (*Vulpes velox*), black-tailed prairie dog (*Cynomys ludoviciana*), olive-backed pocket mouse (*Perognathus fasciatus*), and Richardson's ground squirrel (*Spermophilus richardsonii*) (Jones, Armstrong, and Choate 1985; Johnsgard 2003). There are also a few endemic Plains reptiles, such as the prairie skink (*Eumeces septentrionalis*); but none of these Plains species exhibits the complex speciation and endemicity patterns that are so highly apparent on the Galápagos Islands.

Only one of the nonaerial Great Plains mammals, the marsh rice rat (*Oryzomys palustris*), has any Galápagos relatives of the same genus, although a few migratory bats occur in both regions. As noted earlier, many mammalian groups that are well represented on mainland South America do not exist on the islands. However, several mammals closely associated with humans, including rats, mice, burros, goats, pigs, dogs, and cats, have become established on many islands and have caused great ecological damage at the expense of native species.

A COMPARISON OF GALÁPAGOS AND GREAT PLAINS AVIFAUNA

Because of their flying abilities, birds have been far more successful than mammals, reptiles, or amphibians in colonizing the Galápagos Islands; and no amphibian has yet succeeded in doing so. Among birds, seabirds have been the most successful in occupying the islands; and small songbirds, the least successful. Of the latter, the thirteen endemic finch species known as Darwin's finches have clearly been the most successful, and their beak shapes have adaptively modified to exploit nearly all of the foraging niches of the Galápagos Archipelago. As first visualized by Darwin, some initial invasion by one or perhaps a few ancestral forms has produced an amazing array of bill structures and foraging ecologies. Several mainland songbirds have been proposed as being the nearest living relatives of Darwin's finches. They include a Central American bananaquit (*Coereba*) (Harris 1974) and various grassquits (*Volatinia*, *Melanospiza*, and *Tiaris*) from the Caribbean and Central and South America (Steadman 1982; Sato et al. 1999). The proposed *Tiaris* relationship was based on molecular evidence and may be the most promising. *Tiaris* and *Melanospiza* grassquits also share at least ten of thirteen biological traits with Darwin's finches, especially in their courtship displays, vocalizations, and nest-building behavior (Baptista and Trail 1988).

The available molecular evidence suggests that all the extant Galápagos finches as well as the geographically isolated Cocos Island finch (*Pinaroloxias inornata*) have commonly evolved from some Central or South American finch ancestor within the past 1–2 million years (Petren, Grant, and Grant 1999; Sato et al. 1999). The Cocos Island finch—rather than being genetically distinct from all thirteen Galápagos Islands species, as has often been hypothesized—has evidently descended directly from early Galápagos finch stock. An ancestral population of tree finch stock may have colonized Cocos Island, rather than the current species having evolved separately from a mainland ancestor (Sato et al. 1999; Petren, Grant, and Grant 1999).

The widely distributed warbler finch is now believed to be genetically closest to the most ancestral source of the overall Galápagos finch assemblage (Grant 1999; Petren, Grant, and Grant 1999; and Sato et al. 1999). Because of its warbler-like beak structure, the warbler finch was long regarded as a member of the New World warbler family Parulidae; but it is now firmly placed within the general assemblage of Galápagos finches. Some recent molecular evidence suggests that the warbler finch actually consists of two very distinct genetic lineages (Freeland and Boag 1999; Petren, Grant, and Grant 1999). One lineage (*Certhidea olivacea*) occurs in the large west-central islands and evidently originated early in the finch proliferation, perhaps as early as about 750,000 years ago (Freeland and Boag 1999). The other lineage (*C. fusca*) is found on several of the geologically older and mostly peripheral islands such as Marchena, Española, and Genovesa as well as possibly on the islands of Wolf, Darwin, and Santa Fe. It apparently diverged even earlier than *olivacea* and may most closely genetically approximate the original founding stock for the entire Darwin's finch group (Freeland and Boag 1999).

The vegetarian finch is also now considered from molecular evidence to be a fairly early genetic offshoot, diverging from basal stock after the warbler finch but before the separation of tree finch and ground finch lineages (Sato et al. 1999). These remaining species split genetically into a ground finch–cactus finch assemblage and a tree finch–woodpecker finch assemblage, largely along the lines originally hypothesized on morphological grounds (Lack 1947; Bowman 1961). The long-term field studies of Peter and Rosemary Grant (Grant 1999) regarding the rapid effects by natural selection on local beak shapes and foraging adaptations in Galápagos finches may represent the most important biological field research done on the Galápagos Islands since Darwin's visit (Weiner 1994) and have established the rapidity with which evolutionary changes can occur in small, isolated populations.

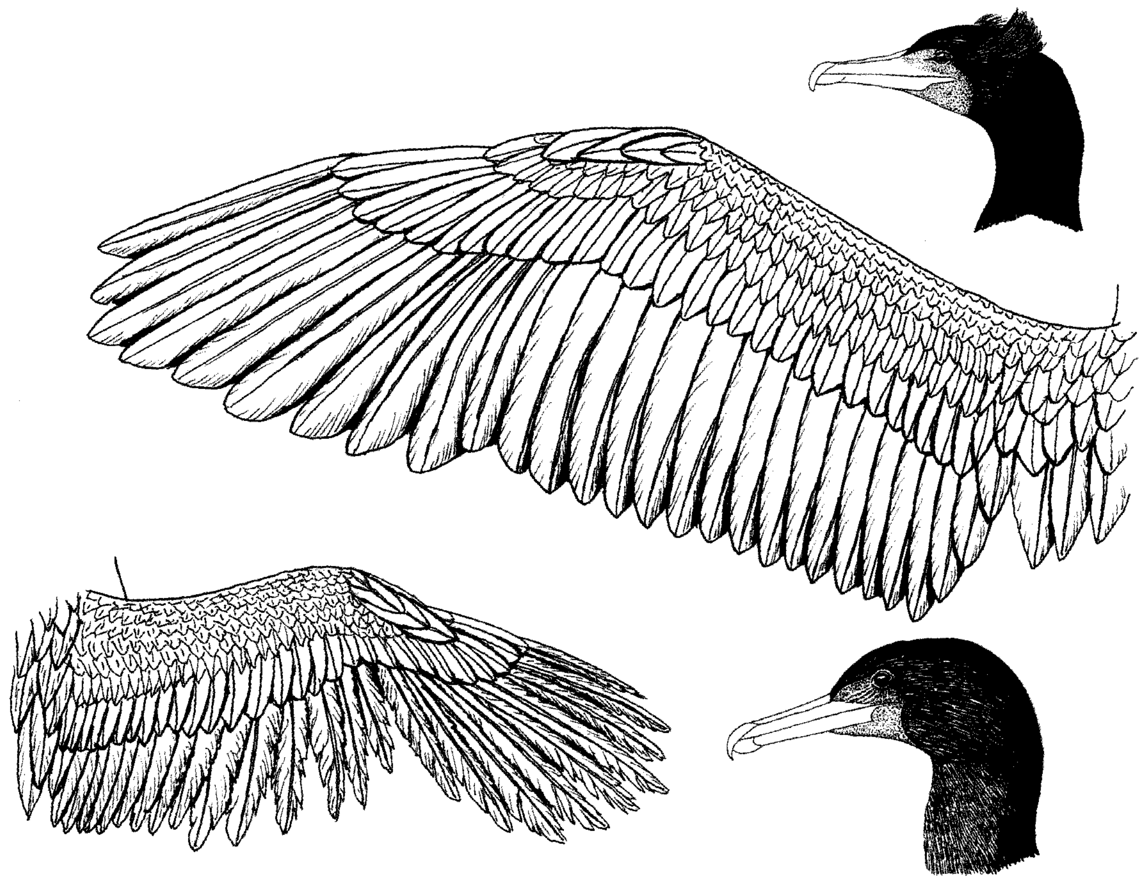
The Galápagos mockingbirds are probably derivative from an ancestral long-tailed mockingbird (*Mimus longicaudatus*) of western South America (Steadman and Zousmer 1988). The localized San Cristobal (*M. melanotis)* and the more widespread Galápagos (*M. parvulus*) mockingbirds closely resemble the South American species, but they have shorter wings and tails than the mainland form, an obvious adaptation to island life. The highly localized Española (*M. macdonaldi*) and Floreana (*M. trifasciatus*) mockingbirds probably evolved from a second South American colonization (Steadman and Zousmer 1988). Shorter wing and tail measurements also occur in the Galápagos population of the vermilion flycatcher (*Pyrocephalus rubinus nanus*), sometimes considered a distinct species. Relatively short wings are also typical of the Galápagos race of yellow warbler (*Dendroica petechia aureola*). In a similar manner, all the Darwin's finches have relatively short wings and tails and fly only rather short distances.

Several endemic Galápagos races or species of birds exist that are both smaller and darker than is typical of continental relatives. Their darker plumages may reflect the dark lava substrate and their smaller size may be in part an adaptation to limited foods, at least for terrestrial species. Some darker and usually smaller populations include the common or brown noddy (*Anous stolidus*), yellow-crowned night heron (*Nycticorax violaceus*), brown pelican (*Pelecanus occidentalis*), white-cheeked pintail (*Anas bahamensis*), barn owl (*Tyto alba*), and short-eared owl (*Asio flammeus*). Other Galápagos species are also generally darker or less brightly colored but are not smaller, such as the American oystercatcher (*Haematopus palliatus*), great blue heron (*Ardea herodias*), and greater flamingo (*Phoenicopterus ruber*).

The probable geographic affinities and biological relationships of endemic Galápagos birds to mainland forms are of particular evolutionary interest. For example, the flightless cormorant's (*Phalacrocorax harrisi*) nearest relative is apparently the double-crested cormorant (*P. auritus*) of North America, a common breeder on the Great Plains. The flightless cormorant's ancestors may have arrived at the islands during glacial times from the north, gradually undergoing atrophy of their wings, eventually becoming the world's only flightless species of cormorant (Steadman and Zousmer 1988).

The endemic lava heron (*Butorides sundevalli*) and striated heron (*B. striata*) are both obviously close relatives of the green heron (*B. virescens*), a species that ranges from the Great Plains south to Panama. The taxonomic relationship of the two Galápagos species to one another, and both of these to the green heron, is still the subject of debate.

The nearest living relative of the endemic lava gull (*Larus fuliginosa*) is possibly the Franklin's gull (*Larus pipixcan*) of the Great Plains. Or perhaps it is the laughing gull (*Larus atricilla*), which occurs along coastal North America and sporadically reaches the southern Great Plains (Steadman and Zousmer 1998). The other endemic Galápagos gull, the swallow-tailed gull (*Creagrus furcatus*), and the arctic-breeding Sabine's gull (*Xema sabini*) are also evidently close relatives. Although each is currently placed in a unique genus, their wing patterns, tail



Comparative wings and heads of the Galápagos Flightless Cormorant (Phalacrocorax harrisi) and the Double-crested Cormorant (P. auritus). Drawn to scale. Print from ink drawing by Paul A. Johnsgard. The Flightless Cormorant may have evolved from colonization by the Double-crested Cormorant during Pleistocene times, and gradually lost its flying abilities when its insular existence no longer required a capacity for flight.

shapes, eye-rings, and bill colors are all similar. The Sabine's gull winters at sea off western South America, from where an ancestral colonization to the Galápagos may have occurred.

The endemic Galápagos hawk (*Buteo galapogensis*) is perhaps closely related to the Swainson's hawk (*Buteo swainsoni*) of the Great Plains. The highly migratory behavior of the Swainson's hawk, breeding in the Great Plains but passing through equatorial regions and wintering in southern South America, might account for a possible early colonization of the islands. The South American variable hawk (*Buteo polysoma*) is another possible candidate for being the nearest ancestral source (Steadman and Zousmer 1988). The variable hawk is notably short-winged, whereas the Swainson's hawk has unusually long and narrow wings for a *Buteo,* which may reflect its long trans-American migration route.

The endemic Galápagos dove (*Zenaida galapogensis*) is in the same genus as the mourning dove (*Z. macroura*) and white-winged dove (*Z. asiatica*) of the Great Plains. However, it is probably more closely related to the West Indian zenaida dove (*Z. aurita*) or to the South American eared dove (*Z. auriculata*) (Steadman and Zousmer 1988).

One other endemic Galápagos land bird, the large-billed flycatcher (*Myiarchus magnirostris*), is very similar to the great crested flycatcher (*M. crinitus*) of the Great Plains. However, it is probably genetically closest to the dusky-capped flycatcher (*M. tuberculifer*), which ranges from Arizona to Argentina (Steadman and Zousmer 1988).

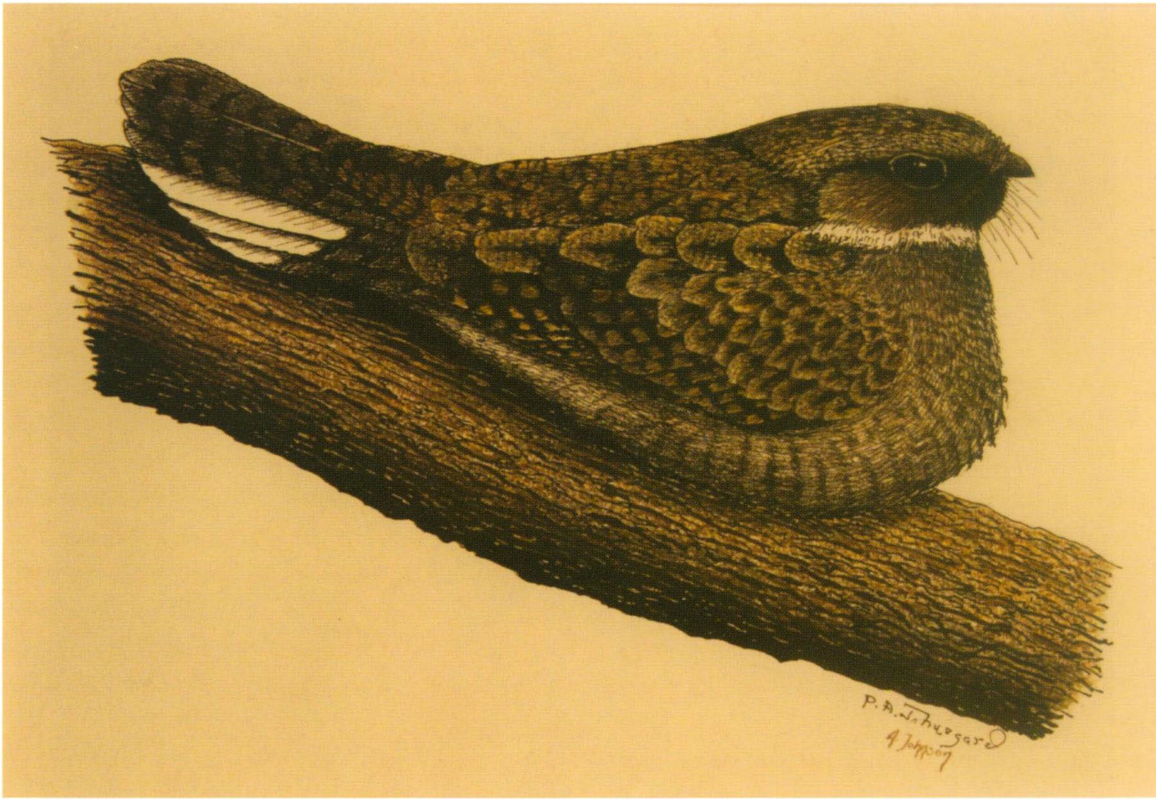
The Galápagos rail (*Laterallus spilonotus*), being somewhat darker than the mainland form, is perhaps no more than a distinctive race of the widespread black rail (*L. jamaicensis*), which occurs within the

Passenger Pigeon (Ectopistes migratorius), adult. Print from ink drawing by Paul A. Johnsgard, colored by Allison Johnson. Great Plains Art Collection [0002.2004.0017]. Extinction is a natural part of evolution, but humans directly caused the extinction of this species. Historically, the species once numbered in uncounted millions, and ranged west to the northern Great Plains.

northern Great Plains and southward to the western coastline of South America. The Galápagos martin (*Progne modesta*) is also barely separable from the southern martin (*P. concolor*) of the South American mainland. It is also a near relative of the widespread purple martin (*P. subis*) of North America, which breeds west to the Great Plains and winters south to Brazil. The dark-billed cuckoo (*Coccyzus melacoryphus*) is an apparently recent arrival from mainland South America and has not yet shown any apparent island modifications. It is a close relative of the black-billed cuckoo (*C. erythropthalmus*), which is common in the northern Great Plains and winters south to Argentina.

Compared with the land birds, there are far fewer Galápagos endemics among the highly mobile sea birds, and these also have few North American counterparts. Two endemic seabird species, the waved albatross (*Diomedea leptodactyla*) and Galápagos penguin (*Spheniscus mendiculus*) have Southern Hemisphere affinities, the penguin being a very close relative of the Peruvian penguin (*Spheniscus humboldti*). The brown pelican (*Pelecanus occidentalis*) is a distinctive Galápagos subspecies that is darker and smaller than the race found along coastal North America, and its size is closer to the mainland Ecuadorian race. There are also endemic Galápagos races of the dark-rumped petrel (*Pterodroma phaeopygia*), Audubon's shearwater (*Puffinus lherminieri*), Elliot's storm petrel (*Oceanites gracilis*), and wedge-rumped storm petrel (*Oceanodroma tethys*). The nearest relatives of these birds occur along coastal South America or are widely scattered across the Pacific (Steadman and Zousmer 1988).

All told, the Galápagos Archipelago supports about 90 species of birds, representing a mean species



Whip-poor-will (Caprimulgus vociferus), adult. Print from ink drawing by Paul A. Johnsgard, colored by Allison Johnson. Great Plains Art Collection [0002.2004.0020]. Three species of "nightjars" are native to the Great Plains. All are nocturnal insectivores, and all are far more easily heard than seen. Each has evolved a distinctive, species-specific territorial vocalization, and the common name "whip-poor-will" provides a good imitation of this species' acoustic signature. The white parts of its plumage that might also provide visual recognition are evident only in flight; otherwise the birds are essentially invisible when the birds are at rest.

diversity of 30 bird species per 1,000 square miles. Mainland Ecuador, with a surface area of 109,483 square miles and vast ranges of elevations and environments, has a bird biota of nearly 1,600 species (Ridgely and Greenfield 2001), representing a mean diversity of 14.6 bird species per 1,000 square miles. By comparison, Nebraska's nearly 78,000 square miles support about 340 regularly occurring birds (Johnsgard 2006), representing a mean diversity of 4.3 regularly occurring bird species per 1,000 square miles, or 5.6 species if all Nebraska's accidentally occurring bird species are also included. It should be noted that the ratio of taxonomic diversity to total land area is not a straight-line relationship, since biota sizes do not increase indefinitely relative to land mass variations. Therefore, such diversity comparisons are best restricted to regions of roughly the same area, such as comparisons between Nebraska and Ecuador rather than between Nebraska and the Galápagos Islands.

The native Great Plains avifauna, although much larger and more diverse, shows some notable evolutionary similarities to its Galápagos counterpart in terms of the proliferation of diverse beak sizes and shapes among the many seed-eating sparrows and finches. As with the large ground and vegetarian finches, massive seed-cracking beaks have developed in such granivorous groups as cardinals (*Cardinalis*) and the convergently evolved grosbeaks (*Pheucticus*, *Guiraca*, and *Pinicola*).

The Great Plains also has its share of species or quasi species that, as a result of climatic trends and vegetational changes, are in fairly recent secondary contact and that hybridize along ecological transition zones, mostly east-west-oriented river systems connecting eastern and western biotas. These include such eastern and western species pairs as the Baltimore and Bullock's orioles (*Icterus galbula* and *I. bullockii*), the indigo and lazuli buntings (*Passerina cyanea* and *P. amoena*), and the rose-breasted and

Bushy-tailed Woodrat (Neotoma cinerea). Print from ink drawing by Paul A. Johnsgard, colored by Allison Johnson. Great Plains Art Collection [0002.2004.0003]. Over 50 species of rodents occur in the five Great Plains states from North Dakota to Oklahoma, but the native rodents in the Galápagos Islands are limited to only four species of rice rats (Neoryzomys).

black-headed grosbeaks (*Pheucticus ludovicianus* and *P. melanocephalus*).

A COMPARISON OF GALÁPAGOS AND GREAT PLAINS REPTILES AND MAMMALS

A review of endemicity and species diversity among Galápagos reptiles and terrestrial mammals indicates a fairly low overall taxonomic diversity among these generally water-avoiding animals. Far fewer genera of reptiles or mammals are present there than occur on the Great Plains; and there are no amphibians, which cannot survive long in salt water. The major reptiles represented are iguanids, which presumably reached the islands by riding on flotsam, and tortoises, which may have also rafted or floated to the islands. In nearly all the Galápagos reptiles, there is a high incidence of interisland endemicity, a reflection of the reduced capacity for most reptiles to cross saltwater barriers.

The Galápagos red bat (*Lasiurus brachyotis*) is somewhat anatomically distinct from continental forms, such as the red bat (*L. borealis*) of the Great Plains and eastern North America; but the hoary bat (*L. cinereus*) of the Galápagos is identical to the species that is found to the north in the Great Plains and southern Canada. The hoary bat is thus evidently a more recent arrival to the Galápagos (Steadman and Zousmer 1988). Both species are highly migratory, wintering south to South America, so their occurrence on the Galápagos is not surprising.

Grizzly Bear (Ursus horribilis), adult. Print from ink drawing by Paul A. Johnsgard, colored by Allison Johnson. Great Plains Art Collection [0002.2004.0008]. Like most large mammalian predators such as the Gray Wolf (Canis lupus), the Grizzly Bear was eliminated from the Great Plains during the late 1800's. Over its North American range it has evolved dozens of geographic races that differ greatly in size and color.

Mountain Lion (Felis concolor), adult. Print from ink drawing by Paul A. Johnsgard, colored by Allison Johnson. Great Plains Art Collection [0002.2004.0015]. This, the largest of the Western Hemisphere cats, had an historic range extending from Canada to the southern tip of South America. Over much of its range deer are its primary prey. The Mountain Lion is slowly recovering some of the Great Plains range it lost during the past century.

Among aquatic but land-breeding mammals, the Galápagos sea lion (*Zalophus californicus*) is slightly smaller than its Californian relative and is sometimes classified as an endemic species (*Z. wollebacki*). The Galápagos fur seal (*Arctocephalus galapogensis*) differs only slightly from closely related mainland forms, and its nearest relative is the substantially larger and widespread South American fur seal (*A. australis*).

The greatest degree of mammalian adaptive radiation has occurred in the several endemic rice rats, which evidently had a relatively early arrival on the Galápagos Islands and have since differentiated into two endemic genera (*Nesoryzomys* and the extinct *Megaoryzomys*). Another genus, *Oryzomys,* also occurs on the mainland of South America, with representatives extending north from the coasts of Peru and Ecuador into the Great Plains as far as Kansas. These rodents are believed to have reached the islands by drift, with *Nesoryzomys* probably arriving earlier than *Oryzomys* (Orr 1966).

There are no complete surveys of the mammals of Ecuador to compare that region's mammalian diversity with the Galápagos; but Salta Province in northwestern Ecuador, with an area of about sixty thousand square miles, supports 144 species of land mammals, the majority of which are bats and rodents (Mares, Ojeda, and Barquez 1989). By comparison the Galápagos Islands' terrestrial mammalian fauna consists of only two bat species and probably eight species of native rice rats distributed over a landmass of about three thousand square miles.

Ernst and Barbour (1992) recognized twelve of the possibly still-extant Galápagos tortoises (*Geochelone*) as full species; but previous authors have instead recognized up to fifteen subspecies within a single collective species. Ernst and Barbour also reported that the domed carapace types are probably ancestral to the saddle-backed type. The saddle-backed carapace type probably evolved more than once, from different ancestors, perhaps under the influence of local needs for reaching higher levels to obtain *Opuntia* leaf-pads. Steadman and Zousmer (1998) noted that the Galápagos tortoise is considerably different from the three extant South American mainland species and that the origin of the Galápagos populations might instead have been from as far away as Africa or Asia. Fossil forms of *Geochelone* have been widely found from the Great Plains and southward, and one giant fossil species (*Geochelone orthopygia*) closely resembling the Galápagos tortoise commonly occurs in Nebraskan Miocene ash deposits from about 10 million years ago.

According to Steadman and Zousmer (1988), the land iguanas (*Conolophus*) may have arrived from South America as recently as about ten thousand years ago and are more similar to the marine iguana than to any South American relative. The two accepted species (*C. subcristatus* and *C. pallidus*) are closely related, and occasionally they hybridize when allowed to come into contact. The marine iguana (*Amblyrhynchus cristatus*) is the only marine-adapted iguanid species in the world and is unique in many ways. It has no obvious, living near relatives other than perhaps the land iguanas, and it has many subspecies that associated with different islands.

The lava lizards (*Tropidurus* or *Microlophus*, depending on the authority), leaf-toed geckos (*Phyllodactylus*), and Galápagos snakes (*Alsophis*) all represent groups having close mainland relatives in western South America. Like the marine iguana, speciation within these reptiles has been notable, with seven endemic lava lizard species, six endemic geckos, and three endemic snakes.

FLORAL ENDEMICITY AND PLANT ADAPTATIONS IN THE GALÁPAGOS

In an early study, Robinson (1902) reported that among 531 Galápagos seed plant taxa the endemism rate was 44.4 percent. More-recent endemism estimates for the islands range from 37–43 percent. Stewart (1911) reported particularly high Galápagos endemism rates in the families Boraginaceae (65 percent), Compositae (67.7 percent), Rubiaceae (77.3 percent), Amaranthaceae (78.7 percent), Euphorbiaceae (86 percent), and Cactaceae (100 percent). Porter (1979) estimated an overall 31 percent endemism among 735 plant taxa; however, this rises to 43 percent if human-caused plant introductions are excluded. Porter also reported the 735 plants consisted of 543 indigenous taxa, including seven endemic genera. Wiggins and Porter (1971) recognized 642 native Galápagos plant species and 60 additional subspecies or varieties, of which total 228 (32 percent) were classified as endemics. By comparison, the endemism rate for the entire Great Plains vascular flora is no more than 2.2 percent, and it is probably less judging from available range maps.

Some endemic species are now being threatened by introduced animals, such as goats and burros, and by hundreds of competing alien plants. By the late 1990s the number of exotic plants on the islands was estimated at nearly 450 species, some of which have been highly invasive and damaging to the islands' native flora and, indirectly, their fauna. Among the worst of these invaders are the quinine tree (*Chinchona succirubra*), multicolored lantana (*Lantana camara*), elephant grass (*Pennisetum purpureum*), and hill raspberry (*Rubus niveus*) (McMullen 1999).

The incidence of Galápagos floral endemism varies by major vegetation zones, with arid-adapted plants accounting for 67 percent of the endemism, mesic-zone plants of higher elevations accounting for 29 percent of the endemism, and shoreline or littoral-zone plants making up the remaining four percent. The high incidence of endemism of plants that are adapted to arid habitats is probably a reflection of the great extent of Galápagos arid habitats and also their presumed relatively old establishment (Johnson and Raven 1973).

A total native Galápagos flora of 700 taxa in an area of 3,042 square miles would represent a mean taxonomic diversity of 230 taxa per 1,000 square miles. The flora of Ecuador, a region some 40 percent larger than Nebraska, is still being surveyed, and its inventory is far from complete. It has been estimated that as many as 16,000 to 18,000 Ecuadorian species might be present (Flora of Ecuador Project), which would represent a mean diversity index of about 155 plant species per 1,000 square miles. This compares with roughly 1,800 Nebraska plant taxa (Kaul, Sutherland, and Rolfsmeier 2006) in an area of nearly 78,000 square miles, or about 20 taxa per 1,000 square miles.

Some close taxonomic similarities can be detected in the plant life of the Galápagos and Great Plains, in spite of their climatic and geographic separation. Though no native plant species are shared by both, if many genera are, some of the counterpart species are very similar in both their appearance and ecological roles.

Substantial adaptive radiation of Galápagos plant taxa has occurred within nineteen genera, with the sunflower-like genus *Scalesia* (twenty taxa) having the highest number of endemic forms. *Scalesia* may be most closely related to South American mainland composites such as the sunflowers *Helianthus* and *Viguiera*. The prickly pear cactus genus *Opuntia* shows the next highest level of taxonomic proliferation, with fourteen taxa. In the Galápagos species, the tree-like (or arborescent) types may be the most primitive taxa, their ancestors probably having originated in the Andes Mountains or coastal Peru (Porter 1979).

Some groups of plants are better represented in the Galápagos than might be expected by simple chance arrival from the available spectrum of mainland flora. Among the species-rich Galápagos plant families are the composites, spurges, amaranths, and legumes as well as grasses and sedges. These groups have evidently been best able to reach the Galápagos Archipelago through efficient long-distance dispersal abilities.

Considering natural dispersal agents, Porter (1983, 1984) estimated that about 80 percent of native Galápagos plant taxa were probably carried in by birds, 13 percent may have been brought by ocean currents, and seven percent were likely to have been carried by wind. Composites (Asteraceae), the best-represented Galápagos family, often have plume-like structures aiding wind dispersal or possess adhesive fruiting structures. Three other species-rich families (Amaranthaceae, Gramineae, and Cyperaceae) are frequently ingested or externally transported by birds (McMullen 1999). Legumes (Leguminaceae) are also well represented; their seedpods are often buoyant, providing a useful preadaptation for possible aquatic transport (Jackson 1985).

With regard to the probable ancestral origins of the Galápagos flora, Wiggins (1966) found a high degree of taxonomic affinity between the plants of the Galápagos and the South American mainland, especially the mainland's western coast. The coastal areas of Peru have a desert climate somewhat similar to that of the Galápagos and might represent a prime source for having supplied the Galápagos with plants via the Humboldt Current and southeast trade winds. Porter (1983) determined that 87 percent of the endemic and 97 percent of the nonendemic plants had their apparent origins in the South American mainland or were derived from more-widespread tropical taxa.

Many of the species-poor Galápagos plant families, such as the Scrophulariaceae and Lamiaceae, are highly adapted for pollination by insects, which are deficient both in diversity and number on the islands. Other families that are specialized for insect pollination and are poorly represented or absent in the Galápagos are the Orchidaceae (eleven taxa), Acanthaceae (six taxa), and Bignoniaceae (entirely absent). There is only one native pollinating bee (*Xylocopa darwinii*) on the islands, and there are very few butterflies. Although there is a fairly high number of nocturnal moths, there are few highly odorous or nocturnally blooming native plants. However, nineteen of the endemic plants do have white flowers, which make them more visible to night-flowing insects.

Wind pollination is also evidently of little significance in the Galápagos (McMullen 1999). However, Rick (1966) reported that Galápagos plants often have a high capacity for automatic self-pollination. Birds such as the cactus finch (*Geospiza scandens*) may incidentally perform a limited amount of pollination, as it often forages on *Opuntia* flowers. Seed dormancy of some Galápagos plants is broken by passage through the digestive tracts of animals such as tortoises or mockingbirds (McMullen 1999).

In addition to three cacti (*Brachycereus*, *Opuntia*, and *Jasminocereus*), spiny shrubs and trees are conspicuously numerous in the Galápagos flora and include ten additional genera (*Acacia*, *Caespalinia*, *Castelia*, *Duranta*, *Grabowskia*, *Mimosa*, *Parkinsonia*, *Prosopsis*, *Scutia*, and *Zanthoxylum*). These twenty total taxa represent about 3 percent of the total flora. Most of these spiny Galápagos genera also have small and usually deciduous leaves, which both reduce browsing opportunities and conserve water transpiration losses during dry seasons. By comparison, the Great Plains has six genera of spiny trees (*Acacia*, *Crataegus*, *Gleditsia*, *Maclura*, *Prosopsis*, and *Robinia*) and five genera of spiny shrubs (*Ribes*, *Rosa*, *Rubus*, *Sarcobatus*, and *Zanthoxylum*), the total representing less than 1 percent of the entire Great Plains flora.

The Galápagos flora is unusually rich in plants of the spurge family, which tend to be poisonous. Compared with the Great Plains, the Galápagos spurges comprise an almost three-fold greater proportion of the archipelago's overall flora. The poison apple (*Hippomane mancinella*), a widely distributed tree-sized spurge, has leaves and fruit that are highly poisonous to humans. However, giant tortoises are known to eat its fruit and to pass on the apparently intact seeds a few days later, and in Central America the fruit is also consumed by iguanas.

FLORAL ENDEMICITY AND PLANT ADAPTATIONS IN THE GREAT PLAINS

In comparison with the Galápagos, the flora of the Great Plains has very low endemism rates and is dominated by herbaceous plants, rather than by the woody plants so typical of the Galápagos. There are 495 taxa of grasses and sedges (Cyperaceae and Gramineae) among the total 2,217 Great Plains taxa, representing 22 percent of the total. By comparison, these two families constitute 89 of the 702 Galápagos plant taxa, or 7.9 percent (an early published estimate was 9.2 percent). Fires, historically frequent on the plains, have strongly favored grasses and sedges over shrubs and trees. When burned, the vast majority of the total aboveground biomass of trees and shrubs is destroyed, whereas fires typically cause relatively little damage to the rapidly regerminating grasses. Furthermore, subfreezing seasonal changes in temperature favor those plants that can readily forfeit their aboveground photosynthetic parts and die back to the ground surface when winter or unusually dry weather arrives. Storing their newly manufactured materials in underground root systems, perennial grasses are able to rapidly replace their photosynthetic leaves the following spring or wet season, whereas annual grasses devote all their energy to seed production within a single growing season.

Wind is an almost constant factor of prairie life; some prairie plants optimize their dissemination of pollen or seeds to coincide with times of maximum wind velocity (Reichman 1987). Unlike in the Galápagos, many Great Plains plants, especially the grasses and sedges, are wind pollinated; seed dispersal by the wind or by the use of adhesive structures that attach to grazing animals is also common in the Great Plains. Spiny seeds, such as those of the widespread puncture vine (*Tribulus terrestris*) and sandbur (*Cenchrus longispinus*), are transported widely by being caught in the fur of mammals.

Because their active areas of cell-division and new plant growth are located near ground level rather than at leaf tips, grasses and sedges are far more tolerant of grazing effects than are trees and shrubs, whose growing points are often destroyed by browsing animals. Indeed, the great array of grazing animals that have occupied the Great Plains since early Cenozoic times have helped grasses and sedges gain ascendancy over trees and shrubs through their grazing adaptations, as has the capacity of the grasses and sedges to weather several years of drought by becoming dormant. For example, at Spring Creek Audubon Prairie, a tallgrass prairie of about 640 acres in Lancaster County, Nebraska, there are roughly 330 vascular plant taxa, including fifty-four species of grasses (70 percent of which are perennials), as compared with twenty-two species of trees and shrubs (Kottas 2000). Likewise, the 240-acre Nine-Mile Prairie, also in Lancaster County, has nearly 400 plant taxa, including sixty-three grasses (73 percent of which are perennials), as compared with twenty-one trees and shrubs (Kaul and Rolfsmeier 1987).

Spines that help reduce or prevent animal browsing are relatively rare among the woody and succulent plants on the Great Plains. There are eleven species of cactus in the Great Plains (Barkley 1977), as compared with eight in the Galápagos. This is roughly three times as many Galápagos cacti relative to that area's total flora as occur in the Great Plains.

Variably toxic leaves, which also reduce or prevent grazing by herbivores, are found among many

Great Plains forbs, especially those adapted to semiarid regions where leaf loss needs to be minimized, including *Asclepias*, *Astragalus*, *Delphinium*, *Helenium*, *Hymenoxys*, *Lathyrus*, *Oxytropis*, *Senecio*, and *Stanleya*. Leaf or stem toxicity is also typical of many Great Plains spurges (Euphorbiaceae). There are thirty-six spurge taxa in nine Plains genera, most or all of which produce a toxic sap that discourages animal consumption. However, the seeds of spurges such as *Croton* and *Euphorbia* are important autumn foods for many birds. Other Great Plains plants such as junipers (*Juniperus*), dogbane (*Apocynum*), and elderberry (*Sambucus*) also have leaves that are sometimes toxic to mammals; but their fruits or seeds are regularly eaten by many birds. After being voided, such seeds might germinate far from the parent plant and facilitate dissemination, in a manner comparable to the spreading of poison apple seeds on the Galápagos Islands.

SUMMARY

Charles Darwin could not have realized the potential that the Galápagos Islands offered for the study of evolutionary biology when he first set foot on San Cristobal more than 170 years ago, nor could he have known how his subsequent ideas would shape all of modern biology. Like Mendel's humble monastery garden, the Galápagos Islands will forever be famously associated with Darwin and his prescient observations there. Because of his insights, we can understand the corresponding evolutionary phenomena and adaptations that have also occurred on the Great Plains and elsewhere. It is appropriate that one of the Galápagos islands, a volcanic peak, a research station, and a group of endemic finches were all named in his honor, as were several of the two hundred–plus animal and plant species that he discovered during the few weeks that he visited the islands. It seems likely that Darwin himself would not have asked for any more lasting recognition than having these namesakes. Yet, on the 200th anniversary of his birth and the 150th anniversary of his *Origin of Species*, biologists worldwide should pause and celebrate the lasting and pervasive influence that Charles Darwin has had on modern science and on world history itself.

Glossary

Adaptive radiation. The evolutionary proliferation of a single genetic line into many species or groups, thereby exploiting a wide range of available habitats or ecological niches.

Archipelago. A localized group of oceanic islands.

Biomass. The total amount of organic matter of a species or community at a particular location and point in time.

Carboniferous period. The geological period lasting from 260 to 345 million years ago, when vast quantities of coal were formed worldwide under tropical swamp-like conditions and when early reptiles appeared.

Cenozoic era. The geological period lasting from 65 million years ago to the present, during which most currently existing groups of animals and plants evolved, such as modern families of birds and mammals.

Cretaceous period. The geological period lasting from 135 to 65 million years ago, the peak of the reptilian reign.

Darwiniana. Objects of historic interest that are associated with Charles Darwin, his life, and his work.

Darwinism. The application of Darwin's theories on evolution. Neo-Darwinism is a modern approach, incorporating more recently available genetic and population information.

Ecological niche. An organism's "profession," including its evolved morphological, physiological, and behavioral features that adapt it to its habitat.

Endemic. Geographically confined to a single location or region, such as the Galápagos Islands or the Great Plains. Endemicity refers to the relative degree of such geographic confinement for an organism or group of organisms.

Eocene epoch. An early part of the Cenozoic era, lasting from 35 to 60 million years ago.

Evolution. In its simplest form: any ordered change. Darwin's theory applied to biological (or "organic") evolution, but evolution also may occur in nonbiological systems, such as planetary evolution and evolution of the chemical elements.

Forb. A broad-leaved herbaceous (nonwoody) plant, thus excluding all linear-leaved plants such as grasses and sedges.

Genus (plural, genera; adjective, generic). A taxonomic category consisting of one or more closely related species. Monotypic genera are those that contain only a single species.

Herbivore. An animal that consume herbaceous (nonwoody) vegetation.

Igneous. A type of mineral formed as a result of having once been molten or partly molten, such as lava.

Iguanid. A member of a large and widespread lizard family (Iguanidae), which includes the Galápagos iguanas and most Great Plains lizards.

Intelligent design. A variant of traditional creationism promoting the belief that living biological systems and organisms are too complex to have evolved without the guiding input of some higher creative power.

Loess. Wind-blown and silt-sized materials that sometimes occur locally on the Great Plains, forming deep and easily eroded ("loose") soils.

Mesic. Characterized by environmental conditions that lack extremes of heat and moisture.

Mesozoic era. The geologic period lasting from 225 to 65 million years ago; the "Age of Dinosaurs" and the period during which early mammals and birds evolved.

Metamorphic. A type of mineral that has undergone a change of state through intense heat or pressure.

Miocene epoch. Part of the Cenozoic era lasting from 23.3 to 5.2 million years ago, when extensive forests and woodlands were slowly being replaced by lush grasslands on the Great Plains.

Morphological. Referring to general anatomical and structural features of an organism.

Natural selection. The Darwinian explanation for adaptive modification of an organism's attributes through genetically based differential survival and reproduction of a population's members. Darwin observed that the populations of animals and plants he had found on the isolated Galápagos Archipelago often closely resembled those of continental South America. He also noted that populations on different Galápagos islands often varied slightly from one another. He thus speculated that the distinctive island biota might have gradually been transformed under conditions of isolation and local adaptation, providing a seminal basis for later hypotheses accounting for the origins of adaptive evolutionary change (natural selection) and gradually increasing biological diversity (speciation).

Oligocene epoch. Part of the Cenozoic era lasting from 35 to 23.3 million years ago, with much mountain building in the Rocky Mountains and arid-adapted grassland expansion in the Great Plains.

Perennial. Occurring in multiple years, or a plant that must survive several years before reproducing.

Paleocene epoch. The oldest part of the Cenozoic era, lasting from 65 to 60 million years ago, marked by the disappearance of most reptilian groups (apparently owing to a catastrophic asteroid collision that altered the earth's climates) and the appearance of most modern groups (orders and families) of birds and mammals.

Paleozoic era. The geological period lasting from about 570 to 225 million years ago, when most invertebrates, plants, and early vertebrates (fishes, amphibians, and reptiles) evolved.

Pleistocene epoch. The part of the Cenozoic era covering much of the past 1.6 million years, during which several continental glaciations covered much of northern North America.

Pliocene epoch. The part of the Cenozoic era lasting from 5.2 to 1.6 million years ago, a period of gradual cooling immediately prior to the Pleistocene, with many grazing animals present on the grasslands of the Great Plains.

Precambrian. The geologic history of the earth prior to the start of the Cambrian period (500 million years ago), when primitive forms of life on earth first evolved.

Rain shadow. An area of reduced rainfall occurring on the leeward side of mountains, owing to excessive precipitation intercepted on the mountains' windward side. This produces a semidesert climate in the western Great Plains.

Riverine. Occurring along or close to a river; often called riparian.

Speciation. The process of species proliferation. In higher animals, speciation typically results from the splitting and prolonged isolation of subpopulations until they have developed sufficient genetic differences to impede or prevent possible future interbreeding between them.

Species (adjective, specific). A population of organisms that potentially might interbreed among themselves but is genetically, structurally, ecologically, or otherwise prevented from breeding with members of other populations. The term species also refers to the second part of a scientific (Latin or Latinized) name, when it is preceded by a more general (generic) name. This combination produces a unique binomial, a dual technical name such as Homo sapiens.

Subspecies. One or more geographically recognizable and structurally distinctive populations of a species. Subspecies are often called "races." Subspecies are identified in print by the addition of a third term to the species' dual scientific name, producing a three-part name, or a trinomial. In botany, the term variety is often used to identify genetic variants that don't qualify as subspecies, and the term morph refers to recognizable genetic variants occurring within animal populations.

Taxon (plural, taxa). Related organisms that belong to a specific taxonomic category, such as a species, genus, or family.

Taxonomy. The practice of investigating evolutionary relationships among a group of organisms and classifying them in such a way that might best reflect these relationships.

Trade winds. The latitudinal bands of winds occurring just to the north and south of the equator, which either consistently blow from the northeast (the northern trade winds) or from the southeast (the southern trade winds). The Galápagos Islands are seasonally influenced by both trade winds.

CITED REFERENCES

Arenz, C. L., and A. Joern. 1986. Prairie legacies: Invertebrates. In *Prairie conservation: Preserving North America's most endangered ecosystem*, ed. F. B. Samson and F. L. Knopf, 91–109. Washington, DC: Island Press.

Baptista, L., and P. W. Trail. 1988. On the origin of Darwin's finches. *Auk* 105:662–71.

Barkley, T. M., ed. 1977. *Atlas of the flora of the Great Plains.* Ames: Iowa State University Press.

Bowman, R. I. 1961. Morphological differentiation and adaptation in the Galápagos finches. *Univ. Calif. Publ. in Zool.* 58:1–302.

Darwin, C. 1845. *Journal of researches into the natural history and geology of the countries visited during the voyage of HMS Beagle round the world under command of Captain Fitzroy.* London: John Murray.

———. 1859. *On the origin of species, by means of natural selection, or the preservation of favoured races in the struggle for life.* London: John Murray.

Ernst, C. H., and R. W. Barbour. 1992. *Turtles of the world.* Washington, DC: Smithsonian Press.

Fitter, J., D. Fitter, and D. Hosking. 2000. *Wildlife of the Galápagos.* Princeton, NJ: Princeton University Press.

Göteburg University and Riksmuseum, Stockholm. Flora of Ecuador Project. http://www2.dpes.gu.se/project/ecuador.

Freeland, J. R., and P. Boag. 1999. Phylogenetics of Darwin's finches: Paraphyly in the tree-finches and two divergent lineages in the warbler finch. *Auk* 116:577–88.

Grant, P. R. 1999. *Ecolo gy and evolution of Darwin's finches.* 2nd ed. Princeton NJ: Princeton University Press.

Harris, M. 1974. *A field guide to the birds of Galápagos.* London: Collins.

Hooker, J. D. 1847. An enumeration of the plants of the Galápagos Archipelago, with descriptions of those that are new. *Trans. Linn. Soc. Lond.* 20:163–233.

Jackson, M. A. 1985. *Galápagos: A natural history.* Calgary: University of Calgary Press.

Johnsgard, P. A. 1979. *Birds of the Great Plains: Breeding species and their distribution.* Lincoln: University of Nebraska Press.

———. 2002. *Prairie birds: Fragile splendor on the Great Plains.* Lawrence: University Press of Kansas.

———. 2003. *Great wildlife of the Great Plains.* Lawrence: University Press of Kansas.

———. 2006. *The birds of Nebraska.* Revised ed. Privately printed, Lincoln, NE.

Johnson, M. P., and P. H. Raven. 1973. Species number and endemism: The Galápagos Archipelago revisited. *Science* 1979:893–95.

Jones, J. K., D. M. Armstrong, and J. R. Choate. 1985. *Guide to mammals of the Plains states.* Lincoln: University of Nebraska Press.

Kaul, R., D. H. Sutherland, and S. B. Rolfsmeier. 2006. *Flora of Nebraska.* Lincoln: Conservation and Survey Division, University of Nebraska–Lincoln.

Kaul, R., and S. B. Rolfsmeier. 1987. The characteristics and phytogeographic affinities of the flora of Nine-Mile Prairie, a western tall-grass prairie in Nebraska. *Trans. Nebr. Acad. Sci.,* 15:23–35.

Kottas, K. 2000. Floristic composition and characterization of Spring Creek Prairie, Nebraska. M.S. thesis, University of Nebraska–Lincoln.

Lack, D. 1947. *Darwin's finches.* Cambridge: Cambridge University Press.

McMullen, C. 1999. *Flowering plants of the Galapágos.* Ithaca, NY: Cornell University Press.

Mares, M. A., R. A. Ojeda, and R. M. Barquez. 1989. *The mammals of Salta Province, Argentina.* Norman: University of Oklahoma Press.

Orr, R.T. 1966. Evolutionary aspects of the mammalian fauna of the Galápagos. In *The Galápagos: Proceedings of the Symposium of the Galápagos International Scientific Project,* ed. R. I. Bowman, 276–81. Berkeley: University of California Press.

Petren, K., B. R. Grant, and P. R. Grant. 1999. A phylogeny of Darwin's finches based on microsatellite DNA length variation. *Proc. Roy. Soc. London* B 266:321–29.

Porter, D. M. 1979. Endemism and evolution in Galápagos Islands vascular plants. In *Plants and islands,* ed. D. Bramwell, 225–56. New York: Academic Press.

———. 1983. Vascular plants of the Galápagos: Origins and dispersal. In *Patterns of evolution in Galápagos Organisms,* ed. R. I. Bowman, M. Berson, and A. E. Leviton, 33–96. San Francisco, CA: Pacific Division, AAAS.

———. 1984. Relationships of the Galápagos flora. *Biol. J. of the Linn. Soc.* 21:243–51.

Reichman, O. J. 1987. *Konza Prairie: A tallgrass natural history.* Lawrence: University Press of Kansas.

Rick, C. M. 1966. Some plant-animals relations on the Galápagos Islands. In *The Galápagos: Proceedings of the Symposium of the Galápagos International Scientific Project,* ed. R. I. Bowman, 215–24. Berkeley: University of California Press.

Ridgely, R. S., and P. J. Greenfield. 2001. *The birds of Ecuador: Field guide.* Ithaca, NY: Cornell University Press.

Robinson, B. L. 1902. Flora of the Galápagos Islands. *Proc. Amer. Acad.* 1902:78–270.

Sato, A., C. O'Huigin, F. Figueroa, P. R. Grant, B. R. Grant, H. Tichy, and J. Klein. 1999. Phylogeny of Darwin's finches as revealed by mDNA sequences. *Proc. Natl. Acad. Sci.* 96:5101–6.

Steadman, D. W. 1982. The origin of Darwin's finches. *Trans. of the San Diego Soc. for Nat. Hist.* 19:279–96.

Steadman, D. W., and S. Zousmer. 1988. *Galápagos: Discovery on Darwin's islands.* Washington, DC: Smithsonian Institution Press.

Stewart, A. 1911. A botanical survey of the Galápagos Islands. *Proc. Calif. Acad. Sci.* 4th ser., 1:7–288.

Weiner, J. 1994. *The beak of the finch: A story of evolution in our time.* New York: Alfred A. Knopf.

Wiggins, I. L. 1966. Origins and relationships of the flora of the Galápagos Islands. In *The Galápagos: Proceedings of the Symposium of the Galápagos International Scientific Project,* ed. R. I. Bowman, 175–82. Berkeley: University of California Press.

Wiggins, I. L., and D. M. Porter. 1971. *Flora of the Galápagos Islands.* Stanford, CA: Stanford University Press.

SELECTED ADDITIONAL REFERENCES

CHARLES DARWIN AND THE HISTORY OF EVOLUTIONARY THEORY

Barlow, N., ed. 1946. *Charles Darwin and the voyage of the Beagle.* New York: New York Philosophical Society.

Brent, P. 1981. *Charles Darwin: A man of enlarged curiosity.* New York: W. W. Norton.

Browne, J. 1995. *Charles Darwin: Voyaging.* New York: Alfred A. Knopf.

———. 2002. *Charles Darwin: The power of place.* New York: Alfred A. Knopf.

———. 2006. *Darwin's "Origin of species."* New York: Atlantic Monthly Press.

Clarke, R. W. 1984. *The survival of Charles Darwin: A biography of a man and an idea.* New York: Random House.

Desmond, A., and J. Moore. 1991. *Darwin: The life of a tormented evolutionist.* New York: W. W. Norton.

Diamond, J., ed. 2006. *Virus and the whale: Exploring evolution in creatures small and large.* Arlington, VA: NSTA Press.

Eldredge, N. 2006. *Darwin: Discovering the tree of life.* New York: W. W. Norton.

Grant, P. R., and B. R. Grant. 2008. *How and why species multiply: The radiation of Darwin's finches.* Princeton, NJ: Princeton University Press.

Himmelfarb, G. 1959. *Darwin and the Darwinian revolution.* New York: W. W. Norton.

Keynes, R. D. 2003. *Fossils, finches and Fuegians: Darwin's adventures and discoveries on the Beagle.* New York: Oxford University Press.

Larson, E. D. 2004. *Evolution: The remarkable history of a scientific theory.* New York: Modern Library.

Levine, G. 2006. *Darwin loves you: Natural selection and the enchantment of the world.* Princeton, NJ: Princeton University Press.

Mayr, E. 1991. *One long argument: Charles Darwin and the genesis of modern evolutionary thought.* Cambridge, MA: Harvard University Press.

———. 2001. *What evolution is.* New York: Perseus Books.

Moorehead, A. 1969. *Darwin and the Beagle.* New York: Harper and Row.

Quammen, D. 2004. Darwin's big idea. *Natl. Geo.* 206 (5): 2–35.

———. 2006. *The reluctant Mr. Darwin: An intimate portrait of Charles Darwin and the making of his theory of evolution.* New York: W. W. Norton.

Ralling, C. 1979. *The voyage of Charles Darwin.* New York: Mayflower Books.

Ruse, M. 2006. *Darwinism and its discontents.* New York: Cambridge University Press.

Sulloway, F. J. 1984. Darwin and the Galápagos. *Biol. J. of the Linn. Soc.* 21:29–59.

———. 2005. The evolution of Charles Darwin. *Smithsonian* 36 (9): 59–69.

Weiner, J. 1994. *The beak of the finch: A story of evolution in our time.* New York: Alfred A. Knopf.

White, M., and J. Gribbsan. 1995. *Darwin: A life in science.* New York: Dutton.

Wilson, E. O. 2006. *The creation: An appeal to save life on Earth.* New York: W. W. Norton.

Zimmer, C. 2001 *Evolution: The triumph of an idea.* New York: HarperCollins.

ADDITIONAL GALÁPAGOS REFERENCES

Beebe, W. L. 1924. *Galápagos: World's end.* New York: Putnam.

Benz, R. 2000. *Ecology and evolution: Islands of change.* Arlington, VA: NSTA Press.

Berry, R. J. 1984. *Evolution in the Galápagos Islands.* New York: Linnaean Society and Academic Press.

Bowman, R. I. 1961. Morphological differentiation and adaptation in the Galápagos finches. *Univ. Calif. Publ. in Zool.* 58:1–302.

Bowman, R. I., ed. 1966. *The Galápagos: Proceedings of the Symposium of the Galápagos International Scientific Project.* Berkeley: University of California Press.

Grant, P . R., and B. R. Grant. 2002. Adaptive radiation of Darwin's finches. *Am. Scientist* 90:130–39.

Huxley, J. 1966. Charles Darwin: Galápagos and after. In *The Galápagos: Proceedings of the Symposium of the Galápagos International*

Scientific Project, ed. R. I. Bowman ed., 3–9. Berkeley: University of California Press.
Kricher, J. 2006. *Galápagos: A natural history.* Princeton, NJ: Princeton University Press.
Larson, E. J. 2001. *Evolution's workshop: God and science on the Galapagos Islands.* New York: Basic Books.
Lewin, R. 1979. *Darwin's forgotten world.* New York: Gallery Books.
Moore, T. D. R. 1988. *Galápagos: Islands lost in time.* New York: Viking Press.
Nelson, B. 1968. *Galápagos: Islands of birds.* London: Longmans.
Perry, R. 1972. *The Galápagos Islands.* New York: Dodd, Mead, and Company.
Swarth, S. 1934. The bird fauna of the Galápagos Islands in relation to species formation. *Biol. Reviews* 9:213–34.
Thorton, I. 1971. *Darwin's islands: A natural history of the Galápagos.* New York: Natural History Press.

THE MAJOR PUBLICATIONS OF CHARLES DARWIN

Journal of Researches during the Voyage of the Beagle. 1839. (2nd ed., 1845).
Zoology of the Voyages of H.M.S. Beagle, ed. C. Darwin. 1838–1843. In five parts (Fossil Mammals, Mammals, Birds, Reptiles, and Fish).
Structure and Distribution of Coral Reefs. 1842. (2nd ed., 1874).
Geological Observations on Volcanic Islands and Parts of South America. 1846. (2nd ed., 1876).
Monographs on the Cirripedia. 1851–1854. 3 vols.
The Origin of Species. 1859. (2nd ed., 1860; 3rd ed., 1861; 4th ed., 1866; 5th ed. 1869; 6th ed., 1872).
On the Various Contrivances by which British and Foreign Orchids are Fertilized by Insects. 1862. (2nd ed., 1877).
Variation of Animals and Plants under Domestication. 1868. 2 vols.
Descent of Man and Selection in Relation to Sex. 1871. 2 vols.
Expression of the Emotions in Man and Animals. 1872.
Insectivorous Plants. 1875.
Movements and Habits of Climbing Plants. 1875.
Effects of Cross- and Self-Fertilization in the Vegetable Kingdom. 1876. (2nd ed., 1878).
Different Forms of Flowers and Plants of the Same Species. 1877. (2nd ed., 1880).
Power of Movement in Plants. 1880.
Formation of Vegetable Mould through the Action of Worms. 1881.
Autobiography of Charles Darwin and Selected Letters, ed. Francis Darwin. 1887. 2 vols. A third volume of letters appeared in 1903, and Nora Barlow published *The Autobiography of Charles Darwin* in 1958, adding some previously deleted text. For a valuable online source to all of Charles Darwin's publications, his voluminous correspondence, and much additional biographical information, see http://darwin-online.org.uk/. Another useful general source of Darwinian information is http://www.aboutdarwin.com/.

DARWIN'S OBSERVATIONS ON THE GALÁPAGOS ISLANDS

"The natural history of these islands is eminently curious, and well deserves attention. Most of the organic productions are aboriginal creations, found nowhere else; there is even a difference between the inhabitants of the different islands; yet all show a marked relationship with those of America, though separated from the continent by an open space of ocean, between 500 and 600 miles in width." *The Voyage of the Beagle*

"Hence, both in time and space, we seem to be bought somewhere near to that great fact—that mystery of mysteries—the first appearance of new beings on earth." *The Voyage of the Beagle*

"The remaining land-birds form a most singular group of finches, related to one another in the structure of their beaks, short tails, form of body and plumage: There are thirteen species, of which Mr. Gould has divided into four subgroups." *The Voyage of the Beagle*

"Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds on this archipelago, one species had been taken and modified for different ends." *The Voyage of the Beagle*

"The inhabitants, as I have said, state that they can distinguish the tortoises from the different islands, and that they differ not only in size, but in other characteristics." *The Voyage of the Beagle*

"If the different islands have their representative species of Geospiza, it may help to explain the singularly large number of species in this one small archipelago, and as a consequence of their numbers the perfectly graduated series in the size of their beaks." *The Voyage of the Beagle*

"But it is the circumstance, that several of the islands have their own species of tortoise, mocking-thrush, finches and numerous plants, these species having the same general habits, occupying analogous situations, and obviously filling that same place in the natural economy of this archipelago, that fills me with wonder." *The Voyage of the Beagle*

"Hence it would appear probable, that the same causes which here make the immigrants of some species smaller, make most of the Galapageian species also smaller, as well as generally more dusky coloured." *The Voyage of the Beagle*

"Reviewing the facts given here, one is astonished by the amount of creative force, if such an expression might be used, displayed on these small, barren and rocky islands; and still more so, on its diverse yet analogous action on points so near each other." *The Voyage of the Beagle*

Darwin's Observations on Evolution

"Analogy would lead me one step further, namely, to the belief that all animals and plants have descended from one prototype . . . probably all the organic beings which have ever lived on this earth have descended from one primordial form into which life was first breathed." *The Origin of Species*

"It is interesting to contemplate a tangled bank, clothed in many plants of many kinds, with birds singing in the bushes, and various insects flitting about, and to reflect that these elaborately constructed forms, so different from one another, and dependent upon one another is such a complex manner, have all been produced by laws acting around us." *The Origin of Species*

"There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved." *The Origin of Species*

"Man may be excused for feeling some pride at having risen, though not through his own exertions, to the very summit of the organic scale; and the fact of his having thus risen, instead of having been aboriginally placed there, may give him hope for a still higher destiny in the distant future." *The Descent of Man*

"For my own part, I would as soon be descended from that heroic little monkey, who braved his dreaded enemy in order to save the life of his keeper, or from that old baboon, who descending from the mountain, carried away in triumph his young comrade from a crowd of astonished dogs, as from a savage who delights to torture his enemies, offers up bloody sacrifices, practices infanticide without remorse, treats his wives like slaves, knows no decency, and is haunted by the grossest superstitions." *The Descent of Man*

"When I view all beings not as special creations, but as the lineal descendant of some few beings which lived long before the Cambrian system was deposited, they seem to be to become ennobled." *The Origin of Species*

"When the views advanced by me in this volume, and by Mr. Wallace, or when analogous views on the origin of species are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history." *The Origin of Species*

"With such moderate abilities as I possess; it is truly surprising that I should have influenced to a considerable extent the belief of scientific men on some important points." *Autobiography*

Great Plains Art No. 9
ISBN 10: 0-938932-19-5

University of Nebraska Lincoln