would be reduced considerably in the absence of ground-water inflow. In addition, if a large fraction of the sedimented diatom silica were not regenerated, the diatom crop in Crystal Lake would be similarly reduced.

Ground water clearly is a major factor controlling the chemical composition and biological dynamics of certain lakes. The role of ground water will be dominant for some constituents and lakes (*14*) but may be minor in others (*15*). Thus, we concur with Winter (*3*) in recognizing the need for understanding ground water–lake relations when constructing lake nutrient and water budgets.

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6. Samples were collected at five to ten depths at the deep-hole station; see Fig. 1 for the collection frequency.
7. We determined DRS on 0.4-μm (Nuclepore) filtrates, following the method of J. D. H. Strickland and T. R. Parsons [*A Practical Handbook of Seawater Analysis* (Fisheries Research Board of Canada, Ottawa, 1972), pp. 65–70]. PBS was analyzed by the method of D. W. Eggiman, F. T. Manheim, and P. R. Betzer [*J. Sediment. Petrol.* **50**, 215 (1980)]. TS was calculated as DRS + PBS. Chlorophyll a was measured according to the method of C. J. Lorenzen [*Limnol. Oceanogr.* **12**, 343 (1967)].
8. Data from 57 piezometers around and beneath the lake were input into flow nets for Darcy's law calculations to determine the monthly ground-water flux to and from the lake.
9. Duplicate traps (3:1 ratio of depth to diameter) were deployed at 17 m; see W. D. Gardner [*J. Mar. Res.* **38**, 41 (1980)] for general design. The relative error between duplicate traps was about 20 percent. Lower accuracy is expected during the well-mixed periods (early May to mid-June and late October to mid-December).
10. The permanent accumulation rate was based on direct analysis of PBS in depth-sectioned sediment cores and a mass sedimentation rate measured by R. Talbot [thesis, University of Wisconsin–Madison (1981)] from excess ^{210}Pb profiles. The range reflects the uncertainty in the area of the depositional zone and the lateral changes in sediment PBS concentrations.
11. Rainfall was measured at a National Atmospheric Deposition Program site located 3 km from Crystal Lake. The mean DRS content was taken from unpublished data of S. J. Eisenreich, P. J. Emmling, and A. M. Beeton for bulk precipitation collected in the area.
12. A mixed-lake mass of 100 kg of silica corresponds to a concentration of about 25 μg liter^{-1}. For comparison, typical concentrations of DRS in northern temperate lakes are 0.46 to 1.18 mg liter^{-1} (*2*).
13. The accuracy of the calculated regeneration flux depends on errors in the other silica fluxes (Eq. 1), estimated to be about 30 percent for gross sedimentation, 50 percent for ground-water inflow, and 20 percent for ΔTS. Thus, errors in regeneration range from about 25 to 30 percent for high fluxes to >100 percent for low values. We constrained Eq. 1 to avoid negative regeneration values by adjusting gross sedimentation. We assume that PBS dissolution in the sediment traps is negligible.
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Geologic Youth of Galápagos Islands Confirmed by Marine Stratigraphy and Paleontology

Abstract. *Six distinctive types of fossiliferous marine deposits occur on the Galápagos Islands that provide evidence for the age of emergence of the islands above sea level and hence a maximum age for the islands' terrestrial biota. These subtidal to supratidal deposits include (i) volcanic tuffs with fossils, (ii) limestones and sandstones interbedded with basalt, (iii) terrace deposits, (iv) beach rock, (v) supratidal talus deposits, and (vi) recently uplifted tidal and subtidal rocks and sand. With the exception of (vi), the deposits were previously assigned ages varying from Miocene to Pleistocene, but all are less than about 2 million years old. This age, together with independently determined geologic ages, indicate that the islands emerged from the sea relatively recently and that all evolution of the islands' unique terrestrial biota occurred within the past 3 to 4 million years.*

The Galápagos Islands are famous for their unique terrestrial biota. Species there evolved in isolation and radiated into a variety of ecological niches. For example, 13 species of Darwin's finches radiated from an apparent single ancestral species (*1*). No fossil evidence has been uncovered that reveals the initial history or age of this biota, hence the earliest time of arrival of any ancestral species and the maximum time available for radiation on the islands can be established only from geologic and marine paleontologic evidence. To date, geologists have suggested that the islands are very young, perhaps no older than 3+ million years (*2, 3*), whereas paleontologists have suggested a Miocene age (10 to 14 million years ago) for some fossil occurrences and Pliocene to Pleistocene ages for others. Thus the age of the initial appearance of the islands above sea level and the time at which they first were available for colonization by a terrestrial biota have not been resolved. The reports of pre-Pleistocene ages based on marine fossils and sedimentary rocks are cited in biological arguments concerning the time of colonization and rates of evolutionary divergence in the fauna (*4*). We describe here six distinctive types of fossiliferous marine deposits that confirm the younger ages proposed by geologists (Figs. 1 and 2).

Marine fossils have long been known from the Galápagos Islands. Darwin (*5*) and Wolf (*6*) reported marine fossils in volcanic rocks high above sea level, but these reports were not investigated subsequently. Fossils reported to be Pleistocene and Pliocene were later described from various sedimentary deposits on several islands (*7–9*). The oldest age inferred for the Galápagos is Miocene and is based on fossils and stratigraphy of limestone deposits on northeastern Isla Santa Cruz (*10*). Radiometric dates (*3, 11–16*) and the islands' plate tectonic history (*2*), however, indicate that the islands did not begin to emerge from the sea until the Pliocene, some 3 to 4 million years ago.

On eight islands we found six types of fossiliferous marine deposits: (i) submarine tuff cones, (ii) limestone and sandstone interbedded with pillow basalts and basalt flows, (iii) subtidal rock and sand deposits preserved on terraces, (iv) beach rock, (v) supratidal talus debris, and (vi) recently uplifted subtidal to supratidal rocks and sand. These deposits bear significantly on the geologic history of the islands, and types (ii) through (iv) have been used in previous interpretations of the islands' age (Fig. 2).

The fossiliferous tuffs occur as broad cones formed during shallow submarine eruptions. Six major tuff cones and cone complexes ring Isla Santa Cruz (*15*) and are thought to represent an early phase of Galápagos volcanism (*16, 17*). The cones are now eroded and are connected to the volcanoes of the main island by subaerial basalt flows. We studied the tuff cones at Cerro Gallina and Cerro Colorado (Fig. 1) (*18*). In the poorly sorted and poorly bedded facies near the vents, boulder-sized fragments of shallow-water coquinas and fossiliferous limestone are incorporated in the tuff. In the better sorted distal facies, individual mollusk shells are relatively common. The oldest radiometric age obtained to date in the Galápagos Islands is a potassium-argon date of 4.8 ± 1.87 million years on the Cerro Colorado tuff at nearby South Plazas Island (*3, 11*). The included limestone clasts there are lithologically and faunally identical to fossiliferous limestones interbedded with reverse-polarity basalts, radiometrically dated at near 2 million years (*16*), that crop out within a few hundred meters of the tuff cone. At Cerro Gallina we collected 20 species of mollusks occurring as individual shells in the tuff from sea level to the top of the eroded cone, and we collected a similar but less diverse fauna from the Cerro Colorado cone (*18*). The specimens are inferred to have been alive or recently dead at the time of eruption because they are infilled with tuff. All the species are alive today in shallow waters of the eastern Pacific Ocean. The large standard deviation in the tuff date, the possible lithologic correlation at Cerro Colorado, and the modern aspect of the tuff-cone faunas suggest that the cones are younger than nearby submarine basalts and limestones.

Fossiliferous marine limestone and tuffaceous sandstone beds are exposed in sea cliffs on Isla Baltra and just north of Cerro Colorado on Isla Santa Cruz. The species are from a variety of intertidal and shallow subtidal associations. The proportion of extinct mollusk species from Isla Baltra led Hertlein (*9*) to assign a Pliocene age to these deposits. It has also been suggested that the rocks near Cerro Colorado were later Miocene (*10*). Radiometric age dates and paleomagnetism of the associated volcanic rocks, however, confirm that the interbedded marine deposits are approximately 2 million years old (*3, 11, 15, 16*).

Marine terrace deposits on the Galápagos occur mostly between 5 and 10 m above sea level and range from pockets of fossiliferous sand on lava platforms and between basalt boulders to stratified sand up to 3 m thick that may be cemented at surface exposures. The fossils in these deposits are generally well preserved and abundant; species diversity is commonly high. On Islas Isabela, San Salvador, and Santa Fé these deposits have molluscan faunas of more than 50 species, and nearly all of these are living today. A terrace deposit just north of Villamil, Isla Isabela, reported previously as being Pleistocene (*7, 8*), is surrounded by a younger lava flow. The radiometric age for Isla Isabela is 0.09 ± 0.04 million years (*3, 11*), and the island is still active. Pleistocene fossils were reported from terraces at James Bay, Isla San Salvador (*8*). The oldest rocks exposed on San Salvador were dated at less than 0.77 ± 0.12 million years (*13*). On Santa Fé fossiliferous terrace deposits at different elevations contain a diverse fauna. The oldest radiometric date for Santa Fé is 2.85 ± 0.06 million years (*3*). One terrace deposit there underlies a lava flow, and volcanism on this island has been extinguished for at least 1 million years (*3*). Thus the terrace deposits in the Galápagos vary widely in age but most are Pleistocene or younger. However, the islands are tectonically and volcanically active; terrace deposits probably have formed throughout their history.

Fossils from beach rock have also been reported as being Pleistocene (*8*). Beach rock, dipping seaward and ce-

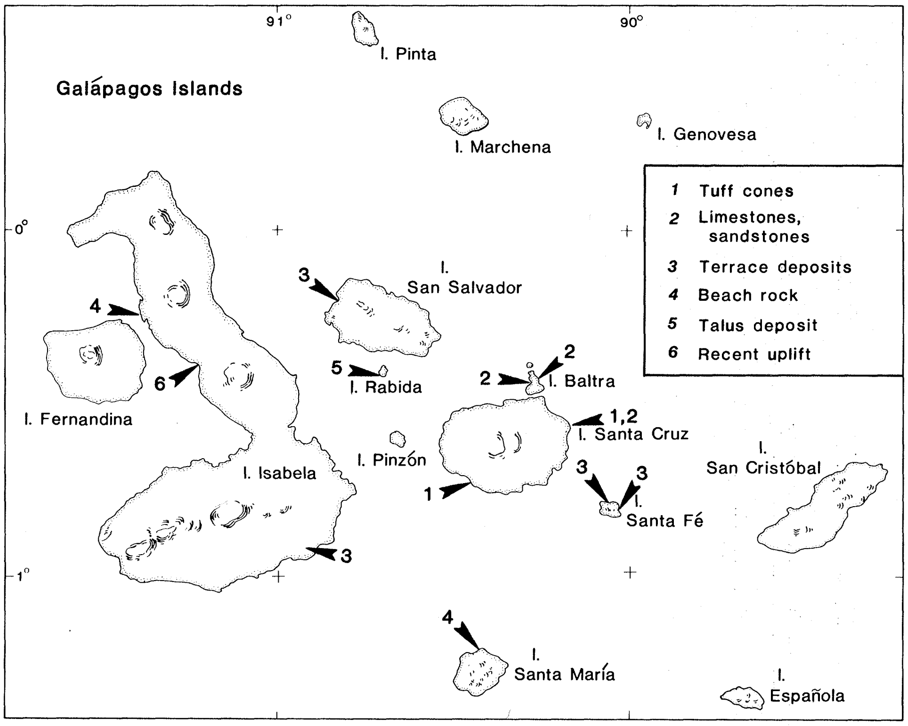

Fig. 1. Map of the Galápagos Islands showing fossil collection localities and types of deposits. Cerro Colorado tuff cone is in the northeastern part of Isla Santa Cruz and offshore South Plazas Island and Cerro Gallina cone is in the southwestern part.

Previous age assignments

Recent	Urvina Bay uplift
Pleistocene	Talus deposits Beach rock James Bay terraces Villamil terrace
Pliocene	Limestones on Baltra
Miocene	Limestones and tuff cone at Cerro Colorado

Revised age assignments

Recent	BRUNHES	Urvina Bay uplift Talus deposits Beach rock
10,000 years		James Bay terraces Villamil terrace
0.72 mya	MATUYAMA	Santa Fé terraces
Pleistocene		Tuff cones???
1.6 mya		Interbedded limestones on Baltra and at Cerro Colorado
2.47 mya	GAUSS	
Pliocene		
5 mya		
Miocene		

Fig. 2. Previous age assignments for fossil deposits and revised age estimates based on this study together with radiometric age dates and paleomagnetic stratigraphy obtained on rocks from the Galápagos. The Pliocene-Pleistocene boundary is now placed at 1.6 million years ago (mya) by others (*19*).

mented in various degrees by $CaCO_3$, crops out at low-tide to mid–high-tide levels on many beaches in the archipelago. The faunas from these rocks include the same species found on adjacent modern beaches. Because beach rock can form very rapidly in tropical and subtropical regions and because these rocks in the Galápagos are associated with modern sea level stands, contain modern faunas, and dip seaward, we infer that these deposits are younger than Pleistocene.

On Isla Rabida, Hertlein and Strong (*8*) reported marine mammal bone and two species of mollusks from scoriaceous talus at the base of steep cliffs above high-tide level. They concluded from the species present that the age was Pleistocene, although they listed the two mollusk species as ranging into the Recent. Our examination of the shore of Isla Rabida revealed that storm-tossed shells and bones of sea lions and birds are now being rapidly buried supratidally by debris falling from the cliffs. We conclude that these deposits at outcrop are also very young, perhaps no more than a few hundred years old.

In 1954 at Urvina Bay, Isla Isabela, the shore was suddenly uplifted 4.5 m shortly before the eruption of nearby Volcan Alcedo (*16*). The uplift exposed supratidal to subtidal bay and rocky shore communities. Now only well-skeletonized forms remain, such as calcareous algae, mollusks, echinoderms, and barnacles. Uplifted biotas may thus be quite recent and do not necessarily imply Pleistocene or older ages, as commonly assumed in the past. The relative importance and scale of localized uplift in forming the present islands have been debated by geologists (*16, 17*). These deposits and terrace deposits confirm the importance of localized uplift in shaping the islands, but they do not indicate similarity of ages.

Shallow-water, tidal, and supratidal marine fossil assemblages in the Galápagos Islands are more abundant and diverse than previously recognized. They occur in at least six geologic settings. In contrast to early paleontologic studies, our observations and conclusions (Fig. 2) corroborate independent geologic evidence (*2, 3*) that the western Galápagos Islands emerged from the sea less than 2 or 3 million years ago. The easternmost islands may be about 1 million years older on the basis of plate tectonic age estimates (*2, 3*), although these estimates do not suggest when the islands appeared above sea level. Radiometric dates on subaerial lava flows indicate that Isla Española stood above sea level at least 3 million years ago (*14*). The marine paleontological record is thus reconciled with the geologic evidence, and together they indicate that all adaptive radiation in the terrestrial biota of the Galápagos Islands occurred within the past 3 to 4 million years.

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Blood-Brain Barrier: Endogenous Modulation by Adrenal-Cortical Function

Abstract. *The blood-brain barrier restricts the passage of molecules from the blood to the brain. The permeability of the barrier to iodine-125–labeled bovine serum albumin was examined in rats that had undergone adrenalectomy, adrenal demedullation, and corticosterone replacement. Adrenalectomy, but not adrenal demedullation, increased the permeability of brain tissue to the isotopically labeled macromolecule; corticosterone replacement reversed this effect. These results indicate that the blood-brain barrier may be hormonally regulated; that is, the pituitary-adrenal axis may physiologically modulate the permeability of the brain microvasculature to macromolecules.*

The blood-brain barrier (BBB) restricts the passage of polar compounds and macromolecules from the blood into the brain interstitium (*1, 2*). This barrier arises from several morphologic characteristics of the brain vasculature; namely, the tight junctions between adjacent endothelial cells and the virtual absence of fenestrations and cytoplasmic pinocytotic vesicles within endothelial cells (*1–3*). Anatomic and physiologic evidence indicates that cerebral microvascular permeability may be responsive to both neural and humoral influences (*4, 5*) and has led to speculation on the roles of these systems in maintaining homeostasis within the central nervous system through actions on the BBB (*5, 6*).

Dexamethasone and other synthetic glucocorticoids have been widely used for the clinical treatment of brain edema (*7*) and have been shown to alter the flux of water across the BBB (*8*). Furthermore, dexamethasone reduces the disruption of the BBB produced by drug-induced acute hypertension (*9*), repeated convulsive seizure activity (*10*), or hypertonic perfusion of the brain (*11*). These observations prompted our speculation that the pituitary-adrenal axis may take part in the endogenous regulation of BBB integrity and that adrenal glucocorticoids may specifically influence the permeability characteristics of the undisrupted brain microvasculature. Therefore, we investigated the effects of adrenalectomy, selective adrenal demedullation, and corticosterone replacement on the permeability of the BBB to ^{125}I-labeled bovine serum albumin (BSA; 69,000 molecular weight) in conscious, freely moving rats. We now report that total adrenalectomy, but not selective adrenal demedullation, significantly increases the permeability of ^{125}I-labeled BSA into the brain and that corticoster-