

## The Herpetofauna of the Rincón Area, Península de Osa, Costa Rica, a Central American Lowland Evergreen Forest Site

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Ten to twelve thousand years ago, when humans first came from the north to enter the vast tropical evergreen lowland forests of Mexico and Central America, these forests stretched for what must have seemed an eternity, from the Veracruz lowlands 2,600 km southeastward into northern South America and beyond. Even eight to ten millennia later, when the Spanish conquistadores arrived on the shores of the American continent, these forests, although heavily disturbed in some areas by native Amerindian cultures, presented an awe-inspiring continuum, a great and dark sea in the words of Fernandez de Oviedo y Valdez (1526), over most of the lowlands of Middle America. Until fairly recently, the humid lowland forest areas of the region have been relatively safe from the destructive agricultural and forestry practices that in postconquest times have denuded, “developed,” or otherwise laid waste much of the drier and upland habitats of tropical America. Now even these long protected remnants of the most diverse and complicated of ecosystems are threatened with total annihilation, first, in the 1970s and 1980s, by the worldwide drive of the Food and Agriculture Organization of the United Nations to convert these natural wonders into cattle land, and now to ever-increasing human population pressures for land and forest products. At the present rate of cutting and development, within the first two decades of this century nearly all of the Central American humid lowland evergreen forest habitats; the products of millions of years of evolution, seem certain of destruction.

Among the most interesting and diverse of the still-extant tracts of lowland evergreen forest in Central America is the relatively undisturbed region of the Península de Osa on the Pacific side of Costa Rica. The Osa forests are part of the geographic unit so beautifully described by Paul H. Allen (1956) as the rainforests of the Golfo Dulce. They are unique in being one of two extensive areas (the other is in Chiapas, Mexico, and adjacent Guatemala) on the Pacific versant of Central America with sufficient annual rainfall to support a broad-leaf evergreen forest similar to that found along much of the Atlantic lowlands from Veracruz to Colombia (fig. 16.1). A few favorable situations in Pacific coastal Panama also support forests of this general type, the largest isolated on the Azuero Peninsula. Specifically, the rainforests of the Golfo Dulce show many similarities and relationships to the Chocó forest of Pacific lowland Colombia, and in this regard, they are very different from other Central American forests.

The Golfo Dulce rainforest formerly occupied a continuous region from approximately Bahía Herradura (fig. 16.2) south below an elevation of 500 m along the Pacific coast of Costa Rica to extreme southwestern Panama, somewhat west of Concepción. Although selected areas of flat terrain within the region were cleared for banana culture by the United Fruit Company beginning in 1938, until thirty years ago extensive and continuous stands of virtually undisturbed forest were still common over most of the area. The flood of cattle-raising developments in the 1980s, followed by renewed clearing and population increases in Costa Rica from 1.2 million people in 1960 to 4.0 million in 2001, has changed all this, and the forest is now practically eliminated except on the fairly inaccessible Península de Osa. This chapter provides an introduction to the herpetofauna of the area, especially around Rincón de Osa, a review of current knowledge, and a comparison of this site with other well-sampled lowland forest localities in Lower Central America.

A substantial area of the Osa Peninsula (from the main dividing ridge westward to the sea) was set aside as the Parque Nacional Corcovado (fig. 16.2) by executive degree of President Daniel Oduber Q. of Costa Rica on 31 October 1975. A number of international agencies, including the Nature Conservancy, the World Wildlife Fund, and the Organization for Tropical Studies, aided Costa Rica in establishing this park (Wright 1976). The courageous and enlightened actions of President Oduber in establishing the park cannot be overestimated. To date, the park has been protected and continued under the administration of Presidents Rodrigo Carazo O., Luis Alberto Monge A., Oscar Arias S., and their successors.

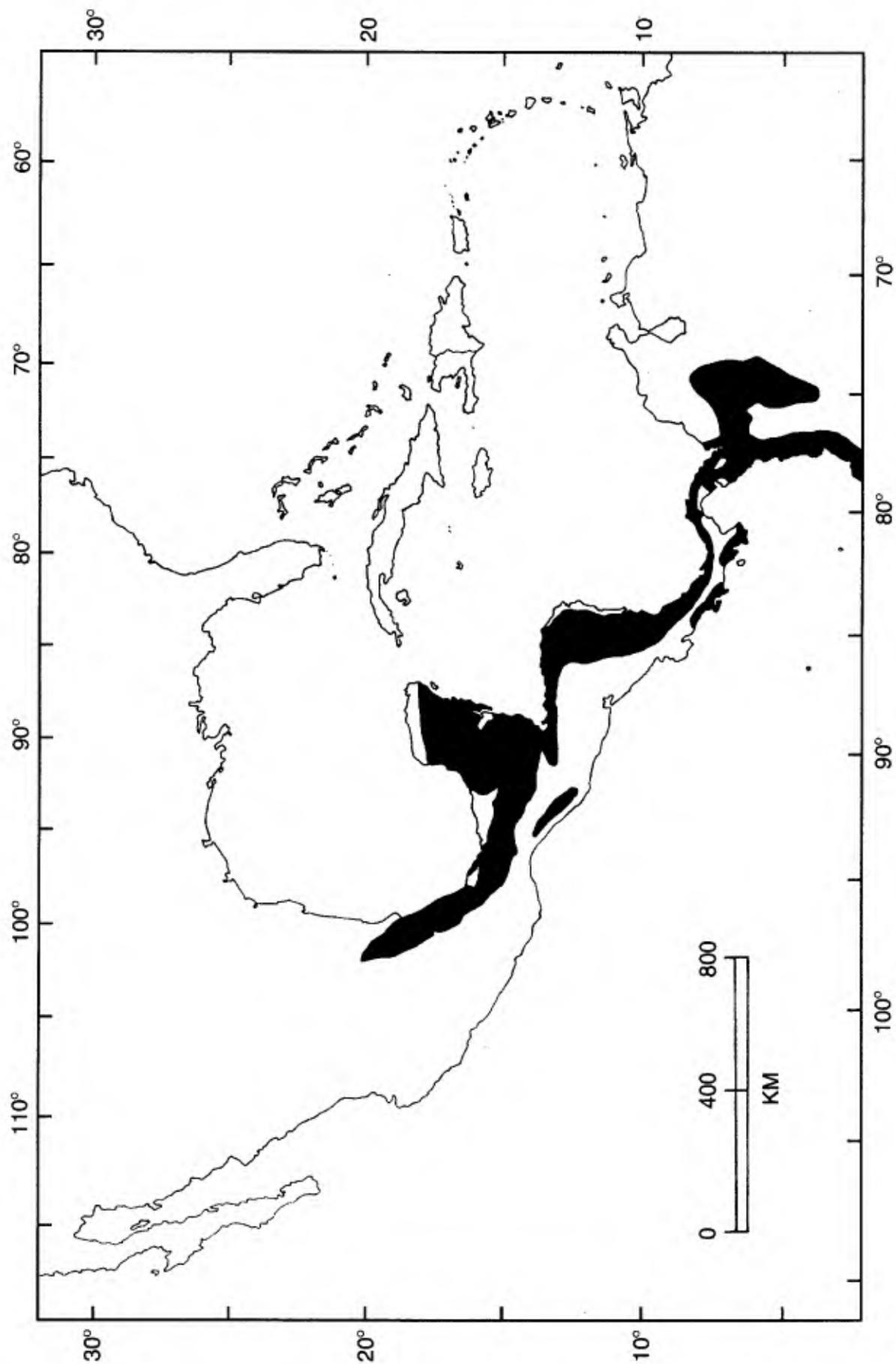


Figure 16.1 Distribution of lowland evergreen rainforests in Middle America and northwestern South America.



Figure 16.2 The Osa Peninsula, with the study site at Rincón and other pertinent localities on the peninsula. (Inset) Distribution of lowland evergreen rainforests in the Golfo Dulce region of southwestern Costa Rica and adjacent Panama.

## Sources of Material

### MATERIAL BASIS OF THE REPORT

Before 1962, the herpetofauna of the Península de Osa was known from a few specimens taken near Puerto Jiménez (Wettstein 1934) and Playa Blanca. In 1962, Savage and the late Charles F. Walker visited the Rincón area for four days and assembled the first large collection of material from the peninsula, and McDiarmid first worked in the Rincón area for nine days in 1966. Since these initial ventures, Savage carried on fieldwork near Rincón for greater or lesser periods in 1964, 1968, and 1973; McDiarmid worked the area in 1967, 1969, 1971, and for a period of more than 60 days in the summer of 1973. Other material was accumulated through the activities of our associates during various time periods (especially by Norman J. Scott Jr.) and forms a further base for the present study. Samples and dates of collection for the Rincón de Osa material housed in the Costa Rica Expeditions Collection are summarized in appendix 16.1. We estimate that about 5,500 person-hours of collecting were recorded from 1961 to 1973. Even so, sampling was quite irregular by month, with about 65% of it occurring in July and August, and no samples taken during five months (January, April, September, October, and December). The bulk of these materials has been deposited in the collections of the Natural History Museum of Los Angeles County. Some material collected by McDiarmid in 1973 is deposited at the National Museum of Natural History. Since 1973, some specimens have been taken at Rincón by the Organization for Tropical Studies courses and by herpetologists from the Universidad de Costa Rica (UCR), primarily the late Douglas C. Robinson, Federico Bolaños, Federico Muñoz, and students from UCR. This material is deposited in the collections of the Museo de Zoología (UCR). All species recorded from Rincón and vicinity are listed in appendix 16.2.

### OTHER SAMPLES FROM THE PENINSULA

The earliest published report on herpetological materials from the Península de Osa was by Wettstein (1934). His samples were taken mostly by Rudolf Zimara and Dr. Otto Koller and forwarded to the Wien Museum. The specimens in this collection are from Puerto Jiménez (Porto Jiménez), or from about 3 km west, near the Río Nuevo, a tributary of the Río Tigre that flows into the western margin of the Golfo Dulce a little north of Puerto Jiménez (fig. 16.2). Among the species from Puerto Jiménez were five lizards and two snakes; a frog and a turtle were taken at Río Nuevo. All are widespread species and, with the exception of the Black Spiny-tailed Iguana, *Ctenosaura similis*, are known from the Rincón

area as well (appendix 16.2). The *Ctenosaura* record is confirmed by recently collected specimens at the Universidad de Costa Rica from that locality and from Piedra El Arcón the outer coast of the peninsula. All these localities in southwestern Costa Rica are along the coast, and it seems likely that south of the main portion of its range in dry forest, spiny-tailed iguanas are restricted to open, sandy, or rocky habitats. The scattered southern Costa Rican records and their essentially coastal distribution may reflect transport by humans, inasmuch as the species was an Amerindian food item.

The only other herpetological specimen taken from the peninsula, before 1962, was one frog, *Dendrobates auratus*, formerly in the Museo Nacional de Costa Rica, as noted by E. R. Dunn (unpub. data).

More recently and since the establishment of the Parque Nacional de Corcovado (Boza 1978; Boza and Sevo 1998), amphibians and reptiles have been collected principally in the area around the original park headquarters at Sirena and between Sirena and Llorona, about 16 km northwest of Sirena. These localities are 26 km south-southwest and 28 km southwest of Rincón, respectively. Some material has been collected at other localities within the park as follows (the approximate distances from Sirena and Rincón are indicated in parentheses): Laguna Corcovado (7 km north-northwest of Sirena, 23 km southwest of Rincón), Laguna Sirena (10 km north-northeast of Sirena, 19 km southwest of Rincón), Pavo Forest (4 km northwest of Sirena, 24 km southwest of Rincón), and Los Patos (19 km northeast of Sirena, 10 km south of Rincón). We were unable to track down all these scattered materials or verify all reports and photographs. Many species reported from the park were collected by students and faculty from the University of Texas, especially Gad Perry and Karen Warkentin, and vouchers that exist are in the collections at the Museo de Zoología, Universidad de Costa Rica, and the Texas Memorial Museum, University of Texas. We have included definite records for species from the park in appendix 16.2.

The snake *Conopsis lineatus* is included tentatively on this list on the basis of a sight record by a competent naturalist (Janzen, in Scott 1983) in second-growth vegetation at Corcovado National Park. Nevertheless, we are skeptical of this report and recommend that efforts be made to verify its presence by a specimen or photograph.

Among specimens at the Museo de Zoología are representatives of five species (three native and two introduced) from the peninsula that are not represented in other samples from Rincón and Corcovado National Park (appendix 16.2). The hylid frog, *Hyla microcephala*, and the colubrid snake, *Enulius sclateri*, are from the Marengo Biological Station just north of the Corcovado National Park boundary, approximately 25 km north-northwest of Sirena and 20 km west of Rincón. A specimen of *Leptodeira rubricata*, a snake found only

in mangroves along the southwestern Pacific coast of Costa Rica and adjacent western Panama, is from near Puerto Jiménez. Two nonnative geckos have recently been collected from the peninsula: *Hemidactylus frenatus* from human habitations in Puerto Jiménez and *Lepidodactylus lugubris* from Quemada, north of Corcovado National Park. We note their occurrence for the sake of completeness but do not include them in our analysis of the native herpetofauna.

Finally, Brian I. Crother and Lisa Aucoin of Southeastern Louisiana University spent 10 days in May 2001 at the Marengo Biological Station with a tropical field ecology course, observing and photographing the biota. Species of amphibians and reptiles that we can identify positively from photographs and notes provided by Crother also have been included in appendix 16.2.

Since 1961, a number of papers mentioning materials from the vicinity of Rincón have appeared. These fall into four categories: (a) monographic studies of particular systematic groups that have included reference to examples from the Costa Rica Expeditions Collections and from the Museo de Zoología at the Universidad de Costa Rica; (b) accounts of common or interesting species presented in *Costa Rican Natural History*, edited by Janzen (1983); (c) ecological or behavioral notes, usually based on incidental studies by students in the field courses of the Organization for Tropical Studies (OTS); and (d) ecological research sponsored or supported by OTS. Germane papers among these are cited at appropriate places in this chapter. The report on the herpetofauna of the leaf litter (Scott 1976) and species accounts in Janzen's (1983) book are especially notable.

## *The Study Area*

### GEOGRAPHY

The Península de Osa projects into the Pacific from the southwest Costa Rican coast (fig. 16.2) and forms the seaward margin for the Golfo Dulce. The peninsula itself is a low-lying series of ridges (highest elevation, 745 m) that is separated from the mainland to the north by a complicated and extensive swampy zone associated with the Río Sierpe. The axis of the peninsula is about 55 km in length and runs from west to southeast. Except for several areas that support small settlements along the Golfo Dulce shore, much of the 1,200 km<sup>2</sup> of the peninsula is covered by undisturbed evergreen forest.

### COLLECTION LOCALITIES

Materials forming the basis of this report are from the area adjacent to Rincón de Osa, a small settlement near the head of the Golfo Dulce (figs. 16.2, 16.3). In

1961 this place was the center for a lumber company, Osa Productos Forestales, that undertook to build roads, survey the forests, and establish housing to accommodate visiting scientists and students, especially those participating in courses presented by the Organization for Tropical Studies. Because plans for utilization of the forests by the lumber company never materialized, most of the areas accessible from Rincón remained relatively undisturbed until the past decade. Our sampling was concentrated along the principal all-weather road, the Carretera al Pacífico, especially within a 5-km radius to the west and south of Rincón (fig. 16.3).

The primary localities and/or particularly significant sites are listed in appendix 16.3. The names of collecting sites were adopted for special areas during our fieldwork. Some of these names are reported in the literature (e.g., Findley and Wilson 1974) and are associated with voucher specimens, so we use them here. The primary localities are indicated on the accompanying map (fig. 16.3) and by reference to standard localities in the list in the appendix. All distances mentioned are straight-line measurements, usually with reference to Rincón.

#### CLIMATE

The climate of the Península de Osa is typical for lowland hot and moist tropical regions with seasonal effects produced by changes in prevailing winds. The climate, according to the Köppen system, is Afi, meaning that the mean temperature for the coldest month is at least 17.8°C, each month has at least 61 mm of precipitation, and the range of temperatures is less than 12.8°C. Although accurate temperature data are lacking, Holdridge et al. (1971) estimated the mean annual temperature as between 26.4°C and 27.8°C, with a mean of approximately 27.5°C for the area near Rincón. The mean annual precipitation (fig. 16.4) at Rincón totals 3,909 mm and at the airfield 4,576 mm, based on ten years and eight years of records, respectively. A definite dry season occurs in January, February, and March, when monthly precipitation averages well below 200 mm, and the number of rainy days averages 8, 5, and 7 per month, respectively. Rainfall begins to increase in late March or early April and rises dramatically to June; thereafter, average monthly precipitation levels off at 400–500 mm through September. Rain falls an average of 21–22 days per month in May, June, July, and August, with a two- to three-week period of little rainfall usually occurring in late July and/or early August. This very short dry season or *veranillo* often is not noticeable in the monthly totals. Very heavy rains commence in late August and peak in October; these months average 26 rainy days, and October typically has more than 700 mm of precipitation. Rainfall decreases sharply through November and December as the next dry season approaches. Holdridge et al. (1971) noted that the Osa Peninsula was part of the Tropical (Lowland) Wet Forest life zone (Holdridge 1967) with a mean annual biotemperature

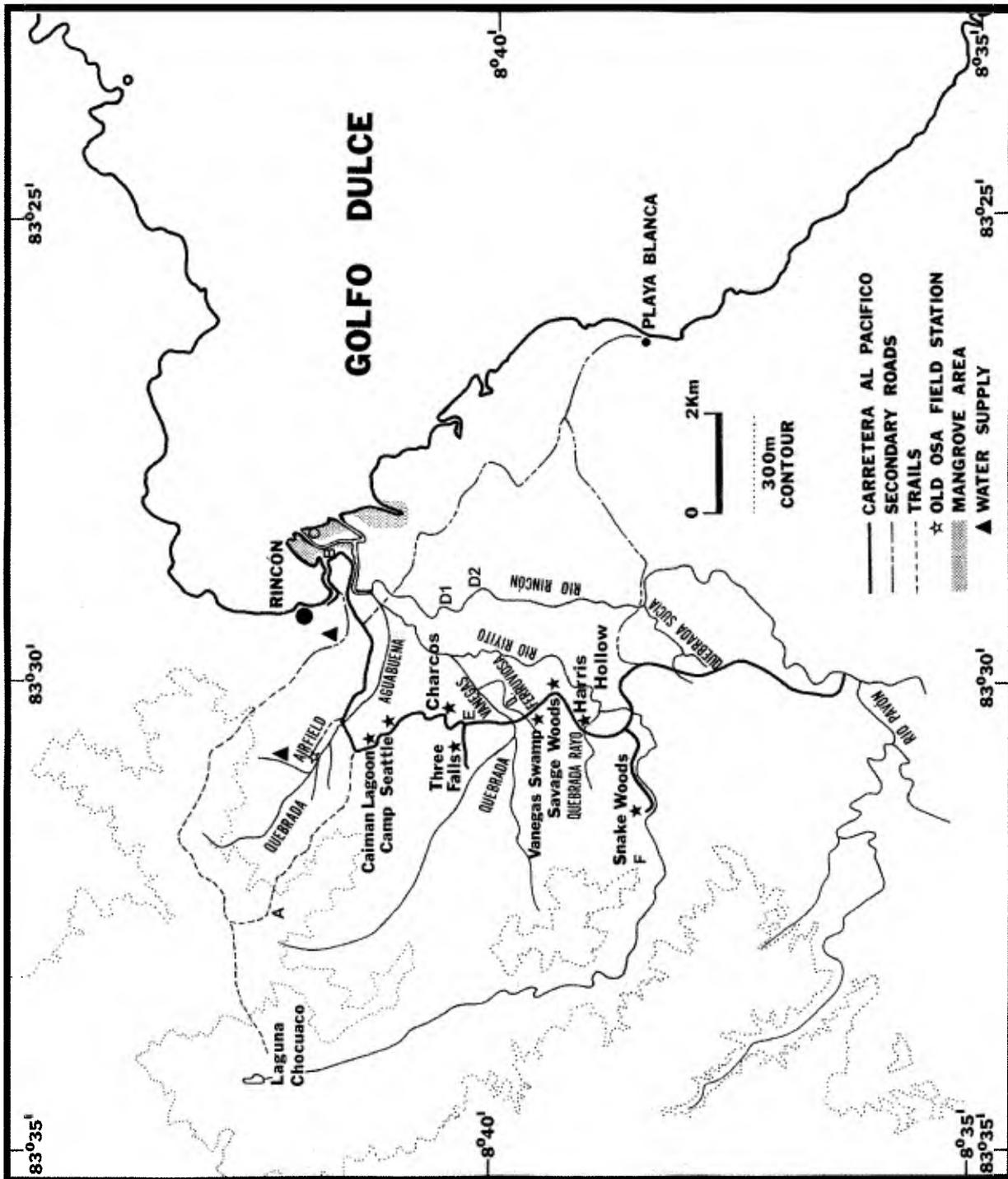


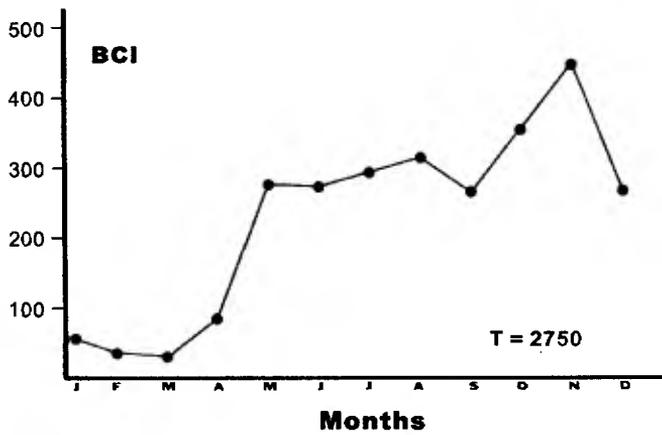
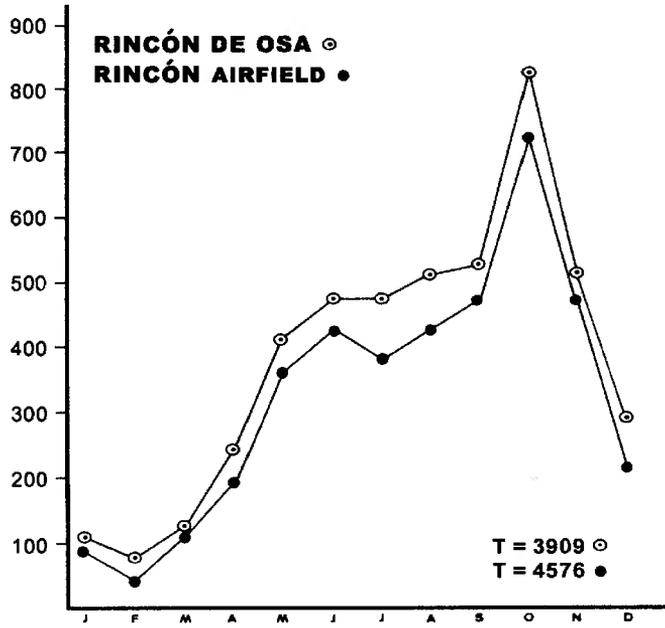
Figure 16.3 The Rincón area, with the major collecting localities for this study.

greater than 24°C and mean annual precipitation between 4,000 and 8,000 mm. Strictly speaking, the area at Rincón (fig. 16.4), with less than 4,000 mm annual precipitation, is in Holdridge's Tropical (Lowland) Moist Forest life zone. This site is in the lee of a steep ridge that reduces the impact of rainstorms coming from the west. Nevertheless, rainfall at Rincón has reached 4,779 mm in a single year (1971).

#### VEGETATION AND SOILS

Holdridge et al. (1971) described in detail the vegetation and soils at seven sites in the vicinity of Rincón. The following summary is generalized from that report, Sawyer and Lindsey (1971), and our own field observations. This forest may be classified as Tropical (Lowland) Wet Forest. A typical Osa site has a tall (45–55 m), multistrata, evergreen forest with a few canopy species that may be briefly deciduous when flowering in the dry season. The number of tree species is high; at one site on the Holdridge Trail, 103 species are present, whereas Sawyer and Lindsey (1971) gave a value of 503 individual trees per hectare at a site in the general area with 195 tree species. The common canopy forms include several species of *Brosimum* and *Protium*, *Anacardium excelsum*, and *Terminalia lucida*. The canopy species usually have clear, smooth, light-barked boles up to 30 m tall, with high buttresses. A lower canopy occurs at 30–45 m and fills in the spaces between the higher canopy trees. An understory with numerous stilt-rooted palms forms a tall, dense layer at 10–20 m. These lower layers commonly include species of *Virola* and *Cryosophila guagara*. A shrub layer consists mostly of dwarf palms reaching a height of about 2 m. The ground layer is minimal; usually only a shallow layer of leaf litter with a few ferns and scattered seedlings is present. Epiphytes, including orchids, bromeliads, and large-leaved herbaceous climbing aroids and cyclanths are common but not conspicuous in the green matrix of the dense forest canopy. Large vines and bush ropes are relatively uncommon, and epiphytic shrubs and strangling trees are rare.

Soils on well-drained sites such as the Holdridge Trail are strongly acidic, red to reddish brown latosols of clay texture. In the flats along the banks of the Río Rincón, the soils are relatively shallow, with leaf litter 2–5 cm deep, an A zone 10–30 cm in vertical extent, and a B zone 40–200 cm but usually 40–70 cm. The soils are deficient in most plant nutrients, although well-drained ridges and uplands tend to have moderate to low amounts of nitrogen, calcium, and manganese.



## The Herpetofauna

The following annotated list includes all species of amphibians and reptiles known to occur in the area near Rincón on the Península de Osa (appendix 16.2). The list serves two functions. First, it provides the basic data for discussion of the herpetofauna known from the vicinity of Rincón, and for ecological and biogeographic comparisons with the herpetofaunas of other sites in Lower Central America (e.g., Sasa and Solórzano 1995). Second, it serves as an introduction to the natural history of these animals for researchers who, in visiting this tropical wet lowland forest for the first or a brief time, wish to maximize their efforts, and to students in OTS courses or other field classes who have little familiarity with amphibians and reptiles, or at best only a minimal knowledge of the species. For these reasons, pertinent ecological data based on our observations of the species at Rincón are delineated. Most of our observations and comments apply to the same species in field situations within Corcovado National Park, where current educational and research activities are concentrated.

Comments on size refer to adult lengths expressed in millimeters. Standard length (snout to vent) is used for salamanders, frogs and toads, and lizards, carapace length for turtles, and total length for caecilians, snakes, and crocodylians. Approximate maximum sizes for the caecilian, salamanders, turtles, and crocodylians are included in the text. Size limits for frogs and toads, lizards, and snakes are in table 16.1.

Relative abundances are approximated by the following values: species are considered *rare* when fewer than 5 adult examples have been collected in the study area; *moderately common* species are represented by 5–10 adult specimens; *common* species include those represented by 11–25 adult individuals; and *abundant* species are those represented in our samples by more than 25 adult specimens. These abundance categories do not apply especially well to snakes, which as a group are much less abundant than most other components (e.g., frogs and lizards) of the herpetofauna and perhaps deserve their own relative abundance categories. However, we decided to use the same categories for all groups because that approach more accurately reflects the probability of encountering one species relative to another at a site. A slightly different approach

Figure 16.4 Seasonal distribution of rainfall at three sites in Lower Central America. Values from Rincón are based on 10 years of data, and those from the Rincón Airfield on 8 years of recordings. Total mean annual precipitation (T) for a comparable 10-year period from La Selva Biological Station was higher than the average (3,850 mm) as calculated from long-term records. In contrast, the total from Barro Colorado Island (BCI) was slightly lower.

Table 16.1 Sizes of anurans and squamates from the Osa Peninsula (in mm)

Size	Taxon		
	Frogs and toads	Lizards	Snakes
Small	<30	<32	<650
Moderate	30–50	32–100	650–1,500
Large	51–80	101–150	1,501–3,500
Very large	>80	>150	>3,500

was taken for species abundance at a dry forest site in northwestern Costa Rica (see Sasa and Solórzano 1995).

Comments on activity patterns, habitat utilization, food habits, and other ecological and behavioral traits of species are based primarily on our experience with specimens from the Rincón area or, in a few instances with rarer species, on our collective experience with the species in Costa Rica. Most descriptive terminology we use is generally understood by field biologists. Our definitions for select terms are as follows: *fossorial* species spend substantial time in soil, often in burrows; *semifossorial* species spend substantial time in and under debris (e.g., logs, rocks, leaf litter, etc.) on the forest floor; *epigeal* species spend substantial time near or on the surface of the ground; *epiphyllous* forms are most often found on leaves or stems of the herb or shrub layer; *arboreal* species are most often encountered on the trunks or limbs of trees from the understory to the canopy; *insectivorous* species eat insects and other arthropods; *myrmecophagous* species feed primarily on ants.

The broad geographical, elevational, and ecological distribution of each species throughout its range also is indicated to provide a basis for evaluating the relationships of the Rincón de Osa herpetofauna to those at other Neotropical lowland evergreen forest sites. Elevational ranges are approximated by the following terms: *lowland*, sea level to 500 m; *premontane*, 501–1,500 m; *lower montane*, 1,501–2,500 m; *montane*, 2,501–3,500 m; and *subalpine* (sub-Andean), 2,500–3,000 m. Vegetation mentioned in the range statements follows the modified Holdridge (1967) system as outlined by Savage (1975).

## AMPHIBIA (46)

### *Gymnophiona* (1)

#### Caeciliidae

*Dermophis occidentalis* Taylor—Small, to 235 mm; nocturnal; feeds primarily on earthworms and insect larvae; fossorial, moderately common in wet season

in deep leaf litter, especially at bases of large buttressed trees in forest; known from lowland and premontane evergreen forest on Pacific versant of southern Costa Rica. This caecilian was called *Dermophis parviceps* in earlier lists (e.g., Scott et al. 1983; Savage and Villa 1986; Villa et al. 1988). Savage and Wake (2001) resurrected *Dermophis occidentalis* for the smaller species with high numbers of primary and secondary annuli from Pacific Costa Rica.

#### *Caudata* (4)

##### Plethodontidae

*Bolitoglossa colonnea* (Dunn)—Moderate size, to 55 mm; nocturnal; insectivorous; epiphyllous on plants along streams; one specimen taken during dry season along Río Riyito; lowland and premontane evergreen forests on both slopes in Costa Rica and western Panama.

*Bolitoglossa lignicolor* (W. Peters)—Moderate size, to 80 mm; nocturnal; insectivorous; epiphyllous on broad-leaved plants; common in forest, occasional in old second-growth vegetation; lowland evergreen forests of southwestern Costa Rica and adjacent Panama.

*Oedipina alleni* Taylor—Elongate, moderate size, to 60 mm; nocturnal; insectivorous; semifossorial; moderately common in shallow leaf litter, beneath logs, and in termite tunnels in logs, in forest and along road cuts; lowland and premontane evergreen forests of southwestern Costa Rica and western Panama. This tropical worm salamander had been called *Oedipina parvipes* by most authors (e.g., Scott et al. 1983; Savage and Villa 1986; Villa et al. 1988), until Good and Wake (1997) resurrected *O. alleni* for the lowland form (also see García-París and Wake 2000).

*Oedipina pacificensis* Taylor—Elongate, moderate size, to 50 mm; nocturnal; insectivorous; semifossorial; abundant in leaf litter, especially near tree buttresses and beneath logs in forest; evergreen forests of southwest Pacific lowlands of Costa Rica and adjacent southwestern Panama. This tropical worm salamander had been called *Oedipina uniformis* by most authors (e.g., Scott et al. 1983; Savage and Villa 1986; Villa et al. 1988), until Good and Wake (1997) resurrected *O. pacificensis* for Pacific lowlands populations.

#### *Anura* (41)

##### Bufonidae

*Bufo coniferus* Cope—Moderate size; nocturnal; primarily myrmecophagous; primarily terrestrial but sometimes found above ground in low vegetation in forest; rare; lowland and premontane evergreen forests from Nicaragua to northwestern Ecuador.

*Bufo haematiticus* Cope—Moderate size; nocturnal; myrmecophagous; abundant in forest and along streams at dawn and dusk; juveniles abundant

along streams in dry season; males call from stream edges in forest during heavy rains and at dawn in wet season; occasionally found asleep on leaves up to 1 m above ground; known from lowland and premontane evergreen and mixed forests from Honduras to central Ecuador.

*Bufo marinus* (Linnaeus)—Very large; nocturnal; eats a wide variety of animal prey from small insects to small amphibians and reptiles, birds, and mammals; abundant along roads and around dwellings between Rincón and old Osa Field Station; breeds in temporary shallow ponds and stream backwaters in wet season, primarily in cleared areas and second-growth vegetation; Wassersug (1971) discussed palatability of tadpoles of this and several other species from Rincón area; widespread from Mexico to South America.

*Bufo melanochlorus* Cope—Moderate size; nocturnal; insectivorous; abundant along forest edge, especially on Carretera al Pacífico during wet season; breeds in small streams during dry season; two males calling from open pond with several *Bufo marinus* in August; widespread in lowland and premontane evergreen forests of Costa Rica.

### Centrolenidae

*Centrolene prosoblepon* (Boettger)—Small; nocturnal; insectivorous; arboreal and riparian; common along small forest streams that flow into Quebrada Aguabuena; males epiphyllous and call from tops of leaves and branches along stream bank; breeding known to occur in June to August; lowland and premontane evergreen forests from eastern Honduras to northwestern Ecuador.

*Cochranella albomaculata* (Taylor)—Small; nocturnal; insectivorous; arboreal and riparian; common; known in Rincón area only from Quebrada Rayo east of Carretera al Pacífico; males epiphyllous, call from tops of leaves 1–2 m above water; amplexing pairs taken in May and July; lowland and premontane evergreen forests from north central Honduras to western Colombia.

*Cochranella granulosa* (Taylor)—Small to moderate; nocturnal; insectivorous; common; arboreal and riparian; found along Quebrada Aguabuena and less frequently in its feeder streams; males epiphyllous, call from tops of leaves up to 4 m above water; breeds from June through September; lowland and premontane evergreen forests of eastern Honduras, Nicaragua, Costa Rica, and Panama.

*Cochranella spinosa* (Taylor)—Small; nocturnal; insectivorous; arboreal and riparian; rare; known from Rincón area from few specimens from water supply stream behind Rincón and single specimen from Quebrada Aguabuena at Carretera al Pacífico; lowland evergreen forests of Costa Rica and Panama, south to northwestern Ecuador.

*Hyalinobatrachium colymbiphylum* (Taylor)—Small; nocturnal; insectivorous; arboreal and riparian; abundant especially along Quebrada Aguabuena and several of its feeder streams, also from Three Falls; males call from under-

side of leaves; breeding occurs from May through September; McDiarmid (1975, 1978) discussed reproductive ecology and behavior of this species and *H. valerioi*; known from lowland and premontane evergreen forests from Costa Rica south to northern and western Colombia.

*Hyalinobatrachium pulveratum* (W. Peters)—Small; nocturnal; insectivorous; arboreal and riparian; moderately common; known from Quebrada Aguabuena and Río Riyito; males epiphyllous, call from tops of leaves and small branches up to 3 m above water; breeding known to occur in late July and August; lowland evergreen forests from north central Honduras south through Nicaragua, Costa Rica, and Panama to northern Colombia.

*Hyalinobatrachium valerioi* (Dunn)—Small; nocturnal; insectivorous; arboreal and riparian; abundant, especially along forest streams flowing into Quebrada Aguabuena, also from Quebrada Rayo; males call from undersides of leaves over water; breeding occurs from May through September; McDiarmid and Adler (1974) and McDiarmid (1978, 1983) discussed male behavior of this form at Rincón; lowland and premontane evergreen forests of Costa Rica to western Colombia.

### Dendrobatidae

*Colostethus flotator* (Dunn)—Small; diurnal; insectivorous; abundant; terrestrial, found in forest leaf litter along streams; males call most commonly in morning; tadpoles with umbelliform oral disc, common in slow waters of small streams in forest; known from lowland and premontane evergreen forests from southeastern and southwestern Costa Rica and Panama to western Colombia. Listed as *Colostethus nubicola* by many recent authors (e.g., Savage and Villa 1986; Villa et al. 1988).

*Colostethus talamancae* (Cope)—Small; diurnal; insectivorous; terrestrial; abundant in leaf litter on forest floor; males call most commonly in afternoon during rain; male found carrying 29 tadpoles on back; males place tadpoles in small puddles of water in depressions on fallen trees or on forest floor; known from lowland evergreen forests of Costa Rica, Panama, and western Colombia.

*Dendrobates auratus* (Girard)—Moderate; diurnal; myrmecophagous; abundant in forest at most localities; tadpoles taken in wet and dry seasons from small depressions on trunks of fallen trees and from tree hollows and bromeliads; primarily terrestrial, frequently found around bases of large trees or spiny palms that provide ample cover; occasionally arboreal, individuals seen climbing up to 3 m on tree trunks; one tadpole taken in bromeliad in tree 20–25 m above ground (McDiarmid and Foster 1975); occurs in lowland evergreen forests of eastern Nicaragua, Costa Rica, Panama, and extreme northwestern Colombia.

*Dendrobates granuliferus* Taylor—Small; diurnal; myrmecophagous; terrestrial; abundant, especially along small forest streams; males and females show

site fidelity; males usually call from elevated sites late in dry season; Goodman (1971) and Crump (1972, 1983) discussed territorial and mating behavior at Rincón de Osa; adult transporting tadpole was photographed by Michael Fogden (Jacobson and Fogden 1984), and details of larval morphology were described by Van Wijngaarden and Bolaños (1992); restricted to lowland evergreen forest below 100 m in southwestern Costa Rica and adjacent Panama; perhaps also native to southeastern Costa Rica (Myers et al. 1995).

*Phyllobates vittatus* (Cope)—Small; diurnal; myrmecophagous; abundant; terrestrial, generally restricted to forest along small streams, less common than *Dendrobates granuliferus* or either species of *Colostethus*; males have been observed wrestling; 3, 4, 8, and 36 tadpoles taken from backs of males; tadpoles taken in shallow, intermittent forest stream near field station; known from lowland evergreen forest in southwestern Costa Rica and adjacent western Panama.

### Hylidae

*Agalychnis callidryas* (Cope)—Large; nocturnal; insectivorous; abundant; arboreal and epiphyllous; breeds in temporary ponds in forest along Río Rincón east of mangroves southeast of Rincón and in forest ponds between Quebrada Aguabuena and airfield; eggs placed on leaves over water; found in lowland and premontane evergreen forests from southern Mexico to central Panama and northern Colombia. Warkentin (1995, 1997, 1999a, 1999b, 2000) studied this species intensively at Corcovado National Park.

*Agalychnis spurrelli* (Boulenger)—Large; nocturnal; insectivorous; arboreal; abundant; occasionally encountered on leaves in forest; incredibly dense breeding aggregations (Scott and Starrett [1974] estimated 13,000 individuals in a breeding aggregation at Caiman Lagoon in August 1970) on vegetation around larger forest ponds; eggs put on leaves over water; known from lowland evergreen forest of southeastern and southwestern Costa Rica and Panama to northwestern Ecuador.

*Hyla ebraccata* Cope—Small (males) to moderate (females); nocturnal; insectivorous; arboreal; abundant; pond-breeding; males epiphyllous, call from vegetation along edges of ponds; eggs placed on leaves over water; amplexing pairs found in June and August; occurs sporadically in temporary and relatively permanent ponds along airfield and Río Rincón, and frequently in Caiman Lagoon and Vanegas Swamp; known from lowland and premontane evergreen and mixed forests of southern Mexico to Guatemala and Belize, and from northeastern Honduras and Nicaragua to northwestern Colombia.

*Hyla rosenbergi* Boulenger—Large; nocturnal; insectivorous; arboreal; abundant; found around small, temporary ponds, puddles, and small streams; males terrestrial or epiphyllous, call from ground (often concealed) or from

vegetation at water's edge; males territorial, construct mud nests at stream edges and along flooded roadways; males known to call from June through August; eggs and tadpoles found in August on Playa Blanca road between Río Riyito and Río Rincón and in small ponds along Río Rincón behind mangroves; occurs in lowland evergreen forests of southwestern Costa Rica and Panama to northwestern Ecuador.

*Phrynohyas venulosa* (Laurenti)—Very large; nocturnal; insectivorous; arboreal; rare, single adult male collected as it called from pond near Vanegas Swamp after a heavy rain in March and one juvenile taken near Caiman Lagoon in June; skin secretions highly irritating; elsewhere in its range this large tree-frog is an explosive breeder, usually for one night after first torrential rains of wet season and probably behaves similarly on Osa Peninsula; wide ranging in lowland forests from Mexico through tropical South America.

*Scinax boulengeri* (Cope)—Moderate; nocturnal; insectivorous; abundant; males epiphyllous, usually call from plant stem in head-down direction, often concealed by dense vegetation along edges of shallow ponds adjacent to Quebrada Aguabuena, at scattered localities along lower parts of airfield, and in Vanegas Swamp; known from lowland evergreen forests from central Nicaragua to northwestern Ecuador.

*Scinax elaeochroa* (Cope)—Moderate; nocturnal; insectivorous; arboreal; common around edges of temporary ponds; males epiphyllous, call from leaves of bushes and tall grass; known from temporary ponds along Río Rincón and lower end of airfield; males heard in June, July, and August; occurs in lowland evergreen forests of eastern Nicaragua, Costa Rica, and adjacent western Panama.

*Smilisca phaeota* (Cope)—Large; nocturnal; insectivorous; abundant; terrestrial and arboreal; found primarily in temporary ponds and puddles; males call from water's edge or while floating in water in March, June, July, and August; breeding apparently initiated by heavy rains; eggs deposited as surface film; frequently encountered in shallow ponds in disturbed areas along road from Rincón to field station; widespread in lowland and premontane evergreen forests from northeastern Honduras to northwestern Ecuador.

*Smilisca sila* Duellman and Trueb—Moderate (males) to large (females); nocturnal; insectivorous; terrestrial and arboreal; rare in Rincón area, known only from rocky, steep stream that forms water supply for old Osa Field Station; breeds during dry season; known from lowland, evergreen forests on Pacific slopes of southern Costa Rica, western Panama, eastern Panama, and northern Colombia.

*Smilisca sordida* (W. Peters)—Moderate (males) to large (females); nocturnal; insectivorous; terrestrial and arboreal; especially abundant during dry season along Quebrada Aguabuena; males call from edges of streams, frequently

from rocks or gravel bars, apparently all year; amplexing pairs found in March, June, July, and August; known from lowland and premontane evergreen and mixed forests from northeastern Honduras to western Panama.

### Leptodactylidae

*Eleutherodactylus crassidigitus* Taylor—Moderate; nocturnal, juveniles diurnal in leaf litter; insectivorous; very abundant throughout forest; males epiphyllous, often calling from branches of understory plants up to 1.5 m above ground; females may be active in leaf litter during day; lowland and premontane evergreen forests of southwestern Costa Rica, through Panama to northwestern Colombia. On the Osa Peninsula, this species has been called *Eleutherodactylus longirostris* by many previous authors (e.g., Scott et al. 1983; Savage and Villa 1986).

*Eleutherodactylus cruentus* (W. Peters)—Small; nocturnal; insectivorous; arboreal; rare, only known specimen from Rincón area was found in an arboreal bromeliad high in forest near the airfield; lowland and premontane evergreen forests from Costa Rica at least to central Panama.

*Eleutherodactylus diastema* (Cope)—Small; nocturnal; insectivorous and myrmecophagous; epiphyllous; common; males call from leaves 1–2 m above ground in forest; lowland and premontane evergreen forests from eastern Nicaragua to western Ecuador.

*Eleutherodactylus fitzingeri* (O. Schmidt)—Moderate; nocturnal; insectivorous; epiphyllous; abundant; males call from leaves along streams, trails, and forest edge, usually less than 1 m above ground; lowland evergreen and deciduous forests of northeastern Honduras, Nicaragua, Costa Rica, and Panama to western Colombia.

*Eleutherodactylus ridens* (Cope)—Small, males much smaller than females; nocturnal; insectivorous, small spiders important in diet; common; males epiphyllous, call from leaves in shrub layer and understory up to 3 m above ground; known from lowland and premontane evergreen forests from eastern Honduras to western Ecuador.

*Eleutherodactylus rugosus* (Cope)—Large; adults nocturnal, juveniles diurnal; insectivorous, eating primarily beetles and occasionally lizards and other frogs; adults in shallow depressions in leaf litter; common on forest floor; known from lowland and premontane evergreen forests of southwestern Costa Rica and adjacent western Panama. Osa populations of this species have been called *Eleutherodactylus biporcatus* by many previous authors (e.g., Scott et al. 1983; Savage and Villa 1986).

*Eleutherodactylus stejnegerianus* (Cope)—Small; diurnal; insectivorous; abundant in leaf litter, aggregates along streams in dry season; known from evergreen and mixed lowland and premontane forests of Pacific slope Costa Rica, and western Panama. At Rincón, this species was referred to as *Eleuthero-*

*dactylus bransfordii* by many previous authors (e.g., Scott et al. 1983; Savage and Villa 1986).

*Eleutherodactylus taurus* Taylor—Large; nocturnal; insectivorous; terrestrial and riparian; abundant; one night a female was seen along a steeply banked section of Quebrada McDiarmid with the legs of a large amblypygid hanging from her mouth; males call from stream banks; restricted to rainforests of Golfo Dulce region in Costa Rica and immediately adjacent southwestern Panama.

*Eleutherodactylus vocator* Taylor—Small, less than 20 mm; usually nocturnal; insectivorous; common; males epiphyllous, call from leaves very near ground, sometimes in late afternoon; adults often taken in leaf litter during day; known in lowland and premontane evergreen forests of Costa Rica, Panama, and northern Colombia.

*Leptodactylus bolivianus* Boulenger—Large to very large, females to 88 mm, males to 94 mm; nocturnal; insectivorous; terrestrial; common; generally found around shallow ponds and marshes, often in areas of second-growth vegetation; males call from deep grass and tangles of vegetation near ponds, sometimes during daylight on dark rainy days; known from evergreen and deciduous lowland forests of Pacific Costa Rica, Panama, and most of tropical South America. Some authors (e.g., Frost 1985; Rand and Myers 1990) have used the name *Leptodactylus insularum* Barbour to refer to this taxon.

*Leptodactylus melanonotus* (Hallowell)—Moderate; nocturnal; terrestrial; rare; known from marshy areas in second-growth vegetation along road from Rincón to airfield and along road to Playa Blanca; tadpoles form schools; widespread in lowlands and premontane zones from Mexico to Ecuador.

*Leptodactylus pentadactylus* (Laurenti)—Very large (adults to over 150 mm); nocturnal; carnivorous; terrestrial; abundant; common along forest edges and in second-growth vegetation, occasionally found along streams and in forest; tadpoles predaceous; ecology of tadpole of this species (Valerio 1971) and tadpoles of other pond breeders from near Rincón (Heyer et al. 1975); lowlands from Honduras throughout Central America and portions of tropical South America primarily in evergreen and mixed forests.

*Leptodactylus poecilochilus* (Cope)—Moderate; nocturnal; insectivorous; abundant; terrestrial, found in second-growth vegetation and along roads between Rincón and field station, and near Camp Seattle; males call from concealed sites beneath ground near shallow temporary ponds; lowlands of western Costa Rica south through northern Colombia and Venezuela.

*Physalaemus pustulosus* (Cope)—Moderate; nocturnal; insectivorous; extremely abundant; terrestrial; commonest in and around temporary, small ponds and puddles in second-growth vegetation or disturbed areas (e.g., around airfield), along roads, and near habitations where it breeds; males heard calling at night from puddle (that filled in a root hollow that formed after a large tree fell in the forest near Quebrada Rayo); eggs placed in foam nests, usually

exposed; known from lowlands and foothills from Mexico to northern Colombia and Venezuela.

### Microhylidae

*Nelsonophryne aterrima* (Günther)—Moderate; nocturnal; myrmecophagous; semifossorial (beneath logs) and in leaf litter; rare, collected once in leaf litter near Three Falls; tadpoles described from Panamanian material (Donnelly et al. 1990); found in evergreen lowland and premontane forests from Costa Rica to northwestern Ecuador.

## REPTILIA (69)

### *Testudines* (3)

#### Emydidae

*Trachemys ornata* (Gray)—Moderate to large, to 600 mm carapace length; diurnal; chiefly herbivorous but opportunistic; aquatic; commonly seen along larger rivers (Río Riyito and Río Rincón); occurs in lowlands on both coasts from Mexico to northern Colombia and northwestern Venezuela.

#### Kinosternidae

*Kinosternon leucostomum* (A. Duméril and Bibron)—Small, to 175 mm carapace length; nocturnal; aquatic; opportunistic and omnivorous; rare in Rincón area, known from single specimen found in pond along Gravel Pit Road; lowland and premontane areas in Atlantic drainages of eastern Mexico south to northern Colombia and in Pacific drainages from central Costa Rica to central western Ecuador.

*Kinosternon scorpioides* (Linnaeus)—Small, to 270 mm carapace length; nocturnal; aquatic; omnivorous; rare, known from near Rincón by single specimen in collections of University of Costa Rica; lowland and premontane areas from Mexico south to Ecuador and northern Argentina.

### *Squamata*—*Sauria* (22)

#### Gekkonidae

*Lepidoblepharis xanthostigma* (Noble)—Small; diurnal; insectivorous but also consumes spiders and mites; terrestrial; common in forest leaf litter, often near streams and occasionally in second-growth areas; lowland evergreen forest from southeastern Nicaragua and Costa Rica to northern Colombia.

*Thecadactylus rapicauda* (Houttuyn)—Large; nocturnal; insectivorous; arboreal; moderately common on large tree trunks, especially between buttresses and in hollows; eggs deposited in leaf litter at base of trees; young hatch in May;

deciduous and evergreen forests at low elevations along Caribbean versant from Chiapas, Mexico, and on Pacific side of Costa Rica southward, to northwestern Ecuador and through northern South America to Brazil and Bolivia; also Lesser Antilles.

*Sphaerodactylus graptolaemus* Harris and Kluge—Small; probably insectivorous; rare in Rincón area, known from single specimen collected as it ran across floor of dormitory of old Osa Field Station; lowland evergreen forests of southwestern Costa Rica and adjacent western Panama.

### Corytophanidae

*Basiliscus basiliscus* (Linnaeus)—Very large; diurnal; young primarily insectivorous, adults omnivorous; terrestrial and arboreal; abundant along larger rivers and streams of Rincón area, and relatively uncommon along smaller, forest streams (e.g., Quebrada Crump, Quebrada Rayo, etc.) and in open, forested areas; frequently found asleep at night on vegetation along streams; lowland deciduous and evergreen forests of southwestern Nicaragua, Pacific Costa Rica, and Panama, south on both coasts of central and eastern Panama to northwestern Colombia and northwestern Venezuela.

*Corytophanes cristatus* (Merrem)—Large; diurnal; insectivorous; abundant; sometimes found on ground but most often seen on vertical stems of understory trees and shrubs, on vines, or on trunks of large trees, where it remains motionless, relying on concealment to escape detection; frequently found asleep in same situations at night; Andrews (1979) reported on diet and field behavior of this lizard at Rincón; occurs in lowland and premontane evergreen forests of Atlantic versant from Mexico to northwestern Colombia and in Golfo Dulce area of Pacific Costa Rica.

### Iguanidae

*Iguana iguana* (Linnaeus)—Very large; diurnal; herbivorous; arboreal; common in Rincón area; may be more abundant than records indicate, especially along large rivers; a few specimens seen and/or collected along Carretera al Pacífico where it parallels Río Rincón south of Rincón, two juveniles near old Osa Field Station, and a few sight records on Río Riyito near Carretera al Pacífico; a wide-ranging species in lowland deciduous and evergreen forests from northern Mexico to Bolivia, Paraguay, and southern Brazil, especially along waterways; also in Lesser Antilles.

### Polychrotidae

*Dactyloa insignis* (Cope)—Large; diurnal; arboreal; rare, known from a single specimen collected from overhanging vegetation along Quebrada Agua-buena; occurs in lowland and premontane evergreen forests of Costa Rica and Panama.

*Norops aquaticus* (Taylor)—Moderate; diurnal; insectivorous; abundant; terrestrial and epiphyllous; riparian, found on banks, rocks, and tree trunks of heavily shaded streams including upper reaches of Quebrada Aguabuena and other streams; often seeks shelter in water; found only in lowland and premontane evergreen forests of Golfo Dulce area in Costa Rica and adjacent southwestern Panama.

*Norops biporcatus* (Wiegmann)—Large; diurnal; insectivorous; arboreal; moderately common on large trees in forest near old Osa Field Station; occasionally found at night asleep on branches 1.5–2 m above ground; found in lowland evergreen forests from Mexico to Venezuela on Atlantic and from Costa Rica to Ecuador on Pacific versants.

*Norops cápito* (W. Peters)—Moderate; diurnal; insectivorous, sometimes eats snails; abundant; often found on ground, on stems of small understory shrubs, and on vines; lowland and premontane evergreen forests from southern Mexico to Panama on Atlantic and from southwestern Costa Rica through Panama on Pacific versants.

*Norops limifrons* (Cope)—Moderate; diurnal; insectivorous but small spiders represent a large proportion of diet; moderately common in old second-growth vegetation along airfield and occasionally along small streams and in forest; one sleeping on leaf at night along stream; lowland deciduous and evergreen forests on Atlantic side from Honduras to Panama and on the Pacific slope from Costa Rica to eastern Panama.

*Norops pentaprion* (Cope)—Moderate; diurnal; arboreal; moderately common but may be abundant in forest canopy; four taken from upper branches of a large tree cut along south slope north of Carretera al Pacífico between airfield and Rincón; lowland deciduous and evergreen forests from southern Mexico to northern Colombia.

*Norops polylepis* (W. Peters)—Moderate; diurnal; insectivorous; abundant; probably most abundant lizard in forests on Osa Peninsula; epiphyllous, usually found on small branches or leaves of understory shrubs up to 2 m above forest floor, often terrestrial on forest floor; Andrews (1971) described the ecology of *Norops polylepis* at Rincón de Osa in some detail, and Perry (1996) studied it near Sirena, Corcovado National Park; occurs only in lowland and premontane evergreen forests of Golfo Dulce region of Costa Rica and adjacent western Panama.

### Scincidae

*Mabuya unimarginata* Cope—Moderate; diurnal; insectivorous; terrestrial; rare; usually found in disturbed habitats; wide ranging in lowland, deciduous and evergreen forests from Mexico to at least eastern Panama.

*Sphenomorphus cherriei* (Cope)—Moderate; diurnal; insectivorous, but isopods represent a large proportion of the diet; terrestrial to semifossorial; mod-

erately common in leaf litter in open forest and under old banana plants near field station; occurs in deciduous and evergreen lowland and premontane forests from southern Mexico to extreme western Panama.

### Gymnophthalmidae

*Bachia blairi* (Dunn)—Moderate; secretive; presumably diurnal; insectivorous; semifossorial; moderately common, known from five specimens collected in leaf-litter accumulations between buttresses of large trees west of old Osa Field Station; McDiarmid and DeWeese (1977) discussed systematic status and natural history of species; lowland evergreen forests of Osa Peninsula and adjacent western Panama.

*Leposoma southi* Ruthven and Gaige—Moderate; diurnal; insectivorous; terrestrial; moderately common in leaf litter on forest floor near old Osa Field Station; Atlantic and Pacific lowland evergreen forests of Costa Rica and Panama to western Colombia.

*Neusticurus apodemus* Uzzell—Moderate; diurnal; presumably insectivorous; terrestrial and riparian; rare, single specimen collected among rocks in the upper reaches of the Airfield Water Supply stream; known elsewhere from two localities in lowland evergreen forest of Golfo Dulce area of Costa Rica.

### Teiidae

*Ameiva festiva* (Lichtenstein and von Martens)—Large; diurnal; insectivorous; abundant; terrestrial, most often seen along forest edge, trails, and heavily vegetated roadsides; most common teiid lizard found in the vicinity of Rincón; Hillman (1969) reported on habitat specificity of three species of *Ameiva* at Rincón de Osa; occurs in lowland and premontane evergreen forests from southern Mexico to northern and western Colombia.

*Ameiva leptophrys* (Cope)—Large; diurnal; insectivorous; abundant and more restricted to forest habitats, especially along forest trails and near small light gaps, than other species of *Ameiva*; known from lowland evergreen forest of Golfo Dulce area of Costa Rica and adjacent western Panama to western Colombia.

*Ameiva quadrilineata* (Hallowell)—Moderate; diurnal; insectivorous; terrestrial; abundant along beaches, riverbanks, unshaded roads, dry beds of larger streams (e.g., Quebrada Aguabuena), and in other, open, bare-ground areas; lowland evergreen forests of Nicaragua to western Panama on Atlantic and southwestern Costa Rica and western Panama on Pacific sides.

### Xantusiidae

*Lepidophyma reticulatum* Taylor—Moderate; probably nocturnal; insectivorous, may eat fruits and other plant material; moderately common; terrestrial

to semifossorial, found in leaf litter, especially between tree buttresses; occurs in lowland and premontane evergreen forests of Pacific slope of Costa Rica.

### *Squamata—Serpentes (42)*

#### **Boidae**

*Boa constrictor* Linnaeus—Very large; crepuscular to nocturnal; feeds on lizards, birds, and mammals; moderately common in Rincón area; known from old second-growth areas around airfield but probably also occurs in primary forest; lowland deciduous, evergreen, and premontane evergreen forests from northern Mexico to Argentina, South America; also Lesser Antilles.

*Corallus ruschenbergerii* (Cope)—Large, to about 1,650 mm; arboreal; elsewhere feeds on frogs, lizards, birds, and mammals; rare; known from single specimen taken in forest near Osa Field Station; lowland evergreen forests from southwestern Costa Rica through Panama to northern Colombia and northern Venezuela; also Trinidad and Tobago. Listed as *Corallus hortulanus* by Scott et al. (1983) and Savage and Villa (1986), and as *Corallus enhydris* by Villa et al. (1988). Henderson (1997) recognized four species for *Corallus hortulanus* and resurrected *Corallus ruschenbergerii* (Cope, 1876) for the Central American species.

#### **Colubridae**

*Amastridium veliferum* Cope—Moderate; terrestrial to semifossorial; eats frogs; rare, known from two specimens collected in forest, one near airfield and another near end of Water Fall Road; lowland and premontane evergreen forests from southeastern Nicaragua to central Panama on Atlantic versant and in southwestern Costa Rica on Pacific versant.

*Chironius carinatus* (Linnaeus)—Large, diurnal; terrestrial, sometimes arboreal; feeds mostly on frogs but elsewhere reported to eat salamanders, lizards, birds, and mammals; rare, young specimens from old second-growth areas near airfield; occurs in lowland wet forests from Costa Rica to western Ecuador and Amazonian Brazil; also Trinidad and Lesser Antilles.

*Chironius grandisquamis* (W. Peters)—Large; diurnal; feeds mostly on frogs but also eats salamanders, lizards, birds, and mammals; moderately common in forest; adults shiny black, juveniles brownish black; adults terrestrial, seen on ground during day and arboreal at night, observed coiled on leaf 4 m above water in Quebrada Rayo, two immatures found at night coiled in branches 1.5 m and 2 m above water on Quebrada McDiarmid; lowland and premontane evergreen forests from Honduras to northwestern Ecuador.

*Clelia clelia* (Daudin)—Large; crepuscular and nocturnal; feeds on snakes and lizards, occasionally mammals; terrestrial; moderately common; adults black, juveniles bright red with black head and white collar; several specimens found crossing road between Rincón and old Osa Field Station during or after

light rain; widespread in lowland deciduous and lowland and premontane evergreen forests from southeastern Mexico to Bolivia.

*Coniophanes fissidens* (Günther)—Small; diurnal; terrestrial; eats primarily frogs, but arthropods, earthworms, lizards, and rarely snakes are eaten; moderately common; on forest floor near old Osa Field Station; lowland and premontane deciduous and evergreen forests from Mexico to central western Ecuador.

*Dendrophidion percarinatum* (Cope)—Moderate; diurnal; terrestrial; eats frogs; common; most often found in forest, especially along small streams; occasionally seen swimming; occurs in lowland evergreen forests from Honduras to western Ecuador and northern Venezuela.

*Dipsas tenuissima* Taylor—Moderate; elongate; nocturnal; arboreal; mollusk eater; very rare only nine known specimens; single example from near Rincón in collection at the Universidad de Costa Rica; restricted to the Golfo Dulce area of Costa Rica and western Panama.

*Drymarchon melanurus* (Duméril, Bibron, and Duméril)—Large (to 3,000 mm); diurnal; known to feed on mammals (e.g., *Sigmodon hispidus*) at Rincón but also takes birds, snakes, turtles, lizards, amphibians, and fish; moderately common; found in second-growth areas around field station and airfield and along major rivers; disjunct and widespread in deciduous, lowland, and premontane evergreen forests from southern United States to western Ecuador and northern Venezuela.

*Erythrolamprus mimus* (Cope)—Moderate; rare; known from one specimen taken near old Osa Field Station; probably diurnal; eats mostly snakes, synbranchid eels, and some lizards; occurs in lowland forests from Honduras to western Colombia and Ecuador, and to northwestern Venezuela, eastern Ecuador, and Peru.

*Geophis hoffmanni* (W. Peters)—Small; earthworm specialist, also eats soft-bodied insect larvae; fossorial; rare in Rincón area; known from single specimen collected near Quebrada Ferruviosa; occurs in lowland, premontane, and montane forests from Honduras to western Panama.

*Imantodes cenchoa* (Linnaeus)—Moderate; very elongate; nocturnal; feeds on lizards and frog eggs; arboreal; moderately common in forest and along streams near old Osa Field Station; may forage 5 m or more above ground; in deciduous and evergreen forests in lowlands and in premontane and lower-montane evergreen forests from southern Mexico to southern South America.

*Imantodes inornatus* Boulenger—Moderate; very elongate; nocturnal; arboreal; forages for sleeping lizards (e.g., small *Basiliscus*, *Norops* spp.) and frog eggs at night in vegetation along streams and trails; moderately common in forest; from lowland, premontane, and lower-montane evergreen forests of Honduras southward to central western Ecuador.

*Leptodeira septentrionalis* (Kennicott)—Moderate; nocturnal; arboreal; common in the Rincón area; often found foraging in low bushes and trees

around ponds or along streams for frogs or frog eggs (e.g., *Agalychnis* spp., *Hyalinobatrachium* spp.); widespread, in lowland deciduous and evergreen forests and in premontane evergreen forests from southern Texas to western Colombia, Ecuador, and northern Peru.

*Leptophis ahaetulla* (Linnaeus)—Large; diurnal; arboreal, sometimes terrestrial; feeds on frogs, lizards, small birds, and bird eggs; moderately common near Rincón; most specimens come from second-growth areas and around inhabited areas; widespread in lowland deciduous and evergreen forests from southern Mexico to southwestern Ecuador, and on the Amazonian side to Argentina.

*Leptophis riveti* Despax—Moderate; diurnal; arboreal; known to eat frogs; rare in Rincón area; known from single specimen taken near old Osa Field Station; occurs in lowland and premontane forests of the Golfo Dulce area of Costa Rica and from central Panama to western Ecuador, Amazonian Peru, and on Trinidad.

*Mastigodryas melanolomus* (Cope)—Moderate; diurnal; terrestrial; eats primarily lizards, but known to consume variety of small vertebrates; moderately common; most often found in second-growth areas and along sunny banks of larger streams; specimens with red and specimens with greenish white venters sympatric near airfield; wide ranging in lowland deciduous and evergreen forests and premontane evergreen forests from Mexico to northern Colombia.

*Ninia maculata* (W. Peters)—Small; nocturnal; semifossorial to terrestrial; feeds on soft-bodied prey, mostly earthworms and slugs, and some insect larvae; rare in leaf litter in Rincón area; lowland, premontane, and montane evergreen forests from Nicaragua to eastern Panama.

*Ninia sebae* (Duméril, Bibron, and Duméril)—Small; body red, head black; nocturnal leaf-litter denizen; feeds primarily on earthworms, slugs, and small land snails; single specimen from near Rincón is in the Universidad de Costa Rica collection; occurs in lowlands and on premontane slopes from Mexico to southwestern Costa Rica.

*Nothopsis rugosus* Cope—Small; presumably nocturnal; feeds on frogs and salamanders; semifossorial to terrestrial; rare in shallow leaf litter in forest west of old Osa Field Station in May; lowland and premontane evergreen forests from eastern Honduras to Panama on Atlantic slope, and in Golfo Dulce area of Costa Rica, Panama, western Colombia, and northwestern Ecuador on Pacific versant.

*Oxybelis aeneus* (Wagler)—Moderate; elongate; diurnal; arboreal; eats mostly frogs, lizards, and birds; rare in Rincón area; juvenile found asleep at night on leaf 2 m above ground along Airfield Water Supply trail; widespread in deciduous, mixed, and evergreen lowland and premontane forests from southern Arizona and Mexico south over northern half of South America to northern Bolivia and southern Brazil.

*Oxyrhopus petolarius* (Linnaeus)—Moderate; primarily nocturnal; eats lizards and small mammals; rare in Rincón area; widespread in lowland and premontane evergreen forests from southeastern Mexico and Costa Rica to western Ecuador, northern South America and south over most of Brazil and the Amazon basin, south to northern Bolivia.

*Pseustes poecilonotus* (Günther)—Large; diurnal; terrestrial, may venture into trees; carnivorous on birds and mammals; moderately common, especially in dry season; adults taken along Carretera al Pacífico between Rincón and airfield and on Ridge Trail about 2 km west of Rincón; widespread in lowland and premontane forests from Mexico to western Ecuador and in Amazon basin to Bolivia and Brazil.

*Rhadinaea decorata* (Günther)—Small; diurnal; terrestrial; feeds on salamanders, frogs, small lizards, and other litter organisms; moderately common in and on leaf litter in forest near old Osa Field Station; widespread in lowland and premontane evergreen forests from Mexico to northwestern Ecuador.

*Scaphiodontophis annulatus* (Duméril, Bibron, and Duméril)—Moderate; diurnal; terrestrial; habits unknown; eats mostly skinks, but also other lizards and sometimes small frogs; rare in Rincón area; lowland and premontane evergreen forests of tropical Mexico south to northern and central Colombia.

*Sibon dimidiatus* (Günther)—Moderate; elongate; nocturnal; arboreal; feeds on mollusks; rare, four specimens found in vegetation at night 4–4.5 m above ground in forest along trails near old Osa Field Station; lowland and premontane evergreen forests of Atlantic versant from southern Mexico to Nicaragua and on Pacific versant of Guatemala, Honduras, and central and southern Costa Rica.

*Sibon nebulatus* (Linnaeus)—Moderate; elongate; nocturnal; arboreal; mollusk eater; rare, two specimens taken at night along trails through forest near station; widespread in lowland, deciduous, and evergreen forests from central Mexico through Central America to Colombia, eastern and western Ecuador and northern Venezuela to northern Brazil.

*Spilotes pullatus* (Linnaeus)—Large; diurnal; arboreal and terrestrial; feeds on mammals and birds and bird eggs; rare in Rincón area; widespread from Mexico through Central America to western Ecuador and Argentina primarily in lowland and premontane evergreen forests.

*Stenorrhina degenhardtii* (Berthold)—Moderate; nocturnal; terrestrial; feeds on scorpions, centipedes, and other arthropods; rare, one specimen taken near Rincón; low elevations from southern Mexico to northwestern Peru and north central Venezuela in deciduous and evergreen forests.

*Tantilla ruficeps* (Cope)—Small; nocturnal; semifossorial; habits unknown but known to eat centipedes elsewhere; rare; found in lowland and premontane evergreen forests from eastern Nicaragua, through Costa Rica to western Panama.

*Tantilla schistosa* (Bocourt)—Small; presumably nocturnal; eats primarily centipedes; rare, in leaf litter in forest west of Osa Field Station; low and moderate elevations from Mexico to central Panama in lowland and premontane evergreen forests.

*Tantilla supracincta* (W. Peters)—Small; semifossorial; eats primarily centipedes; rare, two adults known from area; one collected under a small log in forest near juncture of Gravel Pit Road and Carretera al Pacífico and another unearthed by bulldozer clearing old second-growth vegetation near old Osa Field Station; known from scattered localities in lowland and premontane evergreen forests from Nicaragua through Costa Rica to central Panama and northwestern Ecuador.

*Tripanurgos compressus* (Daudin)—Moderate; nocturnal; terrestrial; only eats lizards; rare in Rincón area, single specimen moving on bank of Quebrada Aguabuena about 300 m below field station at entrance to Quebrada Crump; scattered localities in lowland evergreen forest from Golfo Dulce of Costa Rica and adjacent Panama to western Ecuador and Bolivia, Brazil, and Paraguay.

*Urotheca fulviceps* (Cope)—Small; diurnal and nocturnal; terrestrial to semifossorial; feeds on small leaf litter vertebrates; rare, two specimens, one in leaf litter in forest near old Osa Field Station and on lower slopes (60 m) near Airfield Water Supply in May; known from lowland evergreen forests of Golfo Dulce, central and eastern Panama to northwestern Ecuador.

*Urotheca guentheri* (Dunn)—Small; presumably diurnal; terrestrial; consumes frogs and salamanders; rare, one specimen found in litter sample west of old Osa Field Station in May; lowland, premontane, and montane evergreen forests of eastern Nicaragua, Costa Rica, and western Panama.

*Xenodon rabdocephalus* (Wied)—Diurnal; terrestrial; eats mostly toads but also other anurans; heavy bodied and resembles fer-de-lance (*Bothrops asper*); rare, known from single, small specimen collected along Quebrada Aguabuena; widespread in lowland and premontane evergreen and deciduous forests from Mexico through Central America to western Ecuador and Bolivia.

## Elapidae

*Micrurus alleni* K. Schmidt—Moderate; nocturnal and diurnal; terrestrial; feeds primarily on synbranchid eels and other snakes; rare, one specimen found crawling just after dark near Rincón Airfield (reportedly diurnal at other sites in Corcovado National Park); lowland and premontane evergreen forests of Atlantic eastern Honduras, Nicaragua, Costa Rica, and Panama and Golfo Dulce area of southwestern Costa Rica and adjacent Panama.

## Viperidae

*Bothriechis schlegelii* (Berthold)—Moderate; arboreal; moderately common; feeds on bats (e.g., *Carollia castanea*) and probably birds, frogs, and lizards; col-

lected in small trees and bushes along forest trails northwest of airfield, in Savage Woods and Snake Woods, and along Ridge Trail from Rincón to Laguna Chocuaco; lowland and premontane evergreen forests from southern Mexico to Venezuela and northwestern Peru.

*Bothrops asper* (Garman)—Very large; primarily nocturnal but often moving during day in forest; adults terrestrial, young may be arboreal; eats rodents (e.g., *Sigmodon hispidus*), frogs, and probably lizards; abundant, specimens taken at essentially every major collecting site near Rincón; most frequently encountered at forest edges and in old second-growth vegetation, but also seen swimming in rivers and creeks and coiled along trails and on logs in forest; large individual found at edge of Carretera al Pacífico near Quebrada Aguabuena eating an adult *Leptodactylus pentadactylus*; widespread in evergreen forests from Mexico through Central America to northwestern Ecuador.

*Lachesis melanocephala* Solórzano and Cerdas—Very large; terrestrial; feeds on mammals; rare, in undisturbed forest on Ridge Trail and in Savage Woods; found in lowland evergreen forests of Golfo Dulce region in Costa Rica and western Panama. The population on the Osa Peninsula, referred to as *Lachesis muta* or *Lachesis muta melanocephala* by previous authors (e.g., Scott et al. 1983; Savage and Villa 1986; Villa et al. 1988), was elevated to species status by Zamudio and Greene (1997).

*Porthidium nasutum* (Bocourt)—Small; terrestrial; feeds primarily on frogs; moderately common; most frequently encountered in leaf litter in forest west of the old Osa Field Station, in Savage Woods, and in forest around Airfield Water Supply; small juvenile with a yellowish white tail tip found in forest on 15 August; occurs in lowland evergreen forest from southeastern Mexico along Caribbean Central America to Panama and on Pacific side in Golfo Dulce area of Costa Rica, in western Colombia and northwestern Ecuador.

## *Crocodylia* (2)

### Alligatoridae

*Caiman crocodilus* (Linnaeus)—Moderate to large, to 2.7 m, specimens over 2 m are rare; nocturnal; carnivorous; aquatic; abundant; frequents temporary to relatively permanent ponds along Carretera al Pacífico; lowlands from southern Mexico on the Pacific to northwestern Ecuador, and from Honduras on the Atlantic through Central America to central Brazil and Bolivia in the Amazon Basin.

### Crocodylidae

*Crocodylus acutus* (Cuvier)—Gigantic, to 7 m, specimens over 4 m rare; nocturnal; carnivorous; aquatic; moderately common; found in major rivers; four specimens seen in two nights in March 1966 on Río Riyito near Carretera al

Pacífico; reported to have been abundant in Laguna Corcovado on western side of peninsula and to have been hunted commercially in past years; current populations unknown; former mainland distribution from northwestern Mexico south to northern Peru on the Pacific versant and to northern Colombia and Venezuela on the Caribbean side; also southern Florida and Greater Antilles.

#### MARINE SPECIES

Tosi (1975) listed four species of sea turtles (*Chelonia mydas* [= *Chelonia agassizii* of some authors], *Eretmochelys imbricata*, *Lepidochelys olivacea*, and *Dermochelys coriacea*) from the Osa Peninsula, but we know of no specimens from there. An aerial survey revealed nesting tracks of *Lepidochelys olivacea*, *Chelonia mydas*, and a few *Dermochelys coriacea* at several places along the west coast of the peninsula in October, but none was seen on suitable beaches on the Golfo Dulce side (Richard and Hughes 1972). Other workers (Cornelius 1982; Frazier and Salas 1983) noted that all four forms probably occur in waters off the peninsula and may come ashore, especially on the beaches of the outer coast to nest. Cornelius (1982) commented that *Caretta caretta* is common in Panama and may nest around the Península de Osa. One or a few *Dermochelys coriacea* and *Lepidochelys olivacea* have recently been observed nesting on southern beaches on the outer coast of the peninsula (A. Chaves, pers. comm.) and *Lepidochelys olivacea* on beaches on the mainland south of Golfito. The pelagic or yellow-bellied sea snake, *Pelamis platurus*, occurs along the Pacific coast in warmer waters from southern California to Peru. Snakes often are associated with ocean slicks in deeper water but occasionally wash ashore. Sea snakes have been seen at various places along the outer coast of the Osa Peninsula and taken in the mouth of the Golfo Dulce; specimens have been found on the beach near Llorona and Sirena. Because our treatment deals only with the terrestrial and freshwater components of the herpetofauna, the status of these forms is not considered further.

#### ERRONEOUSLY RECORDED SPECIES

Several lists of species from the Rincón area have been prepared by OTS course instructors in mimeographed form and are the basis for the summary by Schnell (1971) in the OTS handbook. In addition, in 1973 McDiarmid prepared a list of amphibians and reptiles from the peninsula as part of a report to the Costa Rican government on the need to establish a major national park in this unique region. His summary was incorporated into Tosi's (1975) report and list of species. Unfortunately, these lists sometimes contained names of species that were based on misidentifications or other errors. Here, we review some of those reports to clarify the situation.

The following species appear to have been included in one list or the other simply in error or as geographical probabilities for Rincón: caecilians—*Gymnopsis multiplicata*; frogs—*Eleutherodactylus fleischmanni*, *Leptodactylus labialis* (= *L. fragilis*), *Hyla loquax*, *Hyla* or *Ololygon* (= *Scinax*) *staufferi*, *Centrolenella* (= *Hyalinobatrachium*) *fleischmanni*, *Rana palmipes* (= *R. vaillanti*), *Rana warszewitschii*; turtles—*Chelydra serpentina*; lizards—*Anolis* (= *Dactyloa*) *frenatus*, *Anolis* (= *Norops*) *humilis*, *Ameiva undulata*, *Gymnophthalmus speciosus*; snakes—*Leptophis depressirostris*. Although not currently known from the Rincón area, a few of these species (e.g., *Rana warszewitschii*, *Chelydra serpentina*) have been recorded from Corcovado National Park (appendix 16.2). Several forms were listed by synonyms or as misidentifications with closely allied species. They include *Eleutherodactylus crassidigitus* as *E. longirostris*, *Corallus ruschenbergerii* (also called *Corallus hortulanus* by some authors) by its synonym *C. enhydris*, *Chironius grandisquamis* formerly called *C. fuscus* in Costa Rica, *Leptodeira septentrionalis* as *L. annulata*, and *Sibon dimidiatus* as *S. annulatus*. Other erroneously listed species require additional comment.

The frog *Anotheca spinosa* was included on McDiarmid's 1973 list on the basis of a field identification of a tadpole taken 20–25 m above the ground in a bromeliad. Subsequent examination and comparison to other larvae in the laboratory showed the tadpole to be one of *Dendrobates auratus*, and this was subsequently reported by McDiarmid and Foster (1975).

The treefrog *Hyla microcephala* has been listed several times as occurring at Rincón, but the nearest authenticated records for this species at the time were from lowland evergreen forests near Palmar Sur and Golfito (fig. 16.2). A single tadpole that may be of this species was collected from the Vanegas Swamp, but no adults had ever been taken. For these reasons we refrained from listing the species as a member of the Rincón herpetofauna. Recently, an adult *Hyla microcephala* was collected by personnel from the Universidad de Costa Rica at Marenco Biological Station north of Corcovado National Park. This record suggests that the species may yet be collected near Rincón, but we prefer to wait for verifiable specimens before adding it to the Rincón list. We have included the species in the herpetofauna of the Península de Osa (appendix 16.2).

The treefrog *Hyla rufitela* has been included as part of the Osa Peninsula, on the basis of tadpoles and recent metamorphs. A metamorph that RWM identified in the field as *Hyla rufitela* was pale greenish tan with discrete, dark brown dorsal flecks; in part, his identification was based on previous reports of the species from the Osa Peninsula (Duellman 1970, 2001). JMS became suspicious when no adults of *H. rufitela* turned up in any of the Osa collections. Our reexamination of tadpoles and metamorphs in our collections indicates a misidentification; we are now convinced that all are *Hyla rosenbergi*, a species whose larvae and recent metamorphs resemble those of *Hyla rufitela*. Juveniles of both species are cream with dark brown spots in preservative. We suspect that other

reports of *H. rufitela* from the Golfo Dulce region may also be based on misidentifications. Accordingly, we omit *Hyla rufitela* from our list of amphibians from the Osa Peninsula.

Two turtles, *Chelydra serpentina* and *Kinosternon scorpioides*, have also appeared on various lists as coming from Rincón. We know of no specimens of *Chelydra* from the vicinity of Rincón and have not included it in that fauna. However, this large turtle has been recorded recently in the large lagoon-like habitats in Corcovado National Park (appendix 16.2) and probably occurs in similar habitats elsewhere on the Osa Peninsula. The original report of *Kinosternon scorpioides* from Rincón was based on a misidentified specimen of *Trachemys ornata* at the Universidad de Costa Rica. Nevertheless, other specimens of *Kinosternon scorpioides* have been recorded from near Rincón and Sirena, and we have included this turtle in the Rincón fauna.

#### EFFECTIVENESS OF SAMPLING

The only published account attempting to evaluate sampling effort at a comparable tropical locality is that of Myers and Rand (1969) for Barro Colorado Island, Panama. Their data indicate that at this intensively studied site approximately 81% of the species in the herpetofauna known at the time had been collected during the first ten years of sampling (1920–30) but that six species of snakes were added to the list between 1940 and 1967. An additional five species—one frog, three lizards, and a snake—have been added since 1969 (Rand and Myers 1990). Although the area near Rincón has not been subject to the same long-term sampling, it seems likely that the present list is equivalent in terms of search effort to that developed for the Panama site by 1931. In other words, between 80% and 85% of the species in the Rincón herpetofauna have been sampled. During the 13 years of sampling at Rincón, species not previously recorded were added nearly every year, including 1973 (see the chronology of sampling in appendix 16.1). Since that time, only three species—a turtle (*Kinosternon scorpioides*) and two snakes (*Dipsas tenuissima* and *Ninia sebae*)—have been added to the Rincón list, and one species, a frog (*Hyla rufitela*), removed from the list.

By the late 1980s, most OTS courses and researchers had shifted their field activities to Sirena in Corcovado National Park. This move resulted in relatively little being added to the Rincón herpetofaunal list. Even so, the snakes *Dipsas tenuissima* and *Ninia sebae* were first collected near Rincón in the 1990s. However, the increased presence at Sirena added substantially to the total species list of amphibians and reptiles for the Península de Osa. Sampling of amphibians and reptiles in the Parque Nacional de Corcovado over the past ten years has turned up one caecilian, one frog, one turtle, one lizard, and three snakes

(sighting of a fourth species of snake needs verification) that were not recorded from Rincón. These records, together with the collection since 1990 of four previously unreported species (one frog, one lizard, and two snakes) from elsewhere on the Osa Peninsula (appendix 16.2), have increased the peninsular diversity even more. Adding the five species of marine reptiles to this compilation raises the number of native species known from the Osa Peninsula to 133 (135 if the two introduced lizards are included). We are confident that additional fieldwork will add terrestrial and freshwater species to the list of amphibians and reptiles known from the peninsula. On the basis of our knowledge of the fauna of the Golfo Dulce region and experience in sampling lowland wet forest herpetofaunas, we expect that the herpetofauna of the Rincón area will reach 135 species and estimate the herpetofauna of the Península de Osa to be about 149 terrestrial and freshwater species.

Our estimate is reinforced by close examination of the distributional records of species known from elsewhere in the Golfo Dulce forests but as yet not taken near Rincón. A number of conspicuous species that have high population densities in other sections of the Golfo Dulce forests were eliminated from consideration as possible members of the Rincón herpetofauna because they have never been seen elsewhere on the peninsula. As near as we can determine, possible additions other than the seven species from Corcovado National Park and the four from elsewhere on the peninsula (appendix 16.2) include one caecilian, two frogs, three lizards, and five snakes for a total of 22 taxa. Both frog species breed in temporary ponds but neither has been seen nor heard near Rincón and probably do not occur there. Several relatively conspicuous snakes may be added to the Rincón list in the future. Two rarely collected snakes, *Hydromorphus concolor* and *Ungaliophis panamensis*, first reported on the peninsula (at Sirena) in the 1990s, may also eventually appear.

### *Ecological Comparisons*

As previously pointed out by Savage (1966, 1982), the Golfo Dulce forest region of Costa Rica and immediately adjacent southwestern Panama forms an isolated Pacific lowland evergreen forest region. Its closest biotic affinities are with the evergreen forests that, before the last 30 years, extended more or less continuously along the Atlantic lowlands from central Veracruz, Mexico, to Colombia. The Golfo Dulce forest (fig. 16.2) is separated from direct contact with the eastern forests by the Cordillera de Talamanca–Chiriquí axis to the northeast, the lowland semideciduous and deciduous forest areas of western Central America to the north, and the semideciduous and deciduous forests and savannas of western and central Panama to the east. These latter areas also isolate the Golfo Dulce forests and its herpetofauna from the evergreen rain-

forests of western Colombia and Ecuador. In this section, we provide a comparative evaluation of the differences between the Rincón herpetofauna and those from other lowland evergreen sites.

The best-known herpetofauna of a local area within the Isthmian region is that of Barro Colorado Island, Panama Province, Panama. This fauna has been sampled and studied from about 1923, when the island was made a wildlife preserve and research station, onward (Myers and Rand 1969; Rand and Myers 1990). A second intensively studied local herpetofauna occurs at La Selva Biological Station, Heredia Province, Costa Rica. This site, originally under the ownership of Dr. Leslie R. Holdridge, now serves as a major field research station for the Organization for Tropical Studies (Clark 1990; McDade and Hartshorn 1994). This site has been the locus of a detailed analysis of the ecological roles of the species of amphibians and reptiles in the forest community (Lieberman 1986); the herpetofauna was reviewed by Guyer (1990, 1994a, 1994b) and Donnelly (1994a, 1994b). No other areas of Central American or Mexican lowland evergreen forest provide comparable data based on long-term and repetitive sampling. For this reason, the following discussion concentrates on an ecological comparison of the herpetofaunas at La Selva, Rincón, and Barro Colorado Island (BCI).

#### ENVIRONMENTS AT COMPARATIVE SITES

##### *La Selva*

La Selva research station lies on the west bank of the Río Puerto Viejo, a tributary of the Río Sarapiquí (Río San Juan drainage), 5 km southwest of the town of Puerto Viejo in the Atlantic lowlands of Costa Rica (fig. 16.2), at an elevation between 35 and 137 m. La Selva Biological Station has a total area of about 15.3 km<sup>2</sup> (McDade and Hartshorn 1994). The climate in the Köppen system is Af<sub>i</sub>, the same as that of Rincón; the mean annual temperature is 26.2°C; and precipitation averages 3,850 mm per year, with one to two relatively dry months (occurring in January through April) with less than 200 mm of rainfall (Sanford et al. 1994). Rainfall increases from March through July (averages 445 mm), then drops off during August through October to less than 350 mm per month, and finally rises again to above 400 mm per month in November and December (fig. 16.4). La Selva lies in the Tropical (Lowland) Wet Forest life zone (Holdridge 1967) and is slightly drier than most sites near Rincón de Osa. Holdridge et al. (1971) described the vegetation and soil at a typical site within the undisturbed forest at La Selva; at that site, the forest was of three tree strata with the canopy at 50 m. Of approximately 113 tree species at La Selva, 57 species represented by 404 individual trees per hectare occurred at the study site (Sawyer and Lindsay 1971). Hartshorn and Hammel (1994) reviewed the vegetation types

and floristics of the site. Soils on this and other well-drained sites are strongly acid, dark yellowish brown clay latosols that become reddish brown at a depth of 1.5 m; concentrations of magnesium, calcium, potassium, and phosphorus are very low, with concentrations of sodium, manganese, and nitrogen only slightly higher. Sollins et al. (1994) reviewed the soils and soil processes at La Selva.

### ***Barro Colorado Island***

The island, previously a hilltop, was formed in 1914 as the result of the building of the Panama Canal and the damming of the Río Chagres in 1912 to create Gatun Lake. Barro Colorado Island lies in the rather low rolling country of central Panama, north of the continental divide on the Atlantic versant; it is approximately 14.5 km<sup>2</sup> in extent and lies at an elevation of 164 m above sea level and 138 m above Gatun Lake. The climate in the Köppen system is Am; the mean annual temperature is 26.9°C, and precipitation averages 2,750 mm per year, with four dry months (January through April) with less than 100 mm of rainfall. Rainfall increases markedly in April and remains at about 280 mm per month through August; after a slight decrease in amount in September, heavy rains return and peak in November at about 440 mm, just before falling to slightly under 300 mm for December (fig. 16.4). The island is in the Tropical (Lowland) Moist Forest life zone (Holdridge 1967). Croat (1978) listed 365 tree species from the island, of which 211 attain heights of 10 m or more. Bennett (1963) described the vegetation on the island, with the best-developed forest consisting of two tree strata with the canopy at around 30 m in height. Soils at sites with well-developed forest are slightly acid to alkaline, alluvial clay, red to deep-red in color, and somewhat brownish in the uppermost 5 cm. This site has been the focus of intensive and long-term study (see Leigh et al. 1982; Leigh 1999).

### **SPECIES COMPOSITION AND DIVERSITY**

The composition and diversity of the herpetofaunas at the three sites are shown in appendix 16.2. The number of species and percentage that each amphibian and reptile group contributes to the herpetofauna at each site and to the total combined herpetofauna ( $N = 215$ ) are shown in table 16.2. With two exceptions, the herpetofaunas at the three sites are similar in total numbers of species by group. One notable exception is the lower number of frog species recorded from Barro Colorado Island (33) compared with those recorded from La Selva (45) and Rincón de Osa (41). This difference may be directly related to the amount of available water (rainfall and habitats) on Barro Colorado Island, which has lower mean annual precipitation and a more marked dry season

Table 16.2 Herpetofauna among three sites in Lower Central America, combined, and at Santa Cecilia, Ecuador

Taxon	Site														
	Rincón			La Selva			BCI			Combined			Santa Cecilia		
	N	%S	%T	N	%S	%T	N	%S	%T	N	%T	N	%T	N	%T
Amphibia	46	40.0	21.4	49	35.5	22.8	36	33.3	16.7	82	38.1	86	49.7		
Gymnophiona	1	0.9	0.5	1	0.7	0.5	1	0.9	0.5	3	1.4	3	1.7		
Caudata	4	3.5	1.9	3	2.2	1.4	2	1.9	0.9	8	3.7	2	1.2		
Anura	41	35.7	19.1	45	32.6	20.9	33	30.5	15.3	71	33.0	81	46.8		
Reptilia	69	60.0	32.1	89	64.5	41.4	72	66.7	33.5	133	61.9	87	50.3		
Testudines	3	2.6	1.4	5	3.6	2.3	5	4.6	2.3	7	3.3	6	3.5		
Amphisbaenia	0	0.0	0.0	0	0.0	0.0	1	0.9	0.5	1	0.5	1	0.6		
Sauria	22	19.1	10.2	25	18.1	11.6	22	20.3	10.2	43	20.0	27	15.6		
Serpentes	42	36.5	19.5	57	41.3	26.5	42	38.9	19.5	80	37.2	51	29.5		
Crocodylia	2	1.7	0.9	2	1.5	0.9	2	1.9	0.9	2	0.9	2	1.1		
Totals	115	100	53.5	138	100	64.2	108	100	50.2	215	100	173	100		

Source: Donnelly 1994b; Guyer 1994b; Rand and Myers 1990; Duellman 1978.

Note: N, number of species; %S, percentage of contribution of each taxonomic category to the herpetofauna at each site; %T, percentage of total herpetofauna.

(January to April) than the other sites (fig. 16.4). Because many species of amphibians depend on mesic microhabitats and adequate water for breeding, and because many forest species cannot survive long periods of drought, the differences in the amount of rainfall and its seasonal patterns almost certainly are responsible for some of the differences in anuran diversity. In addition to fewer suitable pond habitats than are found at Rincón and La Selva, BCI also lacks permanent streams and is missing many frogs associated with that habitat. One group that reflects this difference is the family Centrolenidae. Three species are known from Barro Colorado Island, but six species occur less than 10 km away on the Río Frijoles, a permanent stream (A. S. Rand, pers. comm.). Similar trends in comparative diversity occur among those amphibian species with direct development, namely, plethodontid salamanders and, in the La Selva to BCI comparison, frogs of the genus *Eleutherodactylus*. Finally, the insular nature of BCI also makes recolonization or invasion by rare species less likely than at the other two sites.

The other exception is the snake fauna, of which 57 species have been recorded from La Selva, 15 more than at BCI and at Rincón. We suggest that part of the difference in snake diversity between La Selva and the Osa Peninsula is the result of inadequate sampling at Rincón de Osa. Support for our assertion can be found by comparing the species list for Corcovado and the other sites to that of Rincón (appendix 16.2); some of the six species known only from elsewhere on the peninsula almost certainly will be taken near Rincón with additional sampling. Between La Selva and BCI, the differences are more likely real. Because fewer species of frogs and toads are part of the Barro Colorado Island herpetofauna and many snake species are frog specialists, the proportion of snake species at BCI (38.9%) is similar to that at La Selva (41.3%). A similar effect is seen in the proportion of reptiles in the total fauna at Barro Colorado Island. In contrast, the lizard faunas are similar in species number and percentages among the three sites. On the basis of these comparisons and our familiarity with herpetofaunas at other Neotropical sites, we expect that a typical herpetofauna from a lowland wet evergreen forest site in Lower Central America will approximate the group composition shown in table 16.2. A taxonomic breakdown of the groups that contribute more than 10% to the total fauna is shown in table 16.3.

Some interesting patterns emerge from comparisons within faunal groups among sites. Leptodactylid species diversity is higher than hylid diversity and contributes the most to frog diversity (34%–37%) at each site; it also is the highest contributor (11%–13%) among amphibians to the total diversity. Three other family groups (Bufonidae, Centrolenidae, Dendrobatidae) generally make up 4%–17% of the frog faunas and 1%–6% of the total herpetofauna. Two notable exceptions to the similarity among faunas in this comparison include the relatively high centrolenid diversity at Rincón (17.1% of frogs and 6.1% of

Table 16.3 Contribution by family of the major components (frogs, lizards, and snakes) of the herpetofaunas of Rincón de Osa, La Selva, and Barro Colorado Island

Taxon	Rincón						Site					
	Rincón			La Selva			BCI					
	N	%G	%H	N	%G	%H	N	%G	%H			
Amphibia	46	—	40.0	49	—	35.5	36	—	33.3			
Anura	41	89.1	35.7	45	91.8	32.6	33	91.7	30.6			
Bufonidae	4	9.8	3.5	3	6.7	2.2	3	9.1	2.8			
Centrolenidae	7	17.1	6.1	7	15.6	5.1	3	9.1	2.8			
Dendrobatidae	5	12.2	4.3	2	4.4	1.4	3	9.1	2.8			
Hylidae	10	24.4	8.7	13	28.9	9.4	10	30.3	9.3			
Leptodactylidae	14	34.1	12.2	16	35.6	11.6	12	36.4	11.1			
Microhylidae	1	2.4	0.9	1	2.2	0.7	0	0	0			
Ranidae	0	0	0	3	6.7	2.2	2	6.0	1.9			
Reptilia	69	—	60.0	89	—	64.5	72	—	66.7			
Sauria	22	31.9	19.1	25	28.1	18.1	22	30.6	20.4			
Anguidae	0	0	0	3	12.0	2.2	0	0	0			
Gekkonidae	3	13.6	2.6	4	16.0	2.9	4	18.2	3.7			

Corytophanidae	2	9.1	1.7	3	12.0	2.2	2	9.1	1.9
Iguanidae	1	4.5	0.9	1	4.0	0.7	1	4.5	0.9
Polychrotidae	7	31.8	6.1	9	36.0	6.5	10	45.5	9.3
Scincidae	2	9.1	1.7	2	8.0	1.4	1	4.5	0.9
Gymnophthalmidae	3	13.6	2.6	0	0	0	1	4.5	0.9
Teiidae	3	13.6	2.6	2	8.0	1.4	2	9.1	1.9
Xantusiidae	1	4.5	0.9	1	4.0	0.7	1	4.5	0.9
Serpentes	42	60.9	36.5	57	65.9	41.3	42	58.3	38.9
Anomalepididae	0	0	0	0	0	0	2	4.8	1.9
Boidae	2	4.8	1.7	2	3.5	1.4	3	7.1	2.8
Tropidophiidae	0	0	0	1	1.8	0.7	0	0	0
Colubridae	35	83.3	30.4	47	82.5	34.1	33	78.6	30.6
Elapidae	1	2.4	0.9	3	5.3	2.2	2	4.8	1.9
Viperidae	4	9.5	3.5	4	7.0	2.9	2	4.8	1.9

Note: N, number of species; %G, percentage of contribution of species in each category to the next higher taxonomic group; %H, percentage of contribution of species in each category to the total number of species at each site (Rincón, 115; La Selva, 138; BCI, 108).

the fauna) and La Selva (15.6% and 5.1%, respectively), and the low dendrobatid diversity at La Selva (4.4% and 1.4%, respectively). The high centrolenid diversity, at least at the Osa Peninsula, may reflect more thorough sampling for centrolenids, because one of us (RWM) focused considerable field time on this group (McDiarmid 1975, 1978), and at BCI, because of the lack of suitable breeding habitats. The low dendrobatid diversity at La Selva is surprising; these diurnal frogs usually are obvious components of a fauna, and we would expect any additional species (e.g., *Dendrobates auratus*) that occurs there to have been recorded previously.

Among lizards, species of polychrotids are the most diverse at all three sites and make up about 32%–46% of the lizard fauna and 6%–9% of the total fauna. The gekkonids are the next most diverse group (approximately 14%–18%) at each site, although at Rincón they are equaled by the gymnophthalmids and teiids. The low diversity of teiids (2 species; 8% of the lizards and 1.4% of the total fauna) and the absence of gymnophthalmids at La Selva, and the higher diversity of these two groups on the Osa Peninsula (3 species in each family, representing a combined 27.2% of lizards and 5.4% of the total fauna) are notable. We are unable to account for the low teiid–gymnophthalmid diversity at La Selva; one teiid, *Ameiva quadrilineata*, may now be extirpated (Guyer 1994). Other species of teiids and gymnophthalmids occur in the northeastern part of Costa Rica (Savage and Villa 1986) and eventually may be recorded from La Selva. The high anguid diversity at La Selva may explain the low teiid–gymnophthalmid diversity because some anguid species are ecologically similar (arboreal and leaf-litter species) to species of teiids and gymnophthalmids and functionally may operate in place of these groups at La Selva. Anguids are unknown at Rincón and BCI, but *Coloptychon* is known from near Golfito and probably occurs near Rincón on the Osa Peninsula.

The snake faunas among the three sites are similar (table 16.3). Colubrids make up approximately 79%–83% of snakes and 30%–34% of the total faunas at each site. Boids, elapids, and viperids each usually account for approximately 2%–10% of the snakes and 1%–3.5% of the totals. The low diversity of elapids from the Osa Peninsula (2.4% of snakes and 0.9% of the total fauna) may be a sampling artifact. At least one, possibly two, other species of *Micrurus* are known from the Golfo Dulce area, and one has been taken in the Corcovado National Park (appendix 16.2).

Duellman (1966, 711–12) compared the numbers of species of amphibians and reptiles from six areas of lowland evergreen forest in Mexico and Central America. His comparisons were based on a survey of samples from relatively large geographic units (e.g., Limón Province, Costa Rica) of substantially greater area than the three intensively studied sites considered here. Generally speaking, species diversity for the large areas would be expected to be higher than for a specific site within one area, because more habitats occur in the for-

Table 16.4 Number of species of amphibians and reptiles recorded from each of six areas of lowland evergreen forest in Mexico and Central America

Area	No. species	Percentage
Southern Veracruz, Mexico	93	38.9
El Peten, Guatemala	84	35.1
Bonanza area, Nicaragua	113	47.3
Limón Province, Costa Rica	127	53.1
Caribbean Canal Zone, Panama	125	52.3
Golfo Dulce area, Costa Rica	94	39.3

Source: Duellman 1966.

Note: The percentage is the proportion of the combined fauna of 239 species found in each region times 100. The current Golfo Dulce herpetofauna is estimated to be approximately 156 species.

mer. Nevertheless, the comparisons are instructive although somewhat out of date because more sampling has occurred in the intervening years, particularly in the Osa portion of the Golfo Dulce region. The total number of species represented in the six areas is 239. The number of species known from each area in 1966 and the percentages of the combined fauna that they represent are shown in table 16.4.

Aside from the Golfo Dulce area, which is now known (Savage 2002) to have a herpetofauna of about 156 species (excluding marine forms and *Conophis*), these data are remarkably similar to ours when the proportions of total available species are compared by area. Thus, the percentage for Limón Province (53.1%, table 16.4) and that for La Selva (64.2%) and Barro Colorado Island (50.2%) from table 16.2 (%T) tend to confirm that the area of highest species richness in the Atlantic versant herpetofauna is in northeastern Costa Rica. The highest species richness in lowland evergreen forests west and north of the Darien, however, seems to be in the Golfo Dulce forests. Our data suggest that although the greatest number of species at a single intensively collected site within these lowland evergreen forests is at La Selva, it is probable that further work will reveal that the highest single-site richness is at a Golfo Dulce forest site and likely on the Osa Peninsula.

Additional data on the overall herpetofaunal similarities at the three sites provide another kind of comparison. Table 16.5 presents values for the coefficient of faunal resemblance (Simpson 1960) for pair-wise (irrespective of species occurrence at other sites) and restricted (species known only from the two sites) pair-wise comparisons. Of the 43 (20%) species in common to all three sites (the percentage of the total herpetofauna for three sites is given in

**Table 16.5** Herpetofaunas from three tropical lowland sites in Central America: Rincón de Osa, Puntarenas Province, Costa Rica; La Selva Biological Station, Heredia Province, Costa Rica; and Barro Colorado Island, Panama Province, Panama

Site	Rincón	La Selva	BCI
Rincón	<b>115</b>	70 (60.9)	58 (52.8)
La Selva	27 (23.5)	<b>138</b>	62 (58.3)
BCI	14 (13.0)	20 (18.5)	<b>108</b>

Note: Values in boldface are total species diversity; values above the diagonal are total species in common between sites and the coefficient of similarity (in parentheses); values below the diagonal are number of species restricted to the two sites and Simpson's coefficient of similarity (in parentheses).

parentheses), 11 (5.1%) are amphibians (all anurans) and 32 (14.9%) are reptiles, as follows: 1 (0.5%) turtle, 9 (4.2%) lizards, 20 (9.3%) snakes, and 2 (0.9%) crocodylians. Of the 27 (12.6%) species that occur only at La Selva–Rincón, 1 (0.5%) is a salamander, 11 (5.1%) are frogs, 3 (1.4%) are lizards, and 12 (5.6%) are snakes; 14 (6.5%) species in common to Osa Peninsula–Barro Colorado Island include 7 (3.2%) frogs, 1 (0.5%) turtle, 3 (1.4%) lizards, and 3 (1.4%) snakes; the 20 (9.3%) species shared uniquely by Barro Colorado Island–La Selva include 8 (3.7%) frogs, 3 (1.4%) turtles, 2 (0.9%) lizards, and 7 (3.3%) snakes.

The actual number (58) of species shared between the Rincón and Barro Colorado Island samples is lower than that shared between La Selva and the Osa Peninsula (70). The coefficients of faunal resemblance of pair-wise comparisons (table 16.5) indicate a strong similarity among all three sites (also see Donnelly 1994a; Guyer 1994a). The Rincón fauna is more similar to that at La Selva than to the BCI fauna; BCI fauna is more similar to La Selva fauna than to that at Rincón. Restricted pair-wise comparisons (table 16.5) indicate greatest similarity between Rincón and La Selva, followed by La Selva and BCI, with Rincón and BCI being the least similar. The faunal similarity between Rincón and La Selva is even stronger than that indicated by the coefficient comparisons because several species pairs (i.e., species whose closest relative occurs at the other site) are known from Rincón and La Selva, respectively, but not from Barro Colorado Island. Among these are *Oedipina pacificensis* and *O. gracilis*, *Dendrobates granuliferus* and *D. pumilio*, *Phyllobates vittatus* and *P. lugubris*, *Eleutherodactylus taurus* and *E. ranoides*, *Sphaerodactylus graptolaemus* and *S. homolepis*, and *Urotheca fulviceps* and *U. pachyura* (appendix 16.2). Interestingly, 48 species known from La Selva do not occur at the other sites. By contrast, 31 species from Rincón and 31 from Barro Colorado Island are not known from the other

two sites. The difference between La Selva and Barro Colorado Island probably reflects the greater species richness at the former locale, and the presence of unique species of southern affinities at the latter. The difference between La Selva and Rincón probably reflects the greater intensity of sampling at the former, particularly among snakes.

Santa Cecilia (Napo Province, Ecuador) is the only other Neotropical evergreen lowland forest site where sampling effort has been comparable to that expended at the three Lower Central American sites just discussed. This upper Amazonian locality was sampled from 1966 to 1973 by field teams from the University of Kansas. The herpetofauna at Santa Cecilia, not including species taken at other nearby localities along the Río Aguarico, comprises 86 species of amphibians and 87 species of reptiles, for an astounding total of 173 species. The general composition of this herpetofauna, including the percentage of each group in the total fauna, is presented in table 16.2.

Comparisons with the three Central American sites indicate that differences between Santa Cecilia and those areas lie in the larger amphibian fauna at the Ecuadorian locale. At Santa Cecilia, amphibians are much more diverse (86 species) and make up 49.7% of the fauna, compared with 33.3%–40.0% at the three Central American sites. Although the anurans at Santa Cecilia make up 47% of the total fauna, the values are 33%, 36%, and 31% for La Selva, Rincón, and Barro Colorado Island, respectively. Among frogs, hylids are more diverse than leptodactylids at Santa Cecilia (less diverse in Central America) and represent 21.4% and 14.4% of the fauna, respectively. For hylids, this is more than twice the contribution to the fauna than in Central America (8.7%–9.4%). The species diversity and percentage contribution for the other frog families are similar to those of the Central American faunas. Lizard diversity is about the same, with 27 species contributing 15.6% of the fauna. At Santa Cecilia, gymnophthalmids (9 species, 5.2%) are more diverse than polychrotids (6 species, 3.5%), whereas at the Central American sites, polychrotids (7–10 species, 6.1%–9.3%) are more diverse than gymnophthalmids (0–3 species, 0%–2.6%). Diversities of other lizard families that are in common are comparable. Interestingly, lizards seem to show more family-level endemism between areas than do amphibian and other reptile groups. Snake diversity (51 species) is lower than that recorded for La Selva (57) but higher than that at Rincón (42) and Barro Colorado Island (42) (table 16.2). The proportion of snakes within the total fauna is lower (29.5%) than for that at La Selva (41.3%), Rincón (36.5%), or Barro Colorado Island (38.9%). Colubrids (36 species) contribute less to snake diversity at Santa Cecilia (70.6% of the snake fauna) than in Central America (33–47 species, 78.6%–83.3%), whereas boids (5 species, 9.8%, at Santa Cecilia vs. 2–3 species, 3.5%–7.1%, at the Central American sites) and elapids (5 species, 9.8% versus 1–3 species, 2.4%–5.3%) have higher diversity.

These differences and similarities, in part, may be related to the amount and

pattern (or lack thereof) of precipitation at Santa Cecilia. This locality is just north of the equator at 340 m elevation and normally receives between 4,200 and 4,300 mm of rainfall per year. There is no definite dry season, but the amount of rainfall is erratic, with some months having in excess of 500 mm and some less than 300 mm. The higher humidity in that area seemingly favors higher frog-species richness compared with that at Barro Colorado Island, which averages much less annual rainfall (2,758 mm) and has a definite dry season. La Selva also averages less annual rainfall (3,850 mm) and has a short dry season, and Rincón (4,576 mm of rainfall/year) has a definite dry season.

Only 4 frogs, 1 turtle, 2 lizards, 11 snakes, and a caiman occur both at Santa Cecilia and at one or more of the Central American sites; suffice it to say that Amazonian and Central American herpetofaunas are very different (also see Donnelly 1994a; Guyer 1994a). Of the species found at Santa Cecilia, 153 (88%) of 173 do not occur at any of the three Central American sites. Or to put it another way, the coefficients of similarity between Santa Cecilia and La Selva, Rincón, and Barro Colorado are 8%, 12%, and 14%, respectively, and essentially reflect the increasing geographic distances of each from Santa Cecilia.

### *Biogeographic Considerations*

The Península de Osa is part of the recently uplifted Isthmian Link that reunited the North and South American continents after their separation during most of the Cenozoic by the marine waters of the Panamanian portal. Not surprisingly, its herpetofauna consists primarily of a mixture of (a) autochthonous Central American taxa and (b) South American groups that apparently dispersed into Lower Central America through the Isthmian connection. In terms of its herpetofauna the peninsula is part of the Golfo Dulce area of endemism (Savage 1982) that extends along the Pacific versant from central Costa Rica to extreme southwestern Panama. A number of forms that occur elsewhere in the Golfo Dulce region and as yet are not reported for the Península de Osa probably occur there. For purposes of this section, only taxa known from the peninsula are included, but the description of historical events and conclusions are applicable to the region as a whole.

At the present time, the Golfo Dulce rainforests form an island of evergreen vegetation separated from contact with similar forest stands by a series of substantial barriers. The first of these is the main mountain axis (2,500–3,800 m) of Lower Central America that borders the Golfo Dulce region on the north and northeast. On the northwest, the region abuts an area of deciduous forest that forms the southern boundary of an extensive subhumid to arid region extending through the Pacific lowlands from Costa Rica to northern Mexico. On the southeast, a lowland, dry forest barrier in Pacific western Panama borders the

Golfo Dulce region. Farther to the east on the Pacific slope of Panama, evergreen forest alternates with subhumid savanna or dry forest habitats to form a filter barrier to exchanges between the rainforests of northwestern South America and areas to the west, including the Golfo Dulce rainforests.

Three major source units have contributed to the herpetofauna of the Golfo Dulce area following the system developed by JMS (Savage 1966, 1982):

1. Old Northern Element (Central American component)—a component of Laurasia affinities that has been disjunct from more northern components of the Old Northern Element during most of later Tertiary and Quaternary and has evolved in situ in tropical Mesoamerica; its isolation was produced by the development of a temperate, semiarid to arid climatic barrier to the north;
2. South American Element—stocks that evolved in situ in South America through its isolation during most of the Cenozoic; and
3. Middle American Element—groups anciently related to South American ones that evolved in situ in tropical North America during the Cenozoic.

For purposes of this account, we recognize 83 major lineages of amphibians and reptiles (exclusive of marine species, introduced forms, and *Conophis*) as represented on the Osa Peninsula as a whole. In our view, major lineages are equivalent to genera, subgenera (in the case of the genus *Eleutherodactylus*), and species groups (for the polyphyletic genera *Bufo* and *Hyla*). In the following comparisons, we indicate the percentage of the total major lineages in the herpetofauna belonging to each of the three biogeographic units described, followed (in parentheses) by the percentage of total species in the fauna belonging to each unit: Central American component of the Old Northern Element 28% (23%), Middle American Element 36% (40%), and South American 36% (37%). Thus, the herpetofauna was assembled primarily from autochthonous Mesoamerican taxa, 64% (63%), with a strong South American representation.

The present distributions and ecologic valence of these lineages and the individual species ally the herpetofauna of the Golfo Dulce region most closely with those from the lowland evergreen forests of the Atlantic versant of Lower Central America (eastern Nicaragua to eastern Panama) and the Pacific versant of Panama. These faunas consist of a base core of Mesoamerican taxa that was enriched by the dispersal of South American groups, primarily from the lowland evergreen forest region of northwestern South America, across the completed Isthmian Link beginning in the Pliocene. Most of these South American groups today occur no farther north than the Golfo Dulce region on the Pacific versant of Central America, while many range northward to various latitudes between Costa Rica and Mexico in the Atlantic slope evergreen forests.

The major steps in the development of the herpetofauna of the area may be summarized as follows:

1. Dispersal event I. Initially the region formed part of a Central American peninsula that gradually emerged from north to south during mid- to late Tertiary; by early Miocene (20 mya), representatives of the Old Northern (Central American component) and Middle American elements were doubtless widespread throughout Central America, and rainforest vegetation was dominant and continuous in distribution; by this time, at the latest, the Golfo Dulce region had a rainforest herpetofauna composed of these elements.
2. Vicariance I. Orogenic activity beginning at about this time led to the fragmentation of rainforest areas into Atlantic and Pacific lowland segments, and associated climatic changes brought about the replacement of lowland rainforest and associated herpetofaunas along the Pacific versant from Costa Rica northward.
3. Dispersal II. With the relinking of Central and South America by the Panamanian Isthmus (approximately 3 mya), representatives of the South American Element dispersed northward into rainforest areas but were prevented from ranging north of the Golfo Dulce region on the Pacific versant by the now fully developed lowland dry forest and thorn woodland zone that extends from northern Mexico to Costa Rica.
4. Vicariance II. Drying trends during the last one to two million years fragmented the formerly continuous lowland rainforest of Pacific Costa Rica and Panama and effectively isolated the Golfo Dulce region when deciduous forest developed to the southwest in western Panama.

From the herpetofaunal perspective, the Golfo Dulce region is an area of endemism among the lowland evergreen forest environments of Central America. Currently, 12 species are recognized Golfo Dulce region endemics: *Oscacilia osae*, *Oedipina alleni*, *Oedipina pacificensis*, *Dendrobates granuliferus* (Myers et al. 1995 reported the occurrence of a population of *D. granuliferus* from the southeastern Atlantic lowlands of Costa Rica; however, there remains a question about whether these animals were accidentally introduced by the Dirección de Fauna Silvestre through the release of confiscated frogs), *Phyllobates vittatus*, *Eleutherodactylus rugosus*, *Eleutherodactylus taurus*, *Sphaerodactylus graptolaemus*, *Norops aquaticus*, *Bachia blairi*, *Neusticurus apodemus*, and *Lachesis melanocephala*. At least 7 other forms—*Bufo melanochlorus*, *Hyalinobatrachium valerioi*, *Colostethus flotator*, *Eleutherodactylus cruentus*, *Micrurus alleni*, *Bothrops asper*, and *Porthidium nasutum*—have distinctive Golfo Dulce populations that may well be regarded as separate species by future workers. Of these 19 taxa, 11 are of Mesoamerican and 8 of South American origins. This suggests

that Mesoamerican ancestors were in the Golfo Dulce region somewhat earlier than the South American groups, indicating slightly different effects and timing of isolation on speciation events. Currently, it is not possible to determine which of the two vicariance events described was principally responsible for the development of the endemic taxa in this herpetofauna, because detailed studies of relationships have not been made for most of them. Mesoamerican taxa may have been derived from ancestral populations isolated from their congeners by the rise of the Talamanca-Baru cordillera to the east and northeast and the development of the deciduous forest environments to the north. However, the fact that both Mesoamerican and South American groups are involved requires that final isolation of the region from southern less-humid habitats occurred after South American lineages were present (i.e., sometime after the Panamanian portal was closed).

### *Postscript*

During the years since our most concentrated fieldwork in the Rincón area, many changes have occurred on the Península de Osa. Most of the forests in which our work was accomplished have been cut, the old Osa Field Station near the airfield has been demolished, and subsistence farming has replaced much of the once imposing natural scene. Nevertheless, Corcovado National Park remains essentially intact. A road now connects Rincón around the head of the Golfo Dulce with the Carretera Interamericana and continues south through Puerto Jiménez to the tip of the peninsula.

Corcovado National Park faced a major crisis in its early days, when the Park Service had to remove the numerous squatters who had established themselves within park boundaries. The squatters did not want to leave so only through payments totaling \$1.7 million were they bought out. Unfortunately, many resettled on the eastern portion of the peninsula outside the park limits.

Another crisis threatened the park in 1985. The new road had brought a flood of eager gold miners to the peninsula, many of whom were also local subsistence farmers and/or former squatters in the park, but most were refugees from the mainland, where cessation of banana operations had left many unemployed. Major placer mining companies had established themselves in the forest "preserves" around the park so that the only way left for individual miners to operate was by illegal gold panning and mining within the park itself. As the crisis developed, some 1,400 miners and many of their hangers-on were in the park seeking gold. Ultimately the miners were evicted at considerable cost, both financially and politically, to everyone involved, but even today illegal mining and logging take place in the park because of understaffing of the Park Service (Wallace 1992).

The 1990s saw a resurgence of ecotourism on the Osa Peninsula, and today a

steady stream of visitors can be seen making their way south along the road to the tip of the peninsula, where they can hike into Corcovado National Park. Between Puerto Jiménez and Carate there are now several privately owned nature lodges set amid large tracts of the remaining forest. The volume of visitors to Corcovado National Park has led the Park Service to give serious consideration to limiting the number of visitors entering the park. Threats to the integrity of the Osa forests have not ceased. In the mid-1990s, serious consideration was given to building a causeway across the Golfo Dulce from Golfito to Puerto Jiménez, a project since abandoned. A proposed chip mill, although based on harvesting plantations of nonnative trees, also set off alarms. Environmentalists saw seed dispersal of nonnative species, chemical pollution of the gulf, and other effects as affecting Corcovado National Park and, together with the local community, have resisted this development.

Fortunately, the Costa Rican people remain committed to the preservation of much of the majesty and profound beauty of the Osa forests through continuing protection within the boundaries of Corcovado National Park. The Park Service has increased efforts to integrate the local community adjacent to the park boundaries more fully into park programs and operations for mutual benefit, especially along the vulnerable northeast margin and around Puerto Jiménez. The economy of the region is now substantially supported by ecotourism involving local Costa Ricans. These developments give promise for long-term stability in maintaining the remnants of the Golfo Dulce rainforests for posterity.

We were privileged to work in the Osa rainforest at a time when it covered the entire peninsula and when few others had the opportunity to experience its magnificence. How can we ever forget seeing our first harpy eagle and king vulture, hearing the peccaries gnashing their teeth in the woods and the howlers howling in the trees 50 m above, or sighting a 2-m-long, black-headed bushmaster barely visible against the leaf litter on the forest floor. But most of all we recall the nights spent in the great forest with good companions searching for glassfrogs along a tropical stream.

## Appendix 16.1

**Table 16A.1 History of collections: dates and collectors of amphibians and reptiles from the vicinity of Rincón de Osa, Osa Peninsula, Puntarenas Province, Costa Rica**

Year	Dates	Collector(s)	Materials
1961	Summer	Lewis Steinmetz	1 <i>Leptodactylus bolivianus</i>
1962	13–18 August	Los Angeles County Museum field party: R. Casebeer, C. McLaughlin, A. Schoenherr, and F. Truxal	general collection
	17–20 August	J. M. Savage and C. F. Walker	general collection
1964	16–19 June	D. Huckaby, J. M. Savage, N. J. Scott, and C. F. Walker	general collection
1965	1–4 March	D. H. Janzen	a few specimens
1966	2–10 March	R. W. McDiarmid in OTS course	general collection
	8–13 November	D. P. Paulson	general collection
1967	7–21 March	D. P. Paulson with OTS course	general collection
	21–22 March	R. W. McDiarmid	general collection
	9 May	D. P. Paulson	2 centrolenids
	22–29 July	A. Starrett with OTS course	frogs and tadpoles
	1–11 August	R. W. McDiarmid with OTS course	general collection
	11 August	W. T. O'Day	tadpoles
1968	27 February–14 March	N. J. Scott with OTS course	general collection
	22 July–6 August	J. M. Savage with OTS course	general collection
	7–13 August	N. J. Scott with OTS course	general collection
	20–29 November	I. Straughan	frogs
1969	5–10 March	N. J. Scott with OTS course	leaf-litter fauna
	14–22 July	N. J. Scott	general collection
	27 July–10 August	R. W. McDiarmid with OTS course	general collection
1970	4 March	N. J. Scott with OTS course	leaf-litter fauna
	30 July–10 August	A. Starrett with OTS course	tadpoles
	8 August	N. J. Scott with OTS course	leaf-litter fauna
1971	2–18 May	R. W. McDiarmid with OTS course	general collection

(continued)

Table 16A.1 (continued)

Year	Dates	Collector(s)	Materials
1973	17–20 March	J. M. Savage and R. T. Harris with OTS course	frogs
	9–22 June	R. W. McDiarmid, W. R. Heyer, and J. J. Talbot	general collection
	30 June–11 July	J. M. Savage and GORE field parties	general collection
	7 July–31 August	R. W. McDiarmid and students	general collection

Note: Field activities after 1973 are summarized in the text.

## Appendix 16.2

This appendix lists all 135 species of amphibians (49) and reptiles (86) reported from the Osa Peninsula, Puntarenas Province, Costa Rica. Records of species from the vicinity of Rincón and the rest of the Osa Peninsula are listed separately. Records for sea turtles and sea snakes are based on sightings along the coast, inside and outside of Corcovado National Park. They are included for completeness, as are records for two introduced geckos. For comparison, all species of amphibians and reptiles known from La Selva Biological Station, Costa Rica, and Barro Colorado Island (BCI), Panama, are included.

Table 16A.2 Herpetofaunal composition and species richness

Taxon	Site			
	Rincón	Osa	La Selva	BCI
Amphibia	(46)	(47)	(49)	(36) <sup>a</sup>
Gymnophiona	(1)	(2)	(1)	(1)
Caeciliidae				
<i>Dermophis occidentalis</i>	+	SI,MA		
<i>Gymnopsis multiplicata</i>			+	
<i>Osaecilia ochrocephala</i>				+
<i>Osaecilia osae</i>		SI,PT		

Table 16A.2 (continued)

Taxon	Site			
	Rincón	Osa	La Selva	BCI
Caudata	(4)	(4)	(3)	(2)
Plethodontidae				
<i>Bolitoglossa colonnea</i>	+	MA	+	
<i>Bolitoglossa lignicolor</i>	+	SI,LC,MA		
<i>Oedipina alleni</i>	+	SI,LC		
<i>Oedipina complex</i>				+
<i>Oedipina cyclocauda</i>			+	
<i>Oedipina gracilis</i>			+	
<i>Oedipina pacificensis</i>	+	SI,MA		
<i>Oedipina parvipes</i>				+
Anura	(41)	(41)	(45)	(33)
Bufonidae	(4)	(4)	(1)	(1)
<i>Bufo coniferus</i>	+	MA	+	
<i>Bufo granulosis</i>				+ <sup>b</sup>
<i>Bufo haematiticus</i>	+	SI,MA	+	
<i>Bufo marinus</i>	+	SI,MA	+	+
<i>Bufo melanochlorus</i>	+	SI,MA		
<i>Bufo</i> cf. <i>typhonius</i>				+
Centrolenidae	(7)	(6)	(7)	(3)
<i>Centrolene prosoblepon</i>	+	LL	+	+
<i>Cochranella albomaculata</i>	+	MA	+	
<i>Cochranella granulosa</i>	+	SI,MA	+	
<i>Cochranella spinosa</i>	+		+	+
<i>Hyalinobatrachium colymbiophyllum</i>	+	MA		
<i>Hyalinobatrachium fleischmanni</i>			+	+
<i>Hyalinobatrachium pulveratum</i>	+	SI	+	
<i>Hyalinobatrachium valerioi</i>	+	SI,MA	+	
Dendrobatidae	(5)	(5)	(2)	(3)
<i>Colostethus flotator</i>	+	SI,LL		+
<i>Colostethus talamancae</i>	+	SI,LL,MA		
<i>Dendrobates auratus</i>	+	SI,MA		+
<i>Dendrobates granuliferus</i>	+	SI,MA		
<i>Dendrobates pumilio</i>			+	
<i>Minyobates minutus</i>				+ <sup>b</sup>
<i>Phyllobates lugubris</i>			+	
<i>Phyllobates vittatus</i>	+	SI,MA		
Hylidae	(10)	(11)	(13)	(10)
<i>Agalychnis calcarifer</i>			+	+
<i>Agalychnis callidryas</i>	+	SI,MA	+	+

(continued)

Table 16A.2 (continued)

Taxon	Site			
	Rincón	Osa	La Selva	BCI
<i>Agalychnis saltator</i>			+	
<i>Agalychnis spurrelli</i>	+	SI,LC,MA		+
<i>Hyla ebraccata</i>	+	SI,MA	+	
<i>Hyla loquax</i>			+	
<i>Hyla microcephala</i>		MA		+
<i>Hyla phlebodes</i>			+	+
<i>Hyla rosenbergi</i>	+	SI,MA		
<i>Hyla rufitela</i>			+	+
<i>Phrynohyas venulosa</i>	+	SI,MA		+
<i>Scinax boulengeri</i>	+	SI,MA	+	+
<i>Scinax elaeochroa</i>	+	SI,MA	+	
<i>Smilisca baudinii</i>			+	
<i>Smilisca phaeota</i>	+	SI,MA	+	+
<i>Smilisca puma</i>			+	
<i>Smilisca sila</i>	+	SI,MA		+
<i>Smilisca sordida</i>	+	SI,MA	+	
Leptodactylidae	(14)	(14)	(16)	(12)
<i>Eleutherodactylus altae</i>			+	
<i>Eleutherodactylus bransfordii</i>			+	
<i>Eleutherodactylus bufoniformis</i>				+
<i>Eleutherodactylus caryophyllaceus</i>			+	
<i>Eleutherodactylus cerasinus</i>			+	+
<i>Eleutherodactylus crassidigitus</i>	+	SI,MA	+	+
<i>Eleutherodactylus cruentus</i>	+	MA	+	
<i>Eleutherodactylus diastema</i>	+	SI,MA	+	+
<i>Eleutherodactylus fitzingeri</i>	+	SI,MA	+	+
<i>Eleutherodactylus gaigeae</i>				+
<i>Eleutherodactylus megacephalus</i>			+	+
<i>Eleutherodactylus mimus</i>			+	
<i>Eleutherodactylus noblei</i>			+	
<i>Eleutherodactylus ranoides</i>			+	
<i>Eleutherodactylus ridens</i>	+	SI,MA	+	+
<i>Eleutherodactylus rugosus</i>	+	SI,MA		
<i>Eleutherodactylus stejnerianus</i>	+	SI,MA		
<i>Eleutherodactylus taeniatus</i>				+
<i>Eleutherodactylus talamancae</i>			+	
<i>Eleutherodactylus taurus</i>	+	SI,MA		
<i>Eleutherodactylus vocator</i>	+	SI,MA		
<i>Leptodactylus bolivianus</i> <sup>b</sup>	+	SI,MA		+
<i>Leptodactylus melanonotus</i>	+	MA	+	

Table 16A.2 (continued)

Taxon	Site			
	Rincón	Osa	La Selva	BCI
<i>Leptodactylus pentadactylus</i>	+	SI,MA	+	+
<i>Leptodactylus poecilochilus</i>	+	RN*,MA		
<i>Physalaemus pustulosus</i>	+	MA		+
Microhylidae	(1)	(0)	(1)	(0)
<i>Gastrophryne pictiventris</i>			+	
<i>Nelsonophryne aterrima</i>	+			
Ranidae	(0)	(1)	(3)	(2)
<i>Rana vaillanti</i>			+	+
<i>Rana taylori</i>			+	
<i>Rana warszewitschii</i>		PT,LC,MA	+	+ <sup>c</sup>
Reptilia	(69)	(75)	(89)	(72)
Testudines	(3)	(8)	(5)	(5)
Chelydridae	(0)	(1)	(1)	(1)
<i>Chelydra serpentina</i>		LC,LS	+	+
Kinosternidae	(2)	(2)	(2)	(1)
<i>Kinosternon angustipons</i>			+	
<i>Kinosternon leucostomum</i>	+	SI,RN*	+	+
<i>Kinosternon scorpioides</i>	+	SI		
Emydidae	(1)	(1)	(2)	(3)
<i>Rhinoclemmys annulata</i>			+	+
<i>Rhinoclemmys funerea</i>			+	+
<i>Trachemys ornata</i>	+	SI,MA		+
Cheloniidae	(0)	(3)	(0)	(0)
<i>Chelonia mydas</i>		marine		
<i>Eretmochelys imbricata</i>		marine		
<i>Lepidochelys olivacea</i>		marine		
Dermochelyidae	(0)	(1)	(0)	(0)
<i>Dermochelys coriacea</i>		marine		
Squamata—Sauria	(22)	(25)	(25)	(22)
Amphisbaenidae	(0)	(0)	(0)	(1)
<i>Amphisbaea fuliginosa</i>				+
Anguidae	(0)	(0)	(3)	(0)
<i>Celestus hylaius</i>			+	
<i>Diploglossus bilobatus</i>			+	
<i>Diploglossus monotropis</i>			+	
Gekkonidae	(3)	(6)	(4)	(4)
<i>Gonatodes albogularis</i>		MA		+
<i>Hemidactylus frenatus</i> <sup>d</sup>		PJ		
<i>Lepidoblepharis sanctaemartae</i>				+

(continued)

Table 16A.2 (continued)

Taxon	Site			
	Rincón	Osa	La Selva	BCI
<i>Lepidoblepharis xanthostigma</i>	+	SI,MA	+	
<i>Lepidodactylus lugubris</i> <sup>d</sup>		QU		
<i>Sphaerodactylus graptolaemus</i>	+	SI,MA		
<i>Sphaerodactylus homolepis</i>			+	
<i>Sphaerodactylus lineolatus</i>				+
<i>Sphaerodactylus millipunctatus</i>			+	
<i>Thecadactylus rapicauda</i>	+	SI,MA	+	+
Corytophanidae	(2)	(2)	(3)	(2)
<i>Basiliscus basiliscus</i>	+	SI,MA,PJ*		+
<i>Basiliscus plumifrons</i>			+	
<i>Basiliscus vittatus</i>			+ <sup>e</sup>	
<i>Corytophanes cristatus</i>	+	SI,LC,MA	+	+
Iguanidae	(1)	(2)	(1)	(1)
<i>Ctenosaura similis</i>		SI,PJ*,PJ,MA		
<i>Iguana iguana</i>	+	SI,MA,LC,PJ*	+	+
Polychrotidae	(7)	(6)	(9)	(10)
<i>Dactyloa frenatus</i>				+
<i>Dactyloa insignis</i>	+			
<i>Norops aquaticus</i>	+	SI,PA,MA		
<i>Norops auratus</i>				+
<i>Norops biporcatus</i>	+	SI,MA	+	+
<i>Norops capito</i>	+	SI,PA,MA	+	+
<i>Norops carpenteri</i>			+	
<i>Norops humilis</i>			+	
<i>Norops lemurinus</i>			+	
<i>Norops limifrons</i>	+	SI,LC,MA	+	+
<i>Norops lionotus</i>				+
<i>Norops oxylophus</i>			+	
<i>Norops pentaprion</i>	+	SI,MA,PJ*	+	+
<i>Norops polylepis</i>	+	SI,LC,MA,PJ*		
<i>Norops vittigerus</i>				+
<i>Norops</i> sp.				+
<i>Polychrus gutturosus</i>			+	+
Scincidae	(2)	(2)	(2)	(1)
<i>Mabuya unimarginata</i>	+	SI,MA	+	+
<i>Sphenomorphus cherriei</i>	+	SI,PA,MA	+	
Gymnophthalmidae	(3)	(3)	(0)	(1)
<i>Bachia blairi</i>	+	SI,MA		
<i>Leposoma southi</i>	+	SI,MA		+
<i>Neusticurus apodemus</i>	+	MA		

Table 16A.2 (continued)

Taxon	Site			
	Rincón	Osa	La Selva	BCI
Teiidae	(3)	(3)	(2)	(2)
<i>Ameiva festiva</i>	+	SI	+	+
<i>Ameiva leptophrys</i>	+	SI,LC,MA		+
<i>Ameiva quadrilineata</i>	+	SI,PA,MA	+ <sup>e</sup>	
Xantusiidae	(1)	(1)	(1)	(1)
<i>Lepidophyma flavimaculatum</i>			+	+
<i>Lepidophyma reticulatum</i>	+	SI,MA		
Squamata—Serpentes	(42)	(44)	(57)	(42)
Anomalepididae	(0)	(0)	(0)	(2)
<i>Anomalepis mexicanus</i>				+
<i>Liotyphlops albirostris</i>				+
Boidae	(2)	(2)	(2)	(3)
<i>Boa constrictor</i>	+	SI,MA	+	+
<i>Corallus annulatus</i>			+	+
<i>Corallus ruschenbergerii</i>	+	SI,MA		
<i>Epicrates cenchria</i>				+
Tropidophiidae	(0)	(1)	(1)	(0)
<i>Ungaliophis panamensis</i>		SI	+	
Colubridae	(35)	(34)	(47)	(33)
<i>Amastridium veliferum</i>	+	SI,MA	+	+
<i>Chironius carinatus</i>	+	SI		+
<i>Chironius grandisquamis</i>	+	SI,MA	+	+
<i>Clelia clelia</i>	+	SI,MA	+	
<i>Coniophanes fissidens</i>	+	SI,MA	+	+
<i>Conopsis lineatus</i>		SI <sup>f</sup>		
<i>Dendrophidion percarinatum</i>	+	SI	+	+
<i>Dendrophidion vinitor</i>			+	
<i>Dipsas tenuissima</i>	+	SI		
<i>Dipsas variegata</i>				+
<i>Drymarchon melanurus</i>	+	PA	+	+
<i>Drymobius margaritiferus</i>			+	
<i>Drymobius melanotropis</i>			+	
<i>Drymobius rhombifer</i>			+	
<i>Enulius flavitorques</i>				+
<i>Enulius sclateri</i>		MA	+	+
<i>Erythrolamprus bizona</i>				+
<i>Erythrolamprus mimus</i>	+	PA	+	
<i>Geophis hoffmanni</i>	+	SI	+	+
<i>Hydromorphus concolor</i>		SI,MA	+	

(continued)

Table 16A.2 (continued)

Taxon	Site			
	Rincón	Osa	La Selva	BCI
<i>Imantodes cenchoa</i>	+	SI,LC,MA	+	+
<i>Imantodes gemmistratus</i>				+
<i>Imantodes inornatus</i>	+	SI	+	
<i>Lampropeltis triangulum</i>			+	
<i>Leptodeira annulata</i>			+	+
<i>Leptodeira rubricata</i>		PJ		
<i>Leptodeira septentrionalis</i>	+	SI,MA	+	+
<i>Leptophis ahaetulla</i>	+	SI,LC,MA,PJ*	+	+
<i>Leptophis depressirostris</i>			+	
<i>Leptophis nebulosus</i>			+	
<i>Leptophis riveti</i>	+			
<i>Liophis epinephalus</i>			+	+
<i>Mastigodryas melanolomus</i>	+	SI,MA	+	+
<i>Ninia maculata</i>	+	MA	+	+
<i>Ninia sebae</i>	+		+	
<i>Nothopsis rugosus</i>	+		+	
<i>Oxybelis aeneus</i>	+	SI,MA	+	+
<i>Oxybelis brevirostris</i>			+	
<i>Oxybelis fulgidus</i>			+	
<i>Oxyrhopus petolaris</i>	+	SI,MA	+	+
<i>Pseudoboa neuwiedii</i>				+
<i>Pseustes poecilonotus</i>	+	SI,MA	+	+
<i>Rhadinaea decorata</i>	+	SI,MA	+	+
<i>Scaphiodontophis annulatus</i>	+	SI,MA	+	
<i>Sibon annulatus</i>			+	
<i>Sibon dimidiatus</i>	+			
<i>Sibon longifrenis</i>			+	
<i>Sibon nebulatus</i>	+	SI,MA	+	
<i>Siphlophis cervinus</i>				+
<i>Spilotes pullatus</i>	+	SI,MA,PJ*	+	+
<i>Stenorrhina degenhardtii</i>	+			+
<i>Tantilla albiceps</i>				+
<i>Tantilla melanocephala</i>				+
<i>Tantilla reticulata</i>			+	
<i>Tantilla ruficeps</i>	+	MA	+	
<i>Tantilla schistosa</i>	+	SI		
<i>Tantilla supracincta</i>	+	PA	+	
<i>Tretanorhinus nigroluteus</i>			+	
<i>Trimetopon barbouri</i>				+
<i>Trimetopon pliolepis</i>			+	

Table 16A.2 (continued)

Taxon	Site			
	Rincón	Osa	La Selva	BCI
<i>Tripanurgos compressus</i>	+	SI		
<i>Urotheca decipiens</i>		SI	+	
<i>Urotheca euryzona</i>			+	+
<i>Urotheca fulviceps</i>	+			+
<i>Urotheca guentheri</i>	+	PA	+	
<i>Xenodon rhabdocephalus</i>	+	SI	+	+
Elapidae	(1)	(3)	(3)	(2)
<i>Micrurus alleni</i>	+	SI,MA	+	
<i>Micrurus mipartitus</i>			+	+
<i>Micrurus nigrocinctus</i>		SI,MA	+	+
<i>Pelamis platurus</i>		marine		
Viperidae	(4)	(4)	(4)	(2)
<i>Bothriechis schlegelii</i>	+	SI,MA	+	+
<i>Bothrops asper</i>	+	SI,LC,MA	+	+
<i>Lachesis melanocephala</i>	+	SI		
<i>Lachesis stenophrys</i>			+	
<i>Porthidium nasutum</i>	+	MA	+	
Crocodylia	(2)	(2)	(2)	(2)
Alligatoridae	(1)		(1)	(1)
<i>Caiman crocodilus</i>	+	SI	+	+
Crocodylidae	(1)		(1)	(1)
<i>Crocodylus acutus</i>	+	LC,MA	+	+
Total species	(115)	(126)	(138)	(108)

Note: Numbers in parentheses indicate the number of species in each taxonomic category for a particular site. Most records of species at localities other than Rincón are within Corcovado National Park from the vicinity of the former headquarters at Sirena (SI). Other records from within the park are noted as follows: LC, Laguna Corcovado; LS, Laguna Sirena; LL, Llorona; PA, Pavo Forest; PT, Los Patos. Specimens from localities outside the park were reported by Wettstein (1934) from Puerto Jiménez (PJ) and Río Nuevo (RN); others have been recorded from Marengo Biological Station (MA), Puerto Jiménez (PJ), Quemada (QU), and marine waters and beaches along the outer coast (marine). Species recorded by Wettstein (1934) are indicated by an asterisk (\*).

<sup>a</sup>Campbell 1999 listed 52 species of amphibians from Barro Colorado Island, but this value included species from the adjacent mainland (Rand and Myers 1990).

<sup>b</sup>Some authors have used *Leptodactylus insularum* for this species. We agree that the Central American species is probably not *L. bolivianus* but prefer to maintain that name until definitive evidence about assignment of names is published.

<sup>c</sup>Species formerly known from Barro Colorado Island but now extirpated (Myers and Rand 1969).

<sup>d</sup>Nonnative species introduced on the Península de Osa.

<sup>e</sup>Species formerly known from La Selva but now possibly extirpated (Guyer 1994a).

<sup>f</sup>Species identification questionable; see text.

## Appendix 16.3 Collecting Localities and Other Important Sites on the Osa Peninsula

*Airfield Water Supply:* Water-collecting site on a small, steep tributary of Quebrada Aguabuena, north of the airfield and 3 km west of Rincón; most specimens were taken along the lower reaches of the stream (60–80 m), but some were from near the top at the ridge (300 m) drained by the water supply stream.

*Caiman Lagoon:* Small lake created by road-building activities in the late 1950s or early 1960s, east of Carretera al Pacífico; another large pond (70 × 50 m) with the same name is west of road; both are about 3 km southwest of Rincón, 35 m.

*Camp Seattle:* Abandoned lumber camp, 3 km southwest of Rincón, just east of Carretera al Pacífico, 30 m.

*Carretera al Pacífico:* Road running southwest from Rincón to Río Rincón near its juncture with Río Pavón; formerly it extended a little farther, but bridges over the Río Riyito and Río Rincón have been washed out.

*Charcos:* Abandoned village site, east of Carretera al Pacífico and north of junction with Water Fall Road, 4 km southwest of Rincón, 20 m.

*Gravel Pit Road:* Side road off Carretera al Pacífico going west to Snake Woods, north of Río Riyito, 60 m.

*Harris Hollow:* Heavily forested depression just east of Carretera al Pacífico, 6 km southwest of Rincón, between Savage Woods and Quebrada Rayo, 10 m.

*Holdridge Trail:* Trail beginning at Carretera al Pacífico near Caiman Lagoon and running northwest onto ridge (400–440 m); connects with Ridge Trail to Laguna Chocuaco; shown but not labeled in figure 16.3.

*Laguna Chocuaco:* Lake 10 km west of Rincón, 200 m.

*Mangrove Area:* Mangrove forest 1–2 km southeast of Rincón on Golfo Dulce shore, near the mouth of Río Rincón; Carretera al Pacífico parallels mangroves for a short distance east of Rincón, 0–3 m.

*Old Osa Field Station:* Field building erected for Tropical Science Center, just south of Rincón Airfield and north of Quebrada Aguabuena, 40 m.

*Playa Blanca:* Settlement on eastern shore of peninsula, 9 km southeast of Rincón, 3 m.

*Puerto Jiménez:* Major settlement on Golfo Dulce on southeastern shore of peninsula, 9.5 km southeast of Playa Blanca, 7 m (fig. 16.2).

*Quebrada Aguabuena:* Tributary of Río Riyito, draining slopes of a small valley south and west of Rincón; samples were taken over most of the length of the stream, which is reduced to intermittent trickles in dry season and may rise 1.5 m in wet season; most material is from about 2 km southwest

- of Rincón near Carretera al Pacífico at 30 m and immediately south of the old Osa Field Station, 3 km west of Rincón at 40 m.
- Quebrada Crump*: Small forest stream flowing eastward into Quebrada Aguabuena, about 300 m southeast of the old Osa Field Station, 40 m (Crump Creek of Findley and Wilson 1974); shown but not labeled in figure 16.3.
- Quebrada Ferruviosa*: Tributary of Río Riyito that crosses Carretera al Pacífico about 5.5 km southwest of Rincón, 20 m.
- Quebrada McDiarmid*: Small forest stream flowing eastward to join Quebrada Aguabuena just south of the old Osa Field Station, 40 m (McDiarmid Creek of Findley and Wilson 1974); shown but not labeled in figure 16.3.
- Quebrada Rayo*: Small tributary of Río Riyito that crosses Carretera al Pacífico about 6.5 km southwest of Rincón, 40 m.
- Quebrada Vanegas*: Small tributary of Río Riyito that crosses Carretera al Pacífico, 5 km southwest of Rincón, 35 m (= Quebrada Banegas on some maps).
- Ridge Trail*: Trail that begins at the terminus of a secondary road south of Rincón and extends north and west onto ridge (> 400 m) and eventually reaches Laguna Chocuaco; shown but not labeled in figure 16.3.
- Rincón Airfield*: Dirt and gravel landing strip suitable for small planes, 2.5 km west of Rincón, 0.5 km northeast and parallel to Quebrada Aguabuena, 40 m.
- Rincón de Osa*: Settlement and former headquarters for Osa Productos Forestales near western head of Golfo Dulce, 4 m.
- Rincón Water Supply*: Small, steep creek immediately west of Rincón, 15–100 m.
- Río Nuevo*: Small settlement, 3 km southwest of Puerto Jiménez, 10 m (fig. 16.2).
- Río Pavón*: Major tributary of Río Rincón, which it joins near Carretera al Pacífico, 11.5 km south-southwest of Rincón, 60 m.
- Río Rincón*: Primary river-draining region that exits to Golfo Dulce via northern and eastern branch around large island, 1.5–2 km east of Rincón.
- Río Riyito*: Major tributary of Río Rincón that crosses Carretera al Pacífico, 7 km southwest of Rincón, 40 m.
- Savage Woods*: Primary forest on river flat of Río Riyito, 5.5 km southwest of Rincón, east of Carretera al Pacífico, 20 m.
- Snake Woods*: Primary forest at end of Gravel Pit Road just north of Río Riyito, 8 km southwest of Rincón and 2 km west of Carretera al Pacífico, 60 m.
- Three Falls*: Waterfalls in small stream crossing Water Fall Road, 1 km west of Carretera al Pacífico, 30 m.
- Vanegas Swamp*: A permanent swamp, 5.5 km southwest of Rincón, 20 m.
- Waterfall Road*: Side road going west from Carretera al Pacífico to Three Falls, 4 km southwest of Rincón, 30 m; shown but not labeled in figure 16.3.

The sites studied by Holdridge et al. (1971) for their vegetation analysis are as follows:

- A. Holdridge Trail, 420 m.
- B. Mora Swamp, 1.5 km southeast of Rincón, near northern Boca de Río Rincón, just east of Carretera al Pacífico, 1.5–2 m.
- C. Mangrove swamp, 2 km southeast of Rincón, near Boca de Río Rincón, on an island between two mouths of the Río Rincón, 0–1 m.
- D1. Eastern bank of Río Rincón, 3 km south of Rincón, 9 m.
- D2. Eastern bank of Río Rincón, 3.5 km south of Rincón, 8 m.
- E. 3.5 km south of Rincón Airfield, 300 m.
- F. 6 km south of Rincón Airfield, 200 m north of Río Riyito, 100–200 m.

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In 1973, the new management of Osa Productos Forestales, which owned 100,000 acres (approximately 41,000 ha) of forest, began promoting land sales to wealthy North Americans; they drew up plans to extend the road across the peninsula, to build retirement communities on the western beaches, and to dredge the Laguna Corcovado to make a large marina. We decided that this development and the ever-increasing clearing and burning near Rincón by squatters made it imperative that we mount a specially intensive collecting program

before all of the forest was gone. Our concern was heightened when we learned that the company was considering sale of the remainder of its holdings to a Japanese company that also was negotiating with the Costa Rican government to clear-cut most of the peninsula. Participants who joined us in this effort (sometimes referred to as GORE I and II) included Doug Allen, Jim and Rosemary DeWeese, Carl Lieb, Andy and Kathy Shumaker, Holly Starrett, Jim Talbot, Ian Straughan, Wayne Van Devender, Dave and Marvalee Wake, and George Zug. We especially thank them for their efforts in making the Osa herpetofauna better known. We also want to acknowledge the many students and faculty who shared the Osa experience with us during our several stints as instructors of courses given by the Organization for Tropical Studies at Rincón; particularly appreciated were interactions with Marty Crump, Jim DeWeese, Ron Harris, Dennis Paulson, Allan Schoenherr, Wade Sherbrooke, Wayne Van Devender, and Don Wilson.

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