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# The Ecology and Systematics of the Amphisbaenian Genus *Bipes*

By

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# ABSTRACT

PAPENFUSS, THEODORE J. The ecology and systematics of the amphisbaenian genus *Bipes*. *Occasional Papers of the California Academy of Sciences*, No. 136, 42 pages, 36 figures, 9 tables, 1982.—The amphisbaenian genus *Bipes* consists of three morphologically distinct species that differ in body size, tail length, number of annuli, and degree of digital reduction. *Bipes biporus* occurs on the Baja California peninsula, *B. tridactylus* in coastal Guerrero, and *B. canaliculatus* (including *B. alvarezi* Smith and Smith here synonymized) in the Balsas Depression of Guerrero and Michoacán. All were once thought to be rare. Between 1971 and 1979 study sites for each species were visited on a number of occasions at different seasons. They could be easily collected by digging and over 3000 had been obtained by the end of this study. Their allopatric distribution is best explained by the tectonic events in western Mexico during the last 20 million years. The ancestral *Bipes* may have been separated into three populations by the formation of the Baja California peninsula and the elevation of the Sierra Madre del Sur of Guerrero.

Caudal autotomy occurs at a single intravertebral fracture plane. There is no regeneration, thus, tail loss is permanent and can provide useful data on predation. The frequency of tail loss is low in *B. biporus* (2.7%) and higher for the mainland species (10.2% for *B. canaliculatus* and 17.0% for *B. tridactylus*). In all species the frequency of autotomized tails increases with age. Increased predation pressure on the mainland species may be due to the presence of coral snakes (*Micrurus*) which are absent from Baja California. Coral snakes can enter the burrow systems of *Bipes* and are known to feed on them.

Life history traits differ for each species. *Bipes tridactylus* mature at a size of about 115 mm and an age of about 21 months. Gravid females have a mean clutch size of 2.2 and reproduce annually. *Bipes canaliculatus* mature at a size of about 185 mm and an age of about 33 months. Although the mean clutch size is 2.8 per gravid female, the mean clutch size per adult female is only 1.02 because an individual female lays only every other year. *Bipes biporus* mature at a size of about 185 mm and an age of about 45 months. The mean clutch size per gravid female is 2.15, but since the reproductive cycle is biennial, the mean clutch size per adult female is only 1.0. There is a 50:50 sex ratio in both *B. tridactylus* and *B. canaliculatus*. In *B. biporus* about twice as many adult females as males were found. It is not known if this difference is due to sampling error, differential mortality, or a skewed primary sex ratio.

All three species are fossorial and live in self-constructed burrow systems. The mainland species were usually found at depths of from 10 to 20 cm. No *B. biporus* were found deeper than 15 cm and over 50% of the individuals were taken from burrows just below the soil crust at a depth of less than 2.5 cm. The differences in preferred depth may relate to thermoregulatory behavior. Both mainland species occur in subtropical areas where soil temperatures are high throughout the year and may exceed preferred body temperatures near the surface. On the other hand, *B. biporus* exhibit behavioral thermoregulation by moving in their burrows between sunny and shaded locations.

# The Ecology and Systematics of the Amphisbaenian Genus *Bipes*

**Theodore J. Papenfuss**[*]

## Introduction

The Amphisbaenia is a suborder of squamate reptiles which includes about 130 species. The members of this suborder are modified for a true burrowing existence. Four families are recognized (Gans 1978): the family Trogonophidae occurs in North Africa and Southwest Asia; the family Amphisbaenidae in Africa, South America, and the West Indies; the family Rhineuridae in Florida; and the family Bipedidae in western Mexico. The last family includes a single genus, *Bipes*, of which there are three species. *Bipes canaliculatus* occurs in the Balsas Depression of Guerrero and Michoacán; *B. tridactylus* in a small geographic area of coastal Guerrero; and *B. biporus* in the Baja California peninsula. Although the genus has been known to science for nearly 200 years, fewer than 50 specimens had been deposited in the museum collections of the world by 1970. The systematics of the amphisbaenians are fairly well understood (Gans 1969), however, there is little information available on their ecology because their fossorial existence makes them difficult to observe or collect. Thus, with the discovery that *B. biporus* could easily be collected by digging in the ground, this study was started in 1971 with the hope of learning something about the ecology of at least one group of amphisbaenians.

## Field Methods

The following data were recorded for specimens observed in the field: date and time of capture, weather conditions, extent of exposure to sun, depth, presence or absence of burrow, soil type, dampness of soil, presence or absence of leaf litter, associated vegetation type and body, substrate, and air temperatures, which were recorded with a Schultheis Reptile Thermometer. All specimens, whether personally observed in the field or brought in by local collectors, were preserved in 10% formalin on the day of capture. Specimens were killed by injection with Nembutal and the following data were recorded before preservation: weight to the nearest 0.1 gram using Pesola 5-gram, 10-gram, or 30-gram scales; body and tail length to the nearest millimeter; and condition of tail (complete or broken). Determination of sex, reproductive condition, and stomach contents were made in the laboratory.

## Selection of Study Sites

The major criterion used to select a study site was information provided by local residents. Farmers know *Bipes* because they are often plowed up. A few days with the local people were sufficient to determine if samples could easily be obtained. This successful method was used extensively throughout Mexico to determine species distribution limits. Wherever *Bipes* occur they are truly abundant. The only limits to sample size are time and money.

Once a study site had been chosen, it was sampled on each visit; however, care was taken not to excavate the same ground more than once. Samples from each site were obtained several times a year over a period of seven years.

Of the three species of *Bipes*, the best sampled is *B. biporus*. Twenty-five samples were collected in all months except February and November at La Paz, Baja California Sur. The mainland localities, inhabited by *B. canaliculatus* and *B. tridactylus*, were visited less often. The principal study areas for these species were visited 10 times during the months of January, April, July, August, September, and December. Secondary study sites for *B. biporus* (Vizcaíno Desert) and *B. canaliculatus* (Petacalco) were discovered later in the study, and only small samples are available from these sites.

## Description of Study Sites and Collecting Methods

### *Bipes biporus:* La Paz, Baja California Sur, Mexico

The 2-km$^2$ study site is located at the north edge of the city of La Paz. It is bordered on the

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FIGURE 1. *Bipes biporus* study site at La Paz, Baja California Sur, Mexico. Specimens were collected by digging at the base of fence posts and under mesquite thickets.

east by the Peninsular Highway, on the south by Calle Colima, and on the north and west by unnamed dirt roads. The area is subdivided by one-lane dirt roads into sections consisting of family plots, abandoned fields, cultivated fields, pasture for cattle, and mesquite-cholla woodland. Sections are enclosed by wooden-post barbed-wire fences often separated from the road by planted mesquite trees (Fig. 1).

A total of 2645 *B. biporus* were collected at the site between 1972 and 1979. Specimens were obtained with shovels by 5 to 20 local children, who would move through the area like a swarm of locusts digging for *Bipes*. Until 1976, a reward of five pesos was paid for each *Bipes* uncovered. However, towards the end of the study, the reward was raised to 10 pesos because of inflation and the devaluation of the Mexican peso. The children were kept in a controlled group, and each time a *Bipes* was uncovered, digging was stopped until field data could be recorded. On each visit a different section of the study area was collected. If at the end of the trip a larger sample size was needed, children were allowed to bring in specimens without field data.

### *Bipes biporus:* 37.3 km NW (by Mex. Hwy. 1) of San Ignacio, Baja California Sur, Mexico

This study site is located in the Vizcaíno Desert along the Transpeninsular Highway. Specimens were collected within a kilometer of the road. The area consists of a substratum of fine sandy soil covered with natural vegetation. Dominant plants include *Yucca valida*, *Pachycereus pringlei*, *Larrea tridentata*, *Lycium* sp., and *Opuntia* sp. (Fig. 2). A total of 74 *B. biporus* were collected at the site in six visits between 1974 and 1978. Because there are no inhabitants at this locality, all material was collected by me and field parties by digging under and around bushes.

### *Bipes tridactylus:* Tecpan de Galeana, Guerrero, Mexico

This site is located on the south bank of the Río Tecpan at the point where the Mexican Highway 200 bridge crosses the river. The town of Tecpan lies on the coastal plain of Guerrero between the foothills of the Sierra Madre del Sur and the Pacific Ocean. The soil on each side of

FIGURE 2. *Bipes biporus* study site in the Vizcaíno Desert, 37.3 km northwest (by road) of San Ignacio, Baja California Sur, Mexico. Specimens were most frequently obtained by digging in mounds of sand at the base of bushes.

the river is very sandy for a distance of several kilometers. The vegetation along the coastal plain is defined as arid tropical scrub forest (Duellman 1965). This low, deciduous, thorn-scrub forest forms dense thickets in some places and shows a savannalike aspect in others. Much of the natural vegetation around Tecpan has been modified by man. Although scattered shade trees remain, the understory has been cleared for the planting of corn, coconuts, and some bananas.

During 1972 and 1973, a total of 56 *B. tridactylus* were obtained here, all collected by Sr. Mariano Rojas, a resident of Tecpan who lived on the south bank of the river. Prior to this study the species was known only from the holotype.

### *Bipes tridactylus:* 6 km SE (by Mex. Hwy. 200) of Tecpan de Galeana, Guerrero, Mexico

Like the nearby town of Tecpan, this locality is on the coastal plain. The original arid tropical scrub forest has been cut for corn fields, coconuts, and cattle grazing (Fig. 3). Between 1974 and 1978, 268 *B. tridactylus* were collected here. Local families obtained most of the specimens by digging under bushes in open cattle pasture land.

### *Bipes canaliculatus:* Río Balsas at Mexican Highway 95, Guerrero, Mexico

This locality is on the north bank of the Río Balsas across the river from the town of Mezcala. Rocky gorges are interspaced with elevated benches of powder-fine sandy soil where arroyos have cut through the rocky hills. As the arroyos approach the river, alluvial fans from 100 m to nearly 1 km wide have formed. Here dense mesquite–palo verde thickets grow above the high-water mark of the river. Behind these thickets the vegetation in the arroyos and on the surrounding hills consists of sparse arid tropical scrub forest. In the dry season the trees are leafless and ground cover is absent from overgrazing by goats.

Between 1971 and 1978, a total of 937 *B. canaliculatus* were collected at this site. All were obtained by local work crews digging in the arroyos and thickets along the river (Fig. 4). Although some specimens were collected with complete field data, most were brought in by the workers at the end of each day.

FIGURE 3. *Bipes tridactylus* study site 6 km southeast of Tecpan de Galeana, Guerrero, Mexico. Much of the original arid tropical scrub forest has been cleared for cattle grazing. Specimens were collected by digging in the sandy soil under bushes.

*Bipes canaliculatus:* Petacalco, Guerrero, Mexico

This site, 200 m from the Pacific Ocean, is located on the south side of Bahía de Petacalco, an estuary 1 km east of the town of Petacalco. It is on the eastern edge of the alluvial plain of the Río Balsas. The main channel of the river, forming the border between Guerrero and Michoacán, is 13 km west. Sandy soil is interspersed with extensive areas of coarse gravel. The original arid tropical scrub forest has been cleared for the planting of coconuts and mangos. *Bipes* were discovered here in 1977, and 21 were collected.

## SYSTEMATIC METHODS

Standardized systematic methods have been used for the diagnoses and descriptions of the three species of *Bipes*. Unlike other members of the Squamata, scales of amphisbaenians are distributed in annuli along the entire length of the body except for the anterior part of the head. Annuli counts are the most useful taxonomic character in amphisbaenians because the lack of landmarks on the head makes it difficult to compare head scales (Gans and Alexander 1962). Much confusion in early amphisbaenian literature was due to the variety of methods used by different authors to count annuli. Standardized methods of annuli counting are now available (Vanzolini 1951; Gans and Alexander 1962). Methods used to record the data found in Table 1 are described below.

SEX.—Because there is no external sexual dimorphism, sex was determined by examination of the gonads.

DORSAL ANNULI.—Counts were made along the right side of the dorsal surface from the first postoral annulus up to and including the dorsal annulus above the ventral annulus bearing the preanal pores.

VENTRAL ANNULI.—Counts were made along the right side of the ventral surface from the first postoral annulus up to and including the ventral annulus bearing the preanal pores.

LATERAL ANNULI.—The dorsal annuli above

FIGURE 4. *Bipes canaliculatus* study site on the north bank of the Río Balsas, across the river from Mezcala, Guerrero, Mexico. This species is easily obtained by digging in the sandy river bank above the high-water line.

the cloacal region are called lateral annuli (Gans and Alexander 1962). These annuli (2 to 6 on each side in *Bipes*) are located between the dorsal annulus above the preanal pores and the first complete caudal ring posterior to the cloaca. The number of lateral annuli is frequently asymmetric and has been recorded separately for the right and left side.

CAUDAL ANNULI.—Counts were made along the right side of the dorsal surface from the first complete annulus posterior to the cloaca up to and including the last annulus with regular segments. Unlike dorsal and ventral annuli, which differ in number and are separated by a lateral sulcus, caudal annuli form a complete ring around the tail of *Bipes*.

INTERCALATED QUARTER-ANNULI.—Intercalated quarter-annuli were found on nearly every *Bipes* examined. They are most numerous on the ventral surface and counts were made for both the right and left sides. These annuli extend from the right or left lateral sulcus on to the ventral surface, but do not continue to the opposite lateral sulcus.

MIDBODY SEGMENTS.—Counts were made on a dorsal and ventral annulus pair selected at random from the midbody region.

PREANAL PORES.—This count is the sum of the pores on both sides.

NUMBER OF CLAWS.—This number is species specific in *B. biporus* and *B. tridactylus*. However, since an occasional specimen of *B. canaliculatus* may have a different number of claws on each foot, data were recorded separately for each foot.

## SYSTEMATIC ACCOUNT

### Genus **Bipes** Latreille, 1801

*Bipes* LATREILLE, 1801:90.
*Bimanus* OPPEL, 1811:18.
*Chirotes* CUVIER, 1817:57.
*Hemichirotes* DUGÈS *in* COPE, 1894:436.
*Euchirotes* COPE, 1894:436.

TABLE 1. MERISTIC DATA FOR *Bipes biporus*, *B. tridactylus*, AND *B. canaliculatus* (*—caudal annuli counts of specimens with autotomized, healed tails; **—caudal annuli counts of specimens with tails autotomized at capture).

| Specimen No. | Sex | Dorsal Annuli | Ventral Annuli | Lateral Annuli | | Caudal Annuli | Intercalated Quarter-Annuli | | Midbody Segments | | Preanal Pores | No. of Claws | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Rt | Lt | | Rt | Lt | Dorsal | Ventral | | Rt | Lt |
| | | | | | | *Bipes biporus* | | | | | | | |
| LA PAZ | | | | | | | | | | | | | |
| CAS 149856 | f | 257 | 162 | 3 | 4 | 25 | 4 | 3 | 30 | 28 | 2 | 5 | 5 |
| CAS 149857 | m | 256 | 164 | 3 | 2 | 29 | 3 | 5 | 31 | 27 | 2 | 5 | 5 |
| CAS 149858 | f | 259 | 156 | 3 | 3 | 25 | 3 | 3 | 29 | 26 | 2 | 5 | 5 |
| CAS 149859 | m | 257 | 154 | 6 | 6 | 29 | 2 | 1 | 29 | 28 | 2 | 5 | 5 |
| CAS 149860 | f | 248 | 159 | 6 | 5 | 29 | 3 | 4 | 29 | 24 | 2 | 5 | 5 |
| CAS 149861 | f | 252 | 153 | 3 | 3 | 24 | 1 | 1 | 29 | 25 | 2 | 5 | 5 |
| CAS 149862 | f | 252 | 155 | 4 | 3 | 29 | 0 | 3 | 30 | 26 | 2 | 5 | 5 |
| CAS 149863 | f | 250 | 154 | 5 | 5 | 26 | 5 | 5 | 29 | 26 | 2 | 5 | 5 |
| CAS 149864 | f | 254 | 161 | 6 | 5 | 29 | 2 | 4 | 31 | 26 | 2 | 5 | 5 |
| CAS 149865 | f | 258 | 163 | 4 | 4 | 29 | 4 | 5 | 28 | 27 | 2 | 5 | 5 |
| CAS 149866 | f | 251 | 157 | 4 | 4 | 25 | 4 | 3 | 30 | 28 | 2 | 5 | 5 |
| CAS 149867 | m | 247 | 151 | 5 | 4 | 28 | 2 | 5 | 29 | 26 | 2 | 5 | 5 |
| CAS 149868 | m | 259 | 153 | 4 | 4 | 26 | 7 | 5 | 29 | 25 | 2 | 5 | 5 |
| CAS 149869 | f | 247 | 153 | 3 | 3 | 28 | 2 | 2 | 29 | 27 | 2 | 5 | 5 |
| CAS 149870 | m | 253 | 154 | 4 | 5 | 31 | 6 | 3 | 30 | 26 | 2 | 5 | 5 |
| CAS 149871 | f | 256 | 165 | 4 | 4 | 29 | 2 | 3 | 27 | 27 | 2 | 5 | 5 |
| CAS 149872 | m | 251 | 148 | 3 | 3 | 25 | 5 | 5 | 30 | 26 | 2 | 5 | 5 |
| CAS 149873 | f | 255 | 158 | 4 | 6 | 26 | 4 | 2 | 31 | 28 | 2 | 5 | 5 |
| CAS 149874 | f | 261 | 158 | 3 | 4 | 27 | 4 | 7 | 26 | 30 | 2 | 5 | 5 |
| CAS 149875 | m | 255 | 152 | 4 | 5 | 27 | 3 | 5 | 26 | 24 | 2 | 5 | 5 |
| CAS 149876 | f | 257 | 148 | 4 | 5 | 24 | 9 | 4 | 28 | 26 | 2 | 5 | 5 |
| CAS 149877 | m | 256 | 150 | 4 | 5 | 25 | 2 | 5 | 30 | 26 | 2 | 5 | 5 |
| CAS 149878 | f | 259 | 164 | 3 | 4 | 25 | 3 | 3 | 32 | 28 | 2 | 5 | 5 |
| CAS 149879 | f | 255 | 159 | 3 | 5 | 28 | 5 | 4 | 29 | 26 | 2 | 5 | 5 |
| CAS 149880 | f | 250 | 148 | 5 | 6 | 28 | 4 | 3 | 31 | 28 | 2 | 5 | 5 |
| CAS 149881 | m | 254 | 159 | 5 | 6 | 26 | 5 | 7 | 28 | 25 | 2 | 5 | 5 |
| CAS 149882 | f | 261 | 155 | 4 | 5 | 26 | 5 | 3 | 28 | 27 | 2 | 5 | 5 |
| CAS 149883 | f | 252 | 163 | 5 | 5 | 26 | 2 | 5 | 29 | 26 | 2 | 5 | 5 |
| CAS 149884 | f | 252 | 151 | 5 | 5 | 24 | 1 | 6 | 31 | 26 | 2 | 5 | 5 |
| CAS 149885 | f | 250 | 149 | 3 | 3 | 24 | 1 | 5 | 30 | 26 | 2 | 5 | 5 |
| CAS 149886 | f | 259 | 161 | 5 | 5 | 27 | 3 | 5 | 29 | 26 | 2 | 5 | 5 |
| CAS 149887 | f | 254 | 151 | 5 | 5 | 26 | 5 | 7 | 29 | 27 | 2 | 5 | 5 |
| CAS 149888 | m | 259 | 156 | 5 | 5 | 26 | 5 | 5 | 29 | 28 | 2 | 5 | 5 |
| CAS 149889 | f | 254 | 148 | 5 | 4 | 27 | 3 | 4 | 29 | 25 | 2 | 5 | 5 |
| CAS 149890 | f | 254 | 158 | 4 | 4 | 25 | 2 | 5 | 27 | 26 | 2 | 5 | 5 |
| CAS 149891 | f | 257 | 164 | 5 | 5 | 27 | 3 | 5 | 32 | 25 | 2 | 5 | 5 |
| CAS 149892 | m | 256 | 157 | 5 | 5 | 26 | 3 | 4 | 27 | 26 | 2 | 5 | 5 |
| CAS 149893 | m | 257 | 167 | 5 | 5 | 28 | 2 | 6 | 28 | 27 | 2 | 5 | 5 |
| CAS 149894 | m | 251 | 159 | 5 | 5 | 28 | 6 | 6 | 30 | 28 | 2 | 5 | 5 |
| CAS 149895 | m | 252 | 153 | 5 | 4 | 27 | 3 | 3 | 29 | 25 | 2 | 5 | 5 |
| CAS 149896 | juv | 252 | 155 | 5 | 5 | 27 | 2 | 4 | 30 | 27 | 2 | 5 | 5 |
| VIZCAINO | | | | | | | | | | | | | |
| CAS 150065 | f | 243 | 148 | 4 | 4 | 27 | 4 | 1 | 28 | 26 | 2 | 5 | 5 |
| CAS 150066 | m | 249 | 151 | 4 | 5 | 27 | 3 | 4 | 30 | 26 | 2 | 5 | 5 |
| CAS 150067 | f | 248 | 145 | 5 | 5 | 26 | 5 | 5 | 29 | 25 | 2 | 5 | 5 |
| CAS 150068 | m | 245 | 147 | 5 | 5 | 26 | 5 | 0 | 29 | 27 | 2 | 5 | 5 |
| CAS 150069 | f | 246 | 150 | 4 | 3 | 6* | 3 | 4 | 32 | 26 | 2 | 5 | 5 |
| CAS 150527 | m | 249 | 148 | 4 | 5 | 27 | 5 | 6 | 29 | 25 | 2 | 5 | 5 |
| CAS 150070 | f | 248 | 153 | 5 | 4 | 28 | 5 | 4 | 30 | 27 | 2 | 5 | 5 |
| CAS 150064 | m | 245 | 144 | 4 | 5 | 26 | 4 | 6 | 30 | 25 | 2 | 5 | 5 |

TABLE 1. CONTINUED.

| Specimen No. | Sex | Dorsal Annuli | Ventral Annuli | Lateral Annuli | | Caudal Annuli | Intercalated Quarter-Annuli | | Midbody Segments | | Preanal Pores | No. of Claws | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Rt | Lt | | Rt | Lt | Dorsal | Ventral | | Rt | Lt |
| CAS 150062 | juv | 248 | 154 | 5 | 5 | 27 | 2 | 3 | 27 | 25 | 2 | 5 | 5 |
| CAS 150088 | m | 242 | 151 | 5 | 5 | 24 | 4 | 2 | 29 | 27 | 2 | 5 | 5 |
| CAS 150071 | f | 249 | 151 | 5 | 4 | 28 | 3 | 6 | 29 | 27 | 2 | 5 | 5 |
| CAS 150072 | f | 244 | 152 | 5 | 6 | 24 | 4 | 3 | 29 | 27 | 2 | 5 | 5 |
| CAS 150073 | f | 244 | 143 | 4 | 5 | 6* | 5 | 2 | 28 | 26 | 2 | 5 | 5 |
| CAS 150074 | f | 247 | 148 | 4 | 4 | 26 | 3 | 3 | 29 | 27 | 2 | 5 | 5 |
| CAS 150075 | f | 249 | 151 | 3 | 5 | 26 | 2 | 4 | 29 | 25 | 2 | 5 | 5 |
| CAS 150076 | f | 250 | 147 | 5 | 6 | 26 | 3 | 3 | 27 | 26 | 2 | 5 | 5 |
| CAS 150077 | m | 245 | 146 | 4 | 5 | 26 | 7 | 2 | 31 | 28 | 2 | 5 | 5 |
| CAS 150078 | f | 248 | 145 | 4 | 5 | 26 | 2 | 2 | 27 | 26 | 2 | 5 | 5 |
| CAS 150079 | m | 245 | 153 | 5 | 5 | 27 | 5 | 4 | 28 | 26 | 2 | 5 | 5 |
| CAS 150080 | f | 248 | 153 | 4 | 5 | 10* | 3 | 4 | 29 | 28 | 2 | 5 | 5 |
| | | | | | | *Bipes tridactylus* | | | | | | | |
| TECPAN DE GALEANA | | | | | | | | | | | | | |
| CAS 150526 | m | 152 | 129 | 3 | 4 | 46 | 2 | 2 | 33 | 34 | 6 | 3 | 3 |
| CAS 149973 | m | 155 | 130 | 3 | 3 | 47 | 1 | 1 | 32 | 34 | 6 | 3 | 3 |
| CAS 149974 | m | 154 | 131 | 3 | 3 | 44 | 2 | 2 | 32 | 36 | 7 | 3 | 3 |
| CAS 149975 | f | 158 | 131 | 3 | 3 | 44 | 1 | 1 | 34 | 34 | 6 | 3 | 3 |
| CAS 149976 | m | 157 | 132 | 3 | 3 | 44 | 3 | 2 | 33 | 36 | 6 | 3 | 3 |
| CAS 149977 | f | 154 | 131 | 2 | 2 | 9* | 1 | 1 | 32 | 35 | 6 | 3 | 3 |
| CAS 149978 | m | 156 | 130 | 3 | 3 | 46 | 4 | 2 | 35 | 36 | 6 | 3 | 3 |
| CAS 149979 | f | 154 | 130 | 2 | 3 | 43 | 3 | 4 | 32 | 34 | 6 | 3 | 3 |
| CAS 149980 | f | 157 | 131 | 3 | 4 | 9* | 1 | 2 | 32 | 34 | 6 | 3 | 3 |
| CAS 149981 | m | 157 | 132 | 3 | 3 | 9* | 2 | 2 | 31 | 33 | 6 | 3 | 3 |
| CAS 149982 | f | 155 | 132 | 3 | 2 | 9* | 0 | 1 | 32 | 29 | 6 | 3 | 3 |
| CAS 149983 | m | 154 | 128 | 3 | 3 | 26 | 3 | 2 | 31 | 34 | 7 | 3 | 3 |
| CAS 149984 | f | 152 | 123 | 3 | 3 | 42 | 6 | 6 | 31 | 36 | 7 | 3 | 3 |
| CAS 149985 | f | 155 | 131 | 4 | 4 | 45 | 3 | 2 | 35 | 33 | 7 | 3 | 3 |
| CAS 149986 | m | 160 | 135 | 4 | 4 | 48 | 0 | 1 | 35 | 32 | 6 | 3 | 3 |
| CAS 149987 | f | 156 | 132 | 3 | 3 | 45 | 1 | 1 | 32 | 35 | 6 | 3 | 3 |
| CAS 149988 | juv | 159 | 134 | 3 | 3 | 45 | 2 | 2 | 34 | 34 | 6 | 3 | 3 |
| CAS 149989 | m | 159 | 132 | 4 | 4 | 42 | 2 | 2 | 34 | 33 | 6 | 3 | 3 |
| CAS 149990 | m | 156 | 134 | 4 | 4 | 42 | 1 | 2 | 29 | 31 | 6 | 3 | 3 |
| CAS 149991 | juv | 159 | 136 | 4 | 3 | 44 | 0 | 1 | 34 | 35 | 6 | 3 | 3 |
| CAS 149992 | m | 157 | 132 | 2 | 3 | 45 | 2 | 3 | 36 | 37 | 6 | 3 | missing |
| CAS 149993 | m | 157 | 130 | 3 | 3 | 43 | 1 | 1 | 34 | 32 | 6 | 3 | 3 |
| CAS 149994 | f | 158 | 129 | 3 | 3 | 44 | 4 | 2 | 35 | 38 | 6 | 3 | 3 |
| CAS 149995 | f | 153 | 126 | 3 | 3 | 44 | 1 | 1 | 35 | 33 | 6 | 3 | 3 |
| CAS 149996 | m | 159 | 136 | 3 | 3 | 8* | 0 | 2 | 36 | 35 | 6 | 3 | 3 |
| CAS 149997 | f | 161 | 137 | 3 | 3 | 48 | 0 | 0 | 39 | 34 | 6 | 3 | 3 |
| CAS 149999 | f | 157 | 133 | 3 | 3 | 9** | 2 | 3 | 35 | 38 | 6 | 3 | 3 |
| CAS 150000 | f | 161 | 138 | 3 | 3 | 8** | 3 | 4 | 34 | 34 | 6 | 3 | 3 |
| CAS 150001 | f | 160 | 135 | 2 | 3 | 45 | 1 | 1 | 34 | 35 | 6 | 3 | 3 |
| CAS 150002 | m | 157 | 133 | 3 | 3 | 46 | 3 | 2 | 37 | 32 | 7 | 3 | 3 |
| CAS 150003 | m | 155 | 124 | 2 | 2 | 47 | 4 | 2 | 30 | 32 | 7 | 3 | 3 |
| CAS 150004 | m | 156 | 132 | 3 | 3 | 46 | 1 | 1 | 35 | 36 | 6 | 3 | 3 |
| CAS 150005 | f | 158 | 130 | 3 | 4 | 8* | 2 | 1 | 33 | 35 | 6 | 3 | 3 |
| CAS 150006 | f | 155 | 129 | 2 | 2 | 9** | 1 | 3 | 34 | 34 | 6 | 3 | 3 |
| CAS 150007 | f | 153 | 129 | 3 | 3 | 8** | 2 | 1 | 36 | 32 | 6 | 3 | 3 |
| CAS 150008 | f | 162 | 135 | 3 | 2 | 8** | 3 | 1 | 35 | 35 | 6 | 3 | 3 |
| CAS 150009 | m | 158 | 129 | 3 | 3 | 8* | 5 | 6 | 35 | 31 | 6 | 3 | 3 |
| CAS 150010 | f | 154 | 131 | 3 | 4 | 44 | 1 | 0 | 30 | 30 | 6 | 3 | 3 |
| CAS 150011 | m | 156 | 130 | 4 | 4 | 8** | 2 | 2 | 32 | 34 | 6 | 3 | 3 |

TABLE 1. CONTINUED.

| Specimen No. | Sex | Dorsal Annuli | Ventral Annuli | Lateral Annuli | | Caudal Annuli | Intercalated Quarter-Annuli | | Midbody Segments | | Pre-anal Pores | No. of Claws | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Rt | Lt | | Rt | Lt | Dorsal | Ventral | | Rt | Lt |
| CAS 150012 | f | 159 | 132 | 3 | 3 | 46 | 2 | 2 | 36 | 33 | 6 | 3 | 3 |
| CAS 150013 | m | 152 | 128 | 3 | 3 | 46 | 4 | 6 | 33 | 37 | 6 | 3 | 3 |
| CAS 150014 | juv | 161 | 138 | 2 | 2 | 47 | 2 | 0 | 37 | 35 | 6 | 3 | 3 |
| CAS 150015 | m | 163 | 135 | 4 | 4 | 48 | 3 | 1 | 34 | 32 | 6 | 3 | 3 |
| CAS 150017 | f | 157 | 131 | 4 | 4 | 45 | 3 | 2 | 37 | 37 | 6 | 3 | 3 |
| CAS 150018 | f | 159 | 132 | 3 | 3 | 46 | 1 | 1 | 31 | 35 | 6 | 3 | 3 |
| CAS 150019 | f | 157 | 128 | 2 | 3 | 44 | 2 | 2 | 30 | 33 | 6 | 3 | 3 |
| CAS 150020 | f | 153 | 130 | 4 | 4 | 45 | 1 | 1 | 32 | 34 | 6 | 3 | 3 |
| CAS 150021 | f | 158 | 132 | 3 | 3 | 46 | 0 | 0 | 34 | 34 | 6 | 3 | 3 |
| CAS 150022 | f | 156 | 131 | 2 | 3 | 48 | 1 | 1 | 32 | 37 | 6 | 3 | 3 |
| CAS 150023 | m | 156 | 133 | 3 | 3 | 46 | 1 | 1 | 32 | 34 | 8 | 3 | 3 |
| CAS 150024 | f | 155 | 128 | 3 | 2 | 44 | 3 | 1 | 34 | 36 | 8 | 3 | 3 |
| CAS 150025 | f | 156 | 133 | 3 | 3 | 45 | 0 | 3 | 35 | 34 | 6 | 3 | 3 |
| CAS 150026 | m | 154 | 131 | 2 | 3 | 44 | 1 | 2 | 35 | 34 | 7 | 3 | 3 |
| CAS 150027 | juv | 157 | 130 | 2 | 2 | 8** | 1 | 0 | 34 | 32 | 6 | 3 | 3 |
| CAS 150028 | m | 154 | 126 | 3 | 2 | 43 | 2 | 1 | 34 | 36 | 6 | 3 | 3 |
| CAS 150029 | m | 158 | 132 | 3 | 3 | 9* | 0 | 0 | 35 | 32 | 6 | 3 | 3 |
| CAS 150030 | juv | 163 | 140 | 2 | 2 | 47 | 1 | 1 | 32 | 32 | 6 | 3 | 3 |
| CAS 150031 | juv | 153 | 129 | 2 | 3 | 44 | 1 | 1 | 32 | 32 | 6 | 3 | 3 |
| CAS 150032 | juv | 157 | 135 | 4 | 3 | 44 | 2 | 1 | 35 | 36 | 6 | 3 | 3 |
| CAS 150033 | juv | 153 | 126 | 3 | 4 | 43 | 2 | 0 | 36 | 35 | 6 | 3 | 3 |
| CAS 150034 | juv | 153 | 128 | 3 | 3 | 45 | 1 | 1 | 35 | 33 | 6 | 3 | 3 |
| CAS 150035 | f | 158 | 128 | 3 | 3 | 46 | 2 | 2 | 33 | 35 | 8 | 3 | 3 |
| CAS 150036 | juv | 157 | 137 | 3 | 3 | 45 | 2 | 3 | 35 | 33 | 6 | 3 | 3 |
| CAS 150037 | juv | 158 | 131 | 3 | 4 | 47 | 1 | 0 | 34 | 36 | 7 | 3 | 3 |
| CAS 150038 | 157 | 135 | 3 | 4 | 42 | 0 | 1 | 33 | 34 | 6 | 3 | 3 | |
| CAS 150039 | f | 154 | 128 | 3 | 3 | 43 | 1 | 1 | 33 | 32 | 6 | 3 | 3 |
| CAS 150040 | f | 157 | 130 | 3 | 3 | 44 | 0 | 1 | 36 | 33 | 6 | 3 | 3 |
| CAS 150041 | f | 155 | 130 | 3 | 3 | 9* | 1 | 3 | 34 | 31 | 6 | 3 | 3 |
| CAS 150042 | m | 157 | 131 | 3 | 2 | 46 | 2 | 0 | 32 | 34 | 6 | 3 | 3 |
| CAS 150043 | f | 156 | 134 | 3 | 3 | 46 | 1 | 2 | 33 | 36 | 6 | 3 | 3 |
| CAS 150044 | juv | 155 | 132 | 3 | 3 | 8** | 0 | 1 | 33 | 31 | 6 | 3 | 3 |
| CAS 150045 | m | 158 | 134 | 3 | 3 | 9** | 0 | 1 | 35 | 35 | 8 | 3 | 3 |
| | | | | | | *Bipes canaliculatus* | | | | | | | |
| MEZCALA | | | | | | | | | | | | | |
| CAS 144774 | m | 203 | 167 | 3 | 2 | 32 | 1 | 2 | 31 | 32 | 6 | 4 | 4 |
| CAS 144775 | m | 213 | 173 | 3 | 3 | 34 | 1 | 2 | 30 | 32 | 6 | 4 | 4 |
| CAS 144776 | m | 211 | 171 | 3 | 3 | 34 | 2 | 3 | 30 | 30 | 6 | 4 | 4 |
| CAS 144777 | f | 207 | 166 | 4 | 3 | 32 | 1 | 4 | 33 | 32 | 6 | 4 | 4 |
| CAS 144778 | f | 205 | 164 | 3 | 3 | 31 | 2 | 6 | 31 | 33 | 6 | 4 | 4 |
| CAS 144779 | m | 207 | 161 | 4 | 4 | 29 | 0 | 1 | 31 | 32 | 6 | 4 | 4 |
| CAS 144780 | f | 211 | 168 | 4 | 3 | 7* | 5 | 5 | 29 | 30 | 6 | 4 | 4 |
| CAS 144781 | m | 209 | 168 | 3 | 3 | 33 | 1 | 4 | 31 | 32 | 7 | 4 | 4 |
| CAS 144782 | m | 208 | 159 | 3 | 3 | 35 | 2 | 2 | 31 | 30 | 6 | 4 | 4 |
| CAS 144783 | f | 215 | 175 | 3 | 3 | 7* | 3 | 3 | 33 | 32 | 6 | 4 | 4 |
| CAS 144784 | f | 213 | 167 | 5 | 4 | 34 | 0 | 4 | 28 | 29 | 6 | 4 | 4 |
| CAS 144785 | m | 210 | 168 | 2 | 2 | 37 | 0 | 4 | 29 | 31 | 6 | 4 | 4 |
| CAS 144786 | f | 202 | 155 | 4 | 4 | 32 | 4 | 7 | 30 | 32 | 6 | 4 | 4 |
| CAS 144787 | m | 206 | 160 | 4 | 4 | 33 | 3 | 2 | 30 | 30 | 6 | 4 | 4 |
| CAS 144788 | m | 206 | 165 | 3 | 3 | 35 | 2 | 0 | 32 | 32 | 6 | 4 | 4 |
| CAS 144789 | m | 207 | 162 | 3 | 4 | 32 | 3 | 3 | 30 | 31 | 6 | 4 | 4 |
| CAS 144790 | f | 218 | 173 | 3 | 3 | 38 | 5 | 2 | 31 | 32 | 6 | 4 | 4 |
| CAS 144791 | f | 220 | 176 | 4 | 3 | 37 | 4 | 3 | 29 | 34 | 6 | 4 | 4 |

TABLE 1. CONTINUED.

| Specimen No. | Sex | Dorsal Annuli | Ventral Annuli | Lateral Annuli |  | Caudal Annuli | Intercalated Quarter-Annuli |  | Midbody Segments |  | Preanal Pores | No. of Claws |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  | Rt | Lt |  | Rt | Lt | Dorsal | Ventral |  | Rt | Lt |
| CAS 144792 | m | 214 | 172 | 4 | 4 | 32 | 2 | 1 | 29 | 30 | 6 | 4 | 4 |
| CAS 144793 | m | 207 | 170 | 3 | 4 | 33 | 3 | 6 | 32 | 33 | 6 | 4 | 4 |
| CAS 144794 | f | 210 | 161 | 2 | 3 | 35 | 3 | 1 | 30 | 31 | 6 | 4 | 4 |
| CAS 144795 | f | 203 | 160 | 4 | 5 | 7* | 3 | 1 | 30 | 31 | 6 | 4 | 4 |
| CAS 144796 | m | 211 | 169 | 4 | 3 | 30 | 2 | 3 | 29 | 31 | 6 | 4 | 4 |
| CAS 144797 | m | 210 | 167 | 4 | 3 | 33 | 2 | 2 | 28 | 31 | 6 | 4 | 4 |
| CAS 144798 | m | 204 | 154 | 4 | 4 | 26 | 4 | 1 | 29 | 30 | 6 | 4 | 4 |
| CAS 144800 | f | 206 | 163 | 4 | 4 | 35 | 1 | 3 | 33 | 35 | 7 | 4 | 4 |
| CAS 144801 | m | 208 | 164 | 4 | 4 | 30 | 1 | 3 | 30 | 28 | 6 | 4 | 4 |
| CAS 144802 | m | 207 | 166 | 3 | 2 | 8* | 1 | 3 | 33 | 32 | 6 | 4 | 4 |
| CAS 144803 | f | 210 | 170 | 4 | 5 | 33 | 0 | 3 | 28 | 30 | 6 | 4 | 4 |
| CAS 144804 | m | 207 | 165 | 4 | 4 | 8* | 1 | 1 | 28 | 28 | 6 | 4 | 4 |
| CAS 144805 | m | 208 | 161 | 4 | 3 | 33 | 1 | 6 | 28 | 30 | 6 | 4 | 4 |
| CAS 144806 | f | 206 | 160 | 3 | 3 | 29 | 0 | 3 | 29 | 29 | 6 | 4 | 4 |
| CAS 144807 | m | 205 | 162 | 4 | 5 | 34 | 2 | 1 | 31 | 31 | 6 | 4 | 4 |
| CAS 144808 | m | 204 | 165 | 3 | 3 | 34 | 0 | 1 | 29 | 32 | 6 | 5 | 5 |
| CAS 144809 | f | 205 | 170 | 3 | 4 | 30 | 1 | 4 | 32 | 30 | 6 | 4 | 4 |
| CAS 144810 | m | 220 | 171 | 4 | 5 | 35 | 1 | 5 | 29 | 31 | 6 | 4 | 4 |
| CAS 144811 | m | 210 | 167 | 5 | 5 | 33 | 3 | 4 | 30 | 31 | 6 | 4 | 4 |
| CAS 144812 | m | 210 | 165 | 6 | 5 | 28 | 0 | 2 | 31 | 33 | 6 | 4 | 4 |
| CAS 144813 | f | 205 | 161 | 3 | 4 | 32 | 4 | 4 | 27 | 29 | 6 | 4 | 4 |
| CAS 144814 | m | 208 | 166 | 4 | 4 | 32 | 2 | 5 | 30 | 31 | 6 | 4 | 4 |
| CAS 144815 | f | 208 | 160 | 5 | 4 | 37 | 2 | 4 | 31 | 31 | 6 | 4 | 4 |
| CAS 144816 | juv | 205 | 158 | 3 | 3 | 35 | 2 | 2 | 28 | 31 | 6 | 5 | 4 |
| CAS 144817 | juv | 205 | 159 | 4 | 4 | 26 | 2 | 2 | 33 | 31 | 6 | 4 | 4 |
| CAS 144818 | juv | 203 | 166 | 5 | 4 | 34 | 0 | 1 | 29 | 30 | 6 | 4 | 4 |
| CAS 144819 | juv | 208 | 162 | 3 | 3 | 28 | 2 | 3 | 30 | 31 | 6 | 4 | 4 |
| TCWC 12593 | ? | 212 | 167 | 4 | 3 | 35 | 2 | 2 | 30 | 28 | 6 | 4 | 4 |
| FMNH 105037 | ? | 209 | 160 | 3 | 4 | 31 | 3 | 1 | 31 | 31 | 6 | 4 | 4 |
| FMNH 105038 | ? | 210 | 163 | 3 | 3 | 34 | 2 | 3 | 28 | 27 | 6 | 5 | 4 |
| FMNH 105039 | ? | 218 | 178 | 4 | 4 | 35 | 4 | 8 | 31 | 31 | 6 | 4 | 4 |
| FMNH 105040 | ? | 208 | 167 | 4 | 4 | 6* | 1 | 1 | 31 | 32 | 6 | 4 | 4 |
| FMNH 105041 | ? | 208 | 165 | 4 | 3 | 34 | 2 | 6 | 31 | 31 | 6 | 4 | 4 |
| FMNH 105042 | ? | 214 | 169 | 2 | 3 | 7* | 4 | 4 | 31 | 32 | 6 | 4 | 4 |
| FMNH 105043 | ? | 204 | 159 | 5 | 5 | 33 | 2 | 3 | 31 | 34 | 6 | 4 | 4 |
| FMNH 105044 | ? | 211 | 172 | 5 | 5 | 8* | 0 | 2 | 31 | 31 | 6 | 4 | 4 |
| FMNH 105045 | ? | 211 | 166 | 4 | 4 | 33 | 1 | 1 | 30 | 30 | 6 | 5 | 4 |
| PETACALCO |  |  |  |  |  |  |  |  |  |  |  |  |  |
| CAS 150048 | f | 204 | 164 | 3 | 3 | 7* | 2 | 2 | 31 | 32 | 6 | 4 | 4 |
| CAS 150528 | m | 208 | 170 | 3 | 3 | 32 | 2 | 2 | 31 | 39 | 6 | 5 | 5 |
| CAS 150049 | m | 217 | 180 | 4 | 3 | 34 | 0 | 3 | 29 | 32 | 6 | 4 | 4 |
| CAS 150050 | m | 218 | 179 | 4 | 4 | 35 | 1 | 5 | 34 | 34 | 6 | 5 | 5 |
| CAS 150051 | f | 213 | 175 | 3 | 3 | 35 | 1 | 4 | 32 | 33 | 6 | 5 | 5 |
| CAS 150052 | juv | 219 | 179 | 3 | 4 | 32 | 5 | 6 | 30 | 35 | 6 | 5 | 5 |
| CAS 150139 | juv | 225 | 179 | 4 | 4 | 37 | 1 | 3 | 28 | 28 | 6 | 5 | 5 |
| CAS 150040 | juv | 215 | 182 | 4 | 4 | 34 | 1 | 4 | 31 | 32 | 6 | 4 | 4 |
| CAS 150041 | m | 210 | 167 | 4 | 4 | 32 | 1 | 3 | 29 | 31 | 6 | 4 | 4 |
| CAS 150042 | m | 213 | 186 | 4 | 3 | 34 | 3 | 5 | 31 | 36 | 6 | 5 | 5 |
| CAS 150043 | m | 205 | 168 | 2 | 2 | 33 | 4 | 4 | 31 | 34 | 6 | 4 | 4 |
| CAS 150053 | f | 231 | 185 | 4 | 4 | 35 | 1 | 4 | 30 | 35 | 6 | 5 | 5 |
| CAS 150054 | f | 209 | 168 | 4 | 4 | 7* | 2 | 4 | 31 | 31 | 6 | 4 | 4 |
| CAS 150055 | f | 211 | 172 | 4 | 3 | 35 | 2 | 3 | 27 | 33 | 6 | 5 | 5 |
| CAS 150056 | f | 210 | 175 | 3 | 3 | 32 | 1 | 4 | 32 | 33 | 7 | 4 | 4 |
| CAS 150057 | f | 205 | 176 | 5 | 5 | 32 | 3 | 4 | 27 | 30 | 6 | 5 | 5 |

TABLE 1. CONTINUED.

| Specimen No. | Sex | Dorsal Annuli | Ventral Annuli | Lateral Annuli | | Caudal Annuli | Intercalated Quarter-Annuli | | Midbody Segments | | Preanal Pores | No. of Claws | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Rt | Lt | | Rt | Lt | Dorsal | Ventral | | Rt | Lt |
| CAS 150058 | f | 211 | 175 | 3 | 4 | 35 | 2 | 1 | 30 | 32 | 6 | 4 | 4 |
| CAS 150059 | f | 208 | 170 | 3 | 2 | 36 | 2 | 4 | 31 | 34 | 6 | 5 | 5 |
| CAS 150060 | m | 222 | 177 | 3 | 3 | 34 | 1 | 2 | 29 | 31 | 6 | 4 | 4 |
| CAS 150061 | m | 219 | 182 | 3 | 4 | 34 | 2 | 1 | 29 | 30 | 6 | 5 | 5 |

## Key to Species of *Bipes*

1a. Preanal pores at least six ........ 2
1b. Preanal pores two ........ *biporus*

2a. Three claws on each limb ........ *tridactylus*
2b. Four, rarely five claws on each limb ........ *canaliculatus*

### **Bipes biporus** (Cope, 1894)

*Euchirotes biporus* COPE, 1894:436. [Type-locality: "Cape San Lucas, Lower California."]
*Bipes biporus:* STEJNEGER AND BARBOUR 1917:72.

DIAGNOSIS.—A form of *Bipes* with five well-developed, claw-bearing digits on each limb; phalangeal formula 3-3-3-3-3. Dorsal annuli 242–261; lateral annuli 2–6; caudal annuli on nonautotomized tails 24–31. Dorsal segments 27–32, ventral segments 24–30 per midbody annulus. Tail 9.5–10.5 percent body length.

DESCRIPTION.—Meristic data for 62 specimens summarized in Table 1. Maximum body length 240 mm. Average adult body length 190–210 mm. No external sexual dimorphism. Dorsal and ventral color of both body and tail white in specimens longer than about 150 mm. Smaller specimens pale pink. Two dorsal annuli for each vertebra. Number of ventral annuli considerably less than number of dorsal annuli; difference not proportional, ranging from 89 to 109 in the 62 specimens examined. Intercalated quarter-annuli on both dorsal and ventral surfaces present, ranging from 2 to 13 on ventral surface. Tail autotomy occurs between 6th and 10th caudal annulus. Two preanal pores.

GEOGRAPHIC VARIATION.—The mean numbers of dorsal and ventral annuli are higher in specimens from La Paz than in specimens from the Vizcaíno Desert (Fig. 5).

DISCUSSION.—The taxonomic history of this species was discussed in detail by Smith and Smith (1977). When Cope (1894) described the species, he erected the new genus *Euchirotes* for it, based on its having five digits, all clawed. He diagnosed *Bipes* as having five digits, one smaller than the others and clawless, and *Hemichirotes* as having three digits, all clawed. The name *Euchirotes* was rejected by Stejneger and Barbour (1917), Schmidt (1922), and all other workers thereafter. As Smith and Smith (1977) pointed out, Gans (1967) provided an authoritative fixation for the name *Bipes biporus*.

Although specimens from the northern part of the range (Vizcaíno Desert) have significantly fewer dorsal and ventral annuli than specimens from the southern part of the range (La Paz), the description of subspecies based on these characters alone is not justified. Environmental factors can affect vertebral number which in turn affects annuli counts. Body annuli in the South American *Amphisbaena alba* decrease from north to south (Vanzolini 1968), explained in part by the lower absolute minimum temperatures and greater average yearly temperature ranges at localities where *A. alba* had lower annuli counts. Vertebral numbers in the banded watersnake, *Natrix fasciata,* increase at both high and low temperatures with minimum counts occurring at intermediate temperatures (Osgood 1968). Fox (1948) suggested that intraspecific variation in scale characters in snakes might be ontogenetic. He found a decrease in scale counts in young snakes born to gravid females that were maintained in the lab at low temperatures during intrauterine development of the young. Klauber (1941) found variable scale counts in 13 species of snakes in desert and coastal parts of San Diego County. He considered temperature and humidity the major environmental factors causing this difference.

Since no meristic characters other than number of dorsal and ventral annuli separate northern and southern populations of *B. biporus*, environmental factors may well account for this difference. The mean annual temperature in the Vizcaíno Desert is from 2 to 5 C lower than the mean annual temperature at La Paz (Hastings and Turner 1965). The specimen of *B. biporus* with the lowest dorsal annuli count (242) is from the coldest part of the Vizcaíno Desert where *Bipes* have been found. This specimen (CAS 150088, Table 1) is from Ejido Jesus María at the northwest edge of the Vizcaíno Desert near the Pacific Ocean. Unfortunately, large series of *B. biporus* are not available from localities between La Paz and the Vizcaíno Desert. Since the distribution of the species is probably continuous, one would predict a gradual increase in annuli number from north to south if this character is environmentally dependent.

**Bipes tridactylus** (Dugès, 1894)

*Hemichirotes tridactylus* Dugès *in* Cope, 1894:437. Dugès 1894:411. [Type-locality: "Tecpan de Galeana, Guerrero," Mexico.]
*Chirotes tridactylus:* Dugès 1896:480.
*Bipes tridactylus:* Smith and Necker 1944:180.

Diagnosis.—A form of *Bipes* with three well-developed, claw-bearing digits on each limb. First digit not visible; fifth digit reduced, without a claw; phalangeal formula 0-3-3-3-2. Dorsal annuli 152–163; lateral annuli 2–4; caudal annuli on nonautotomized tails 42–48; dorsal segments 29–37; ventral segments 29–38 per midbody annulus. Tail 19–30 percent of body length.

Description.—Meristic data for 72 specimens summarized in Table 1. Species smallest in genus, reaching a maximum body length of 160 mm. Average adult body length 120–150 mm. No external sexual dimorphism. Dorsal color of both body and tail brown. Ventral color of both body and tail cream. Dorsal color extends across lateral suture and on to ventral annuli, gradually lightening along sides to produce counter-shaded effect. Two dorsal annuli for each vertebra. Ventral annuli fewer than dorsal annuli; reduction not proportional, ranging from 20 to 31 in the 72 specimens examined. Dorsal and ventral intercalated half-annuli present, most frequently on ventral surface, where 0–12 occur (Table 1). Tail autotomy occurs between 8th and 10th caudal annuli. Usually 6 preanal pores; sometimes 7 or 8 (Table 1).

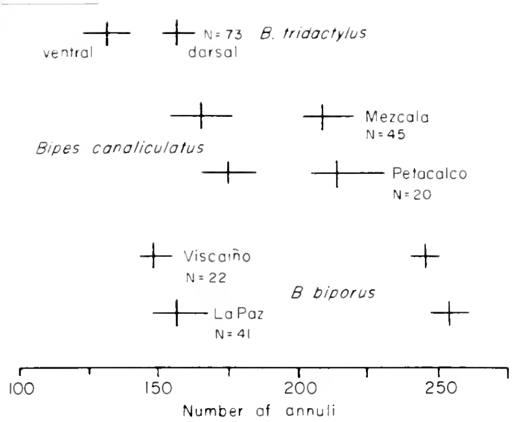

Figure 5. Dorsal and ventral annuli counts in *Bipes*. Horizontal line = range; vertical line = mean. Sample size is given for each locality.

Discussion.—Smith and Smith (1977) discussed the taxonomic history of this species. When Dugès (1894) described this species, he erected the genus *Hemichirotes* based on the character of three clawed digits. Smith and Necker (1944) included this species in the genus *Bipes*. They considered the three species to be about equally distinct, and since *B. canaliculatus* and *B. biporus* were considered congeneric at the time, they felt that it was preferable to adhere to that precedent. Gans (1967) provided an authoritative fixation for the name *Bipes tridactylus*.

Dugès's description was based on a single mutilated specimen, and until the present study, no additional specimens were known. His specimen had only eight caudal annuli, and Dugès used the character of "tail but little longer than head" in his diagnosis. It is now known that tail autotomy occurs frequently in this species, and an autotomized but healed tail looks "normal." It is not surprising that Dugès used the apparent "short tail" in his diagnosis. In fact, *B. tridactylus* has a longer tail than the other species of *Bipes*.

**Bipes canaliculatus** (Bonnaterre, 1789)

*Bipes canaliculatus* Bonnaterre, 1789:68. [Type-locality: "Mexico"; restricted to "Mexcala, Guerrero," Mexico

(Smith and Taylor 1950). Holotype: name based on "le canéle" of Lacépède 1788:613.]

*Lacerta lumbricoides* SHAW, 1795:212. [Type-locality: "Mexico." Restricted to "Mexcala, Guerrero," Mexico (Smith and Taylor 1950).]

*Lacerta mexicana* DONNDORFF, 1798:135. [New name for "le cannelé." Type-locality: "Mexico" by implication; restricted to "Mexcala, Guerrero," Mexico (Smith and Taylor 1950).]

*Lacerta sulcata* SUCKOW, 1798:147. [New name for "le cannelé." Type-locality: restricted to "Mexcala, Guerrero," Mexico (Smith and Taylor 1950).]

*Chamaesaura propus* SCHNEIDER, 1801:211. [New name for "le cannelé" and *Lacerta lumbricoides* Shaw. Type-locality: restricted to "Mexcala, Guerrero," Mexico (Smith and Taylor 1950).]

*Bipes caniculatus* [sic] *multiannulatus* ALVAREZ, 1966:147–152. [Type-locality: "Pizandaran, 14 kilómetros al norte de El Infiernille Michoacán," Mexico.]

*Bipes alvarezi* SMITH AND SMITH, 1977:39–40. [Type-locality: "Mexcala, Guerrero," Mexico.]

DIAGNOSIS.—A form of *Bipes* with four well-developed, claw-bearing digits on each limb; fifth digit reduced, usually without a claw. Dorsal annuli 202–231; lateral annuli 2–6; caudal annuli 26–38 on nonautotomized tails. Dorsal segments 27–34, ventral segments 28–39 per midbody annulus. Tail 14–16 percent body length.

DESCRIPTION.—Meristic data for 75 specimens summarized in Table 1. Maximum body length 240 mm; average adult body length 190–210 mm. No sexual dimorphism. Dorsal color brown, ventral color cream; color change abrupt, occurring at suture between dorsal and ventral annuli. Color of tail same as that of body, without abrupt change. Two dorsal annuli for each vertebra. Ventral annuli always fewer than dorsal annuli; difference not proportional, ranging from 27 to 50 in the 75 specimens examined. Intercalated quarter-annuli present on dorsal and ventral surfaces; found most frequently on ventral surface; range from 1 to 12 per specimen; usually more on the left side of ventral surface than on right side. Tail autotomy occurs at 7th caudal annulus; occasionally at the 6th or 8th. Usually six preanal pores; seven in 3 of 70 specimens.

GEOGRAPHIC VARIATION.—The mean numbers of dorsal annuli, ventral annuli, and caudal annuli are higher at Petacalco than at Mezcala (Fig. 5). The presence of a claw on the fifth digit is common at Petacalco and rare at Mezcala (Table 1). A claw on the fifth digit is present in 12 of 20 specimens from Petacalco, but only 1 of 45 specimens from Mezcala has a claw on each fifth digit and 3 specimens have a claw on the right fifth digit only.

DISCUSSION.—*Bipes canaliculatus* is the only species in need of taxonomic revision. First described by Bonnaterre (1789), an additional four names and descriptions appeared between 1795 and 1801 (see synonomy). Gans (1967) has suggested that all five descriptions are based on the same specimen; therefore, all are junior objective synonyms of *B. canaliculatus*. Smith and Taylor (1950) restricted the original type-locality "Mexico" to Mezcala, Guerrero, because (1) all known specimens with precise locality data had been collected there, and (2) as Mezcala is the Río Balsas crossing point of the Mexico City–Acapulco highway, the 18th century trade route between these two cities probably crossed the river at or near the same point.

Alvarez (1966) described *B. canaliculatus multiannulatus* from the Tepalcatepec valley of Michoacán and diagnosed it as follows: 6 preanal pores; 5 fingers on each hand; 148–181 ($\bar{x}$ = 169.4) ventral annuli; 215–275 ($\bar{x}$ = 246.1) dorsal annuli. Alvarez compared his series of 60 specimens from Michoacán with a series of 12 *B. canaliculatus* from Mezcala reported on by Smith (1949). Alvarez did not examine Smith's specimens, so he was not able to standardize his method of counting annuli with that of Smith. Even so, of the four diagnostic characters for *B. canaliculatus multiannulatus*, only the dorsal annuli count of 215–275 distinguished this subspecies from Smith's Mezcala sample, which had a reported 194–201.

Only the dorsal annuli count would seem to separate these two forms. Although Smith (1949) did not state how he counted dorsal annuli, Alvarez counted from behind the frontals to the last annulus on the tail. The inclusion of the dorsal annuli on the tail with the dorsal annuli on the body has led to confusion in the literature during the last hundred years, and to the description of an invalid species of *Bipes*. Smith and Smith (1977) described *Bipes alvarezi* from Mezcala. The holotype and paratypes included the series of *B. canaliculatus* Smith reported on in 1949. The main diagnostic character of this new species was a low dorsal annuli count (194–201) compared to a high dorsal count (215–275) for *B. canaliculatus*. In order to justify the existence of a second species in the Balsas drainage, Smith and Smith redesignated the type-locality of *B. canaliculatus* as the mouth of the Río Balsas, Guerrero-Michoacán, and reported the sympatric occurrence of *B. alvarezi* and *B. canaliculatus* at Mezcala. This was based on a single specimen of *Bipes* reported by Davis and Dixon (1961) with 252 dorsal annuli, a count well above those reported by Smith (1949) from Mezcala and within the range of specimens from Michoacán. In their review of 19th century literature on *B. canaliculatus*, Smith and Smith (1977) found that all reported specimens of *B. canaliculatus* had dorsal annuli counts higher than 201 (the highest Smith observed at Mezcala), and they reasoned that the Mezcala material could not be *B. canaliculatus* but rather represented an undescribed species.

Duméril and Bibron (1839) reported 260 dorsal annuli in the specimen of *Chirotes canaliculatus* they examined. Strauch (1883) reported 209 and 214 dorsal annuli for the two specimens he had; and Boulenger (1885) 220 and 224 for two specimens in the British Museum. Smith and Smith (1977) totaled the dorsal and caudal annuli counts of these authors and arrived at a range of 230–300. Thus, they felt that the material from Mezcala, with a maximum dorsal annuli count of 201, represented a new species, which they described as *Bipes alvarezi*.

Smith and Smith (1977) also stated that digital reduction in Mezcala specimens (*B. alvarezi*) differed from that in animals from Michoacán (*B. canaliculatus*). In the Mezcala series the first digit was reduced; in the Michoacán series the fourth and fifth digits were reduced.

I examined 45 specimens of supposed *B. alvarezi* from Mezcala, 20 specimens of supposed *B. canaliculatus* from the mouth of the Río Balsas at Petacalco (Table 1), the holotype (FMNH 105039) and 8 paratypes (FMNH 105037–38; 105040–45) of *B. alvarezi*, and the specimen of *B. canaliculatus* with high dorsal annuli counts collected by Davis and Dixon (TCWC 12593).

Using Vanzolini's (1951) methods the range of dorsal annuli counts for the Petacalco sample is 204–231 ($\bar{x}$ = 213.6 ± 7.1 SD); for the Mezcala sample 202–220 ($\bar{x}$ = 208.4 ± 4.2 SD); for the holotype of *B. alvarezi* 218; for the type-series of *B. alvarezi* 204–218 ($\bar{x}$ = 210.3 ± 3.7 SD). The Davis and Dixon specimen has 212 dorsal annuli (Table 1). From these data it is evident that the character supposedly separating *B. alvarezi* from *B. canaliculatus* is illusory. Smith and Smith's low dorsal annuli counts resulted from their use of a counting method other than that of Vanzolini (1951). The report of 252 "dorsal annuli" by Davis and Dixon (1961) includes all annuli to the tip of the tail (Table 1). The range of 215–275 for *B. canaliculatus multiannulatus* is stated to include all annuli from the parietals to the tip of the tail. This large range of 60 annuli includes both specimens with complete tails and those that have lost their tails. Specimens with complete tails have between 26 and 38 caudal annuli, while those with lost tails have only 7 or 8 caudal annuli. The lowest dorsal annuli count found at Mezcala (202) is only two less than the lowest found at Petacalco (Fig. 5). Although Smith and Smith stated that in their Mezcala series the first digit was reduced, in fact, it is the fifth digit that is reduced in all specimens I have examined from both Mezcala and Petacalco. Further, the first four digits always bear well-developed claws. In the Mezcala specimens the tiny fifth digit is usually clawless. Of the 45 specimens examined from Mezcala, 1 has a small claw on the fifth digit of each foot and 3 have small claws on the fifth digit of the right foot. Twelve of the 20 Petacalco specimens have a claw on the tiny fifth digit.

*Bipes alvarezi* must be synonymized with *B. canaliculatus* inasmuch as there are no features separating specimens from the lower Río Balsas (Petacalco) and the upper Río Balsas (Mezcala). When Alvarez (1966) described *B. canaliculatus multiannulatus*, he was not aware that Smith (1949) had counted annuli by a different method. Clearly, he did not examine any specimens from Mezcala. However, his multi-annulated subspecies does have a significantly higher number of both dorsal and ventral annuli than the Mezcala sample, although the ranges nearly overlap (Fig. 5). This difference is similar to that found in northern and southern populations of *Bipes biporus* in which subspecies have not been recognized. Until material from intermediate localities is available, it seems best not to recognize subspecies in *B. canaliculatus*.

## DISTRIBUTION

The three species of *Bipes* have allopatric distributions (Fig. 6). *Bipes canaliculatus* occurs in the Balsas-Tepalcatepec Basin of Guerrero and Michoacán, *B. tridactylus* is restricted to a small

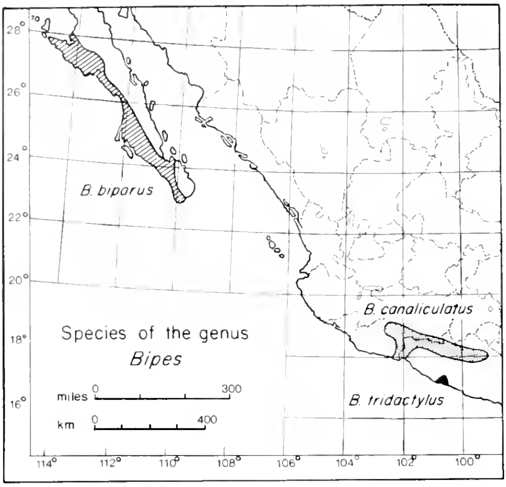

FIGURE 6. Distribution of species in the genus *Bipes*.

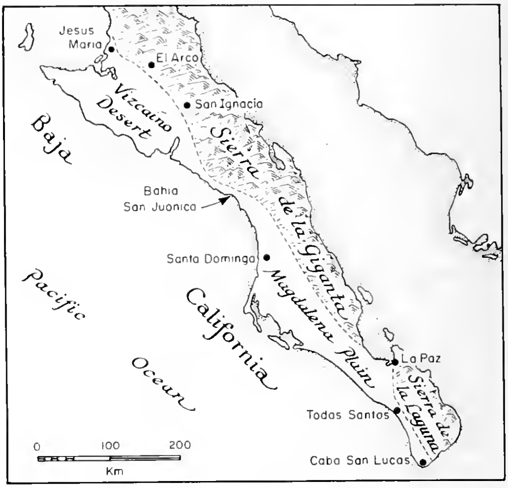

FIGURE 7. Distribution of *Bipes biporus* in Baja California. The limits of the distribution of *Bipes biporus* is outlined by the dashed line. Towns and geographic features are discussed in the text.

area of coastal Guerrero, and *B. biporus* is found on the Baja California peninsula, occurring from Cabo San Lucas in the south to the northwest edge of the Vizcaíno Desert in the north, a distance of over 700 km and including the state of Baja California Sur and a small part of Baja California Norte (Fig. 7).

Except in the vicinity of La Paz, *B. biporus* is absent from the Gulf of California drainage of the peninsula. The species is restricted to the continuous belt of sandy soil that starts in the south at Cabo San Lucas and continues north through the Vizcaíno Desert. Between Cabo San Lucas and Todos Santos suitable habitat is restricted to a narrow plain only one to five kilometers wide between the foothills of the Sierra de la Laguna and the Pacific Ocean. At Todos Santos this plain widens into the Magdalena Plain, which extends north from Todos Santos nearly 400 km to the vicinity of Bahía San Juanico where the foothills of the Sierra de la Giganta approach the Pacific Ocean. The only point where the Magdalena Plain reaches the Gulf of California is at La Paz. North of Bahía San Juanico, a narrow coastal plain separates the Magdalena Plain by about 50 km from the southern limits of the Vizcaíno Desert as defined by Nelson (1921). Less than 20 km north of Villa Jesus María, the Vizcaíno Desert ends where mountains reach the Pacific Ocean (Fig. 7). This point appears to be the absolute northern limit of the distribution of *B. biporus*. A careful search of sandy valleys to the north has yielded nothing.

*Bipes tridactylus* has been found only in the vicinity of the type-locality, Tecpan de Galeana, 90 km northwest of Acapulco (Fig. 8). Specimens have been taken at two localities: the south bank of the Río Tecpan at the town of Tecpan, and 6 km southeast (by Mex. Hwy. 200) of Tecpan. Inquiries of farmers at all towns and rivers along the coast of Guerrero between Acapulco and the mouth of the Río Balsas have determined that *Bipes* is absent except at the vicinity of the type-locality. The restriction of this species to a 20-km stretch of coastal Guerrero may be due to a combination of coastal lagoons and low-lying marsh areas that flood in the rainy season and frequent rocky hills that extend from the Sierra Madre del Sur out to the coast.

*Bipes canaliculatus* occurs in the Balsas-Tepalcatepec Basin and reaches the coast only at the mouth of the Río Balsas (Fig. 8). This arid, interior basin is one of the major physiographic features of southwestern Mexico. It begins in northwestern Oaxaca and southwestern Puebla and extends west-northwest through Guerrero into Michoacán. The Río Balsas lies between the Cordillera Volcanica and the Sierra Madre del Sur, whereas the Río Tepalcatepec lies between the Cordillera Volcanica and the Sierra de Coalcomán. The Río Balsas flows into the Pacific Ocean through a narrow gorge which divides the Sierra Madre del Sur from the Sierra de Coalcomán. The aridity of the basin is caused by the rain-shadow effect of these two coastal mountains, both of which reach heights in excess of 3000 m.

Although locality records are scanty, *B. canaliculatus* is probably widely distributed throughout much of the basin. The species appears to be absent from the vicinity of Piaxtla, Puebla, but specimens are available from Balsas, Tecuaiziapán, and Mezcala (often spelled Mexcala or Mescala), all in Guerrero (Smith and Smith 1977). The species is found throughout the Tepalcatepec Valley of Michoacán. Specimens have been reported from Pizandaran, Gambara, and Los Nopales (Alvarez 1966). This study documents the occurrence of *B. canaliculatus* on the coastal plain of Guerrero at Petacalco, on the eastern edge of the delta of the Río Balsas.

Such a disjunct distribution pattern is found in several other reptilian groups, including snakes of the genera *Nerodia* and *Elaphe*, and lizards of the genera *Ctenosaura* and *Phyllodactylus*. In all groups, the nearest relative of a species in southern Baja California is found on the mainland of Mexico, and in each case the genus is absent from northern Baja California, the head of the Gulf of California, and northwestern Mexico. Van Denburgh (1895) pointed out that several of the reptile species of the Cape region of Baja California had their nearest relative on the mainland of Mexico, but he made no attempt to explain the disjunct distribution. Schmidt (1922) also recognized this distributional pattern and suggested that the Cape region species with relatives on the mainland must have at one time had a continuous distribution north through Baja California, around the head of the Gulf and down into mainland Mexico. Savage (1960) assumed that the peninsula was geologically very old, and for Cape region species with relatives on the Mexican mainland, he stated (page 199):

> The Gulf of California has acted as a strong barrier to biotic dispersion between the Mexican mainland and Baja California throughout peninsular history. The stability of the peninsula and the long term existence of a salt water barrier to the east have required that all terrestrial immigrants enter the region from the north.

However, Leviton and Tanner (1960) cited geologic evidence for a trans-gulfian land mass joining Baja California to the mainland and suggested that *Eridiphas slevini* reached the peninsula by means of this land mass rather than by dispersal around the head of the Gulf of California.

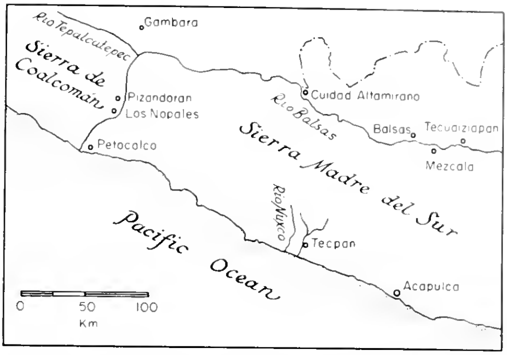

FIGURE 8. Distribution of *Bipes tridactylus* and *Bipes canaliculatus* on the Mexican mainland. Towns and physical features shown on the map are discussed in the text.

During the last ten years, studies in the field of plate tectonics have demonstrated that the Baja California peninsula is neither old nor stable, but was once a part of the Mexican mainland that has been tectonically disrupted and is still in a state of instability. Anderson (1971) presented evidence that Baja California was torn away from the mainland between four and six million years ago. He also suggested that the Cape region may have originated as a separate segment that broke off further to the south and moved northward, colliding with the rest of the peninsula as it moved west and north from the adjacent mainland. Gastil and Jensky (1973) have shown that the La Paz region of Baja California was connected to the mainland of Mexico in the vicinity of the state of Nayarit. The Cape region, south of La Paz, was joined to the mainland in the Jalisco-Colima area. They point out that the offset between Nayarit and La Paz cannot be achieved by simply closing the Gulf of California, but that for proper alignment there must be 435 km of right lateral strike-slip displacement. Although the Gulf was well established 4–5 million years BP, it opened from south to north and the tectonic events leading to its formation started much earlier. The alignment of the Cape region with Jalisco-Colima is at least 14 million years old.

Based on the geologic evidence for the formation of the Baja Peninsula, it is now possible to test an alternate hypothesis to that of Schmidt and Savage: that Cape region reptiles did not all arrive by invasion from the north, but rather some elements rafted northward with the Baja California land mass after it separated from the mainland. This hypothesis eliminates the necessity of epic marches from southern Mexico, around the head of the gulf, and down into the Cape region, followed by extinction in northern Baja California and northwest Mexico.

This hypothesis was first suggested by Murphy (1975) in his discussion of the relationships of the Baja California subspecies of the blind snake, *Leptotyphlops humilis*. Based on morphological characters, he found that *L. h. levitoni* and *L. h. lindsayi* were allied to *L. h. dugesi* of the Mexican mainland. Kim et al. (1976), in an electrophoretic study of *Bipes* species, hypothesized a divergence time for these species of about 15 million years. This time estimate is very close to the geologic estimate of 14 million years for the alignment of the Cape region with the west coast of Mexico. Wyles and Gorman (1978) in an albumin immunological comparison of the insular Baja California lizard *Sator angustus* with 49 other sceloporine lizards, found that save for *Sator grandaevus* of Cerralvo Island, *S. angustus* was most closely related to *Sceloporus utiformis* of the Mexican mainland to the south. The hypothesized time of divergence was 14 million years. Murphy and Papenfuss (1980), using electrophoresis, estimated a divergence time of 15 million years for the lizards *Phyllodactylus unctus* of the Cape region and *P. paucituberculatus* of Michoacán. Seib (1980), in an analysis of reptile distribution patterns of Baja California, suggested that a large component of the Baja herpetofauna could be best explained by vicariant events rather than by dispersal from the north as proposed by Savage. The occurrence of *Bipes biporus* in Baja California is certainly due to vicariance.

*Bipes canaliculatus* and *B. tridactylus* are no more closely related to each other than either is to *B. biporus* (see Kim et al. 1976). Geologic events associated with the uplift of the Sierra Madre del Sur of Guerrero have been summarized by Duellman (1965). The Tecpan de Galeana coastal region of Guerrero is separated from the Balsas-Tepalcatepec Basin by these mountains, which were formed in several stages beginning at the end of the Cretaceous. Additional uplifting occurred during the Miocene and again in the late Pliocene and Pleistocene. The Nei genetic distance (based on the methods of Sarich 1977) between *B. canaliculatus* and *B. tridactylus* of 1.012 ± 0.289 suggests that the two species were separated between 14.8 and 26.6 million years ago.

Although *B. canaliculatus* reaches the coast of Guerrero at the mouth of the Río Balsas 180 km northwest of Tecpan de Galeana, a careful search for *Bipes* along the intervening coastal plain has yielded none. It is possible that additional species of *Bipes* will be discovered in the future. Although two of the species are widely distributed, the limited range of *B. tridactylus* shows that this relictual genus can survive in small pockets of suitable habitat. This ancient and perhaps once widespread group may have been isolated elsewhere by the complex tectonic events and climatic changes in western Mexico. I have searched along most of the west coast from Chiapas to Sonora and Arizona. The only area where local residents seem to be familiar with *Bipes* is the Colima-Michoacán border near the town of Tecomán, Colima. *Bipes* can be expected there. The Ahuijullo depression is a lowland connection between the lowlands of Colima and the Tepalcatepec Valley of Michoacán, and Duellman (1965) has demonstrated that there is considerable faunal exchange through the Ahuijullo depression.

Although Taylor (1938) discussed the possible occurrence of *Bipes* in southeastern Arizona, based on several convincing accounts from local inhabitants, no specimen has ever appeared. R. C. Stebbins (University of California, Berkeley, pers. comm.) suggests that these accounts and more recent stories that he has heard may refer to a lizard, *Gerrhonotus kingi*. He has observed *G. kingi* crawling slowly on the ground using only its forelimbs while its hind limbs are folded against the body. This species is known to occur at the various localities mentioned by Taylor. Also, the possibility of *Bipes* in the Mexican state of Chiapas (Smith and Smith 1977) has not been confirmed. In discussions with Dr. Alvarez

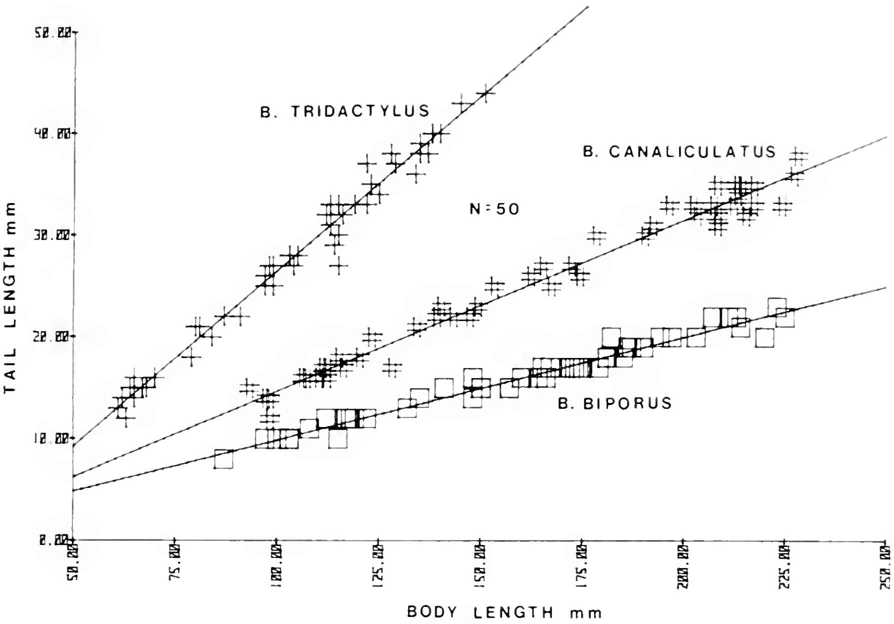

FIGURE 9. Relation of tail length to body length in *Bipes*. Measurements for 50 specimens of each species are plotted. Only specimens with complete tails were used.

del Toro of the Museo de Historia Natural, Tuxtla Gutierrez, Chiapas, Mexico, I was told that crushed specimens had been seen by an engineer in a road construction site near the town of Cintalapa. However, Dr. del Toro stated that he had not seen the specimens himself. I showed numerous farmers in the Cintalapa area a specimen of *B. canaliculatus*, and without exception they stated that they had never seen such an animal before. The name "ajolote," used to describe *Bipes* in Baja California, is used to describe *Gerrhonotus liocephalus* in the state of Chiapas.

## TAIL LENGTH, TAIL LOSS, AND PREDATION

### Tail Length

Tail length is diagnostic for each species of *Bipes* (see systematic section). Linear regressions of tail length against body length show high correlation and no interspecific overlap (Fig. 9). *Bipes biporus* has the shortest, *B. tridactylus* has the longest, and *B. canaliculatus* has an intermediate relative tail length. It is constant throughout the range of the two widely distributed species (*B. biporus* and *B. canaliculatus*). The regressions shown in Figure 9 are for specimens from the major collection sites, La Paz and Mezcala. *Bipes biporus* from the Vizcaíno Desert and *B. canaliculatus* from Petacalco have relative tail lengths that fall within the range of specimens from the main collecting sites.

Two factors are associated with shifts in relative tail length: change in number of annuli and change in number and size of caudal vertebrae. A cleared-and-stained specimen of *B. canaliculatus*, the species with intermediate tail length, had 17.5 caudal vertebrae posterior to the intravertebral fracture plane in the ninth caudal vertebra. The total of 25 caudal vertebrae had 37 caudal and lateral annuli associated with them. The 1.5:1 ratio of annuli to caudal vertebrae represents a reduction from the dorsal-annuli–to–trunk-vertebrae ratio, which is 2:1 in all *Bipes*.

One cleared-and-stained specimen of *B. biporus* had 20 caudal vertebrae with a fracture plane in the eighth, 12.5 vertebrae posterior to

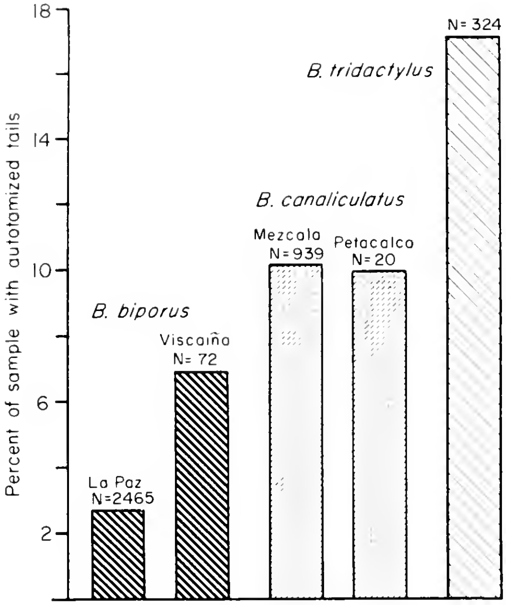

FIGURE 10. Frequency of tail autotomy in *Bipes*. Each bar represents the percent of the sample with autotomized tails. Sample size (N) is for the entire sample of each species and includes individuals with and without autotomized tails.

the eighth, and 32 associated annuli. The ratio of annuli to caudal vertebrae was 1.6:1. The individual vertebrae are shorter in *B. biporus* than in *B. canaliculatus*.

A specimen of *B. tridactylus* had 29 caudal vertebrae, a fracture plane in the eighth, 21.5 vertebrae posterior to the eighth, and 50 associated annuli. The ratio of annuli to caudal vertebrae was 1.7:1. The individual vertebrae are longer in *B. tridactylus* than in *B. canaliculatus*.

In summary, the ratio of annuli to caudal vertebrae remains relatively constant (1.5–1.7:1) in all three species of *Bipes*. Both the number and size of annuli and vertebrae are greater in long-tailed *B. tridactylus* than in short-tailed *B. biporus*.

## Tail Loss

All species of *Bipes* show caudal autotomy. There is a single point for intravertebral autotomy located less than 10 caudal annuli posterior to the cloaca. Once autotomy has occurred, the shortened tail heals but there is no regeneration, so a *Bipes* can lose its tail only once in its lifetime. Tail autotomy occurs in many amphisbaenians (Vanzolini 1951; Gans and Alexander 1962). To some extent it follows phylogenetic lines. There is no autotomy in the families Rhineuridae and Trogonophidae. All Bipedidae show autotomy. In the widespread family Amphisbaenidae, tail autotomy may be present or absent and, in general, is present more often in small than in large species (Gans 1974).

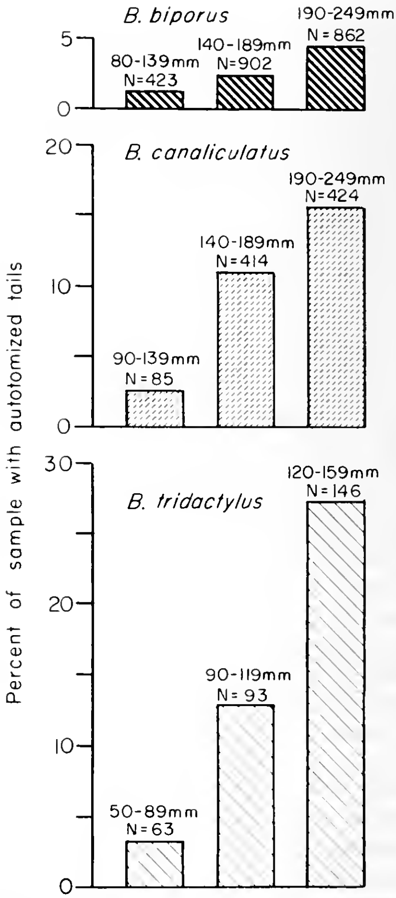

FIGURE 11. Frequency of tail autotomy in *Bipes*. The sample of each species has been divided into three size classes. Each bar represents the percent of the sample with autotomized tails. Sample size (N) is for the entire sample of each species and includes individuals with and without autotomized tails.

Although autotomy can occur in all three species of *Bipes*, the frequency of occurrence of tail loss varies among them (Fig. 10). In each species the frequency of occurrence of tail loss increases with body size (Fig. 11). This increase demonstrates that there is a relation between age and tail loss. Although the data presented in Figure 11 are not age specific by year, obviously large *Bipes* are usually older than small *Bipes*.

## Predation

There are considerable data demonstrating that tail autotomy is a defense mechanism against predation and that older animals are more likely to have encountered predators during their life than are younger animals.

Cagle (1946) found that only 10% of the juveniles, as opposed to 33% of the males and 29% of the females, had regenerated tails in a sample of 126 of the gecko lizard *Hemidactylus garnotti*. Werner (1968) observed that 17.3% of the juveniles, 49.2% of the females, and 59% of the males of a sample of 250 of the gecko *Hemidactylus turcicus* had regenerated tails. Pianka (1970a) could determine no significant difference between the sexes in frequency of regenerated tails in the whiptail lizard *Cnemidophorus tigris*; however, he did demonstrate a significant increase in frequency of regenerated tails correlated with latitude north to south. He also found a north-to-south increase in both number of species and number of individuals of lizard-eating snakes and lizard-eating birds. Pianka suggested that the differences between northern and southern populations of *C. tigris* reflected real differences in the amount of predation and not just increased intraspecific aggression. Vitt et al. (1974) concluded that frequency of tail break increased with size in both male and female desert spiny lizards (*Sceloporus magister*). The frequency was always greater in males than females, and based on observations of male–male territorial encounters and the presence of tail and body scars on the males, he suggested that a significant portion of the dimorphism in tail-break frequency might be due to fighting in males. Parker and Pianka (1975) noted a near two-fold increase in frequency of tail loss from north to south in juvenile *Uta stansburiana*. They suggested that this difference could be a direct result of the southward increase in the number of predators. Congdon et al. (1974) reported experiments with the gecko *Coleonyx variegatus* and a natural snake predator, *Hypsiglena torquata*. In 30 predator–prey encounters using *Coleonyx* with tails, 11 of the geckos escaped while losing portions of their tails and 19 were captured by 10 *Hypsiglena*. In seven encounters with tailless geckos all were captured. Greene (1973) observed that *Amphisbaena fuliginosa*, a species with tail autotomy, showed a defensive tail display when touched. If he dug up the specimen, it immediately started to burrow into the substratum. When the animal was touched, it raised its tail and waved it from side to side. Based on these observations and those of Vanzolini (1951) for a sample of 129 *A. fuliginosa* of which 28 had incomplete tails, Greene concluded that autotomy is probably facilitated by tail display in this species.

Shaffer (1978) used tail autotomy as an index of relative predation on salamanders along an altitudinal transect in Guatemala. He found that the frequency of tail loss decreased with increasing altitude and suggested that predation pressure on salamanders was more intense at low elevations. He also found that female neotropical salamanders had higher frequencies of tail loss than males. This higher frequency was probably because brooding females tend to remain with the egg mass even when disturbed.

Two general observations can be made from tail-autotomy data: (1) sexual differences in behavior may account for frequency differences in some species; and (2) tail autotomy is an important anti-predator mechanism. In the three species of *Bipes*, the observations that frequency of tail loss increases with body size and that there is no significant difference between the sexes (chi-square test: $P > .05$) suggest that tail loss is due to predation. The more than six-fold difference (2.7% versus 17.0%) between *B. biporus* and *B. tridactylus* in caudal autotomy suggests much greater predation pressure on the latter species. Predation pressure on *B. canaliculatus* falls between the other two species.

A subterranean existence enables *Bipes* to avoid many potential predators. *Bipes* live in self-constructed burrows and virtually never come to the surface. Of the more than 3800 individuals obtained for this study, only three were found active on the surface at night. The rest were dug from underground. Although birds prey on diurnal lizards, they are not likely to be important predators on *Bipes*. Predators on *Bipes* must either dig them up or encounter them underground in burrow systems. Mammalian predators such as badgers and skunks could dig up *Bipes*; however, most potential mammal predators are nocturnal, and *Bipes* retreat deep-

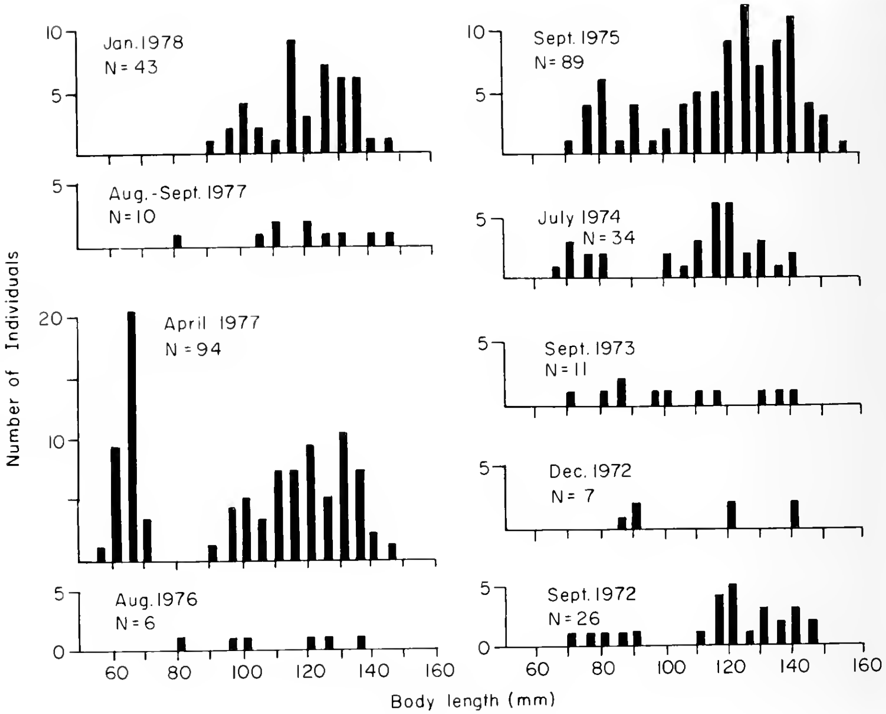

FIGURE 13. Size frequency distribution of all *Bipes tridactylus* collected. Size classes are based on 5-mm increments in body length.

The *Micrurus* must eat the tail before it can pursue the *Bipes*. The longer the *Micrurus* spends eating the tail, the greater the chance the *Bipes* has of escaping. Greene (1973) found that ingestion in *Micrurus* was inhibited by prey movement. Autotomized tails of *B. tridactylus* will move back and forth for several minutes after they have been dropped. Tail movement would give a *Bipes* additional time to escape.

Tail length and frequency of tail loss must be related to predation pressure on *Bipes*. In the absence of a specialized *Bipes* predator in Baja California, *B. biporus* does not "need" a long tail. However, on the mainland of Mexico, selection has favored a long tail as a defense against predation. Both *B. canaliculatus* and *B. tridactylus* have longer tails and greater frequencies of tail loss than does *B. biporus*.

## GROWTH AND REPRODUCTION

### *Bipes tridactylus*

Although sample sizes for *B. tridactylus* are smaller than for the other two species, large samples for September 1975, April 1977, and January 1978 have made it possible to determine female age at first reproduction, clutch size, egg-laying season, approximate incubation time, size of young at hatch, growth rate during the first year, and an estimate of survivorship to maturity. Samples, some very small, from other months and years provide supporting data (Fig. 13).

Among 43 *B. tridactylus* collected 14–16 January 1978, 27 were females. All but 1 of the 21 females larger than 115 mm in body length contained large yolked oviducal eggs (Fig. 14). None of the remaining six, ranging in body length from 90 to 104 mm, showed any sign of reproductive activity. Their ovaries contained only small follicles less than 1 mm in diameter. There was a size gap of 11 mm between the largest nongravid female and the smallest gravid female, and a considerable weight difference between the largest nongravid females and the smallest gravid females. Weights for three nongravid females between 100 and 104 mm in body length ranged from 2.3 to 2.6 g ($\bar{x}$ = 2.5 g), whereas weights for five gravid females between

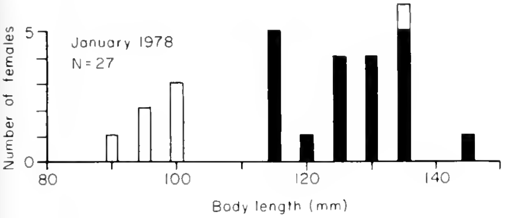

FIGURE 14. Size frequency distribution of female *Bipes tridactylus*. Open boxes represent non-gravid females, solid ones gravid females. Sample collected 14–17 January 1978.

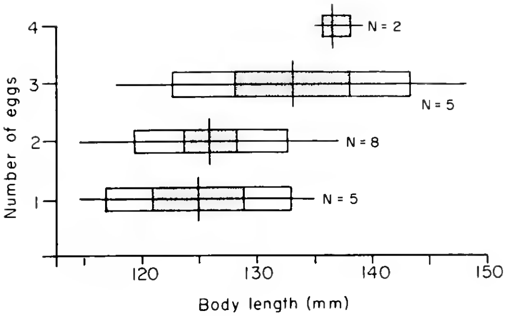

FIGURE 15. Oviducal egg number of *Bipes tridactylus*. The egg number ranges from one to four. Each Dice-Lerras diagram represents the size range of females producing a given egg number. Horizontal line is range; vertical line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error. There is no significant difference in body length between females producing one, two, or three eggs. Females producing four eggs are significantly larger than those producing one or two eggs (Student's *t*-test; $P < .05$).

115 and 118 mm in body length ranged from 3.7 to 5.3 g ($\bar{x} = 4.7$ g). Large females have more oviducal eggs than do small females (Fig. 15). This pattern of a larger clutch size with an increase in body size is found in many snakes and lizards (Fitch 1970). The number of oviducal eggs ranged from one to four ($\bar{x} = 2.2$).

All females with large ova appeared distended and ready to lay. One brought back to the laboratory laid two eggs on 26 January, 10 days after capture. Had all 44 eggs from the total sample hatched, there would have been a nearly exact replacement of the total sample of 43 *Bipes* that were collected. However, 100-percent egg survival seems unlikely. Factors that may cause egg death include desiccation due to unfavorable soil conditions, destruction by mold or bacteria, and loss to predators.

Data on reptile egg survivorship suggest considerable interspecific and even intraspecific variation. Some studies have found nearly complete hatching success. In *Uta stansburiana*, the number of hatchlings was equal to or even exceeded the number predicted from data on clutch size and clutch frequency (Tinkle 1967), and hatching success was nearly 100 percent in *Sceloporus graciosus* (see Tinkle 1973). However, Ruth (1977) estimated only 40 percent of *S. graciosus* eggs hatch; the figure is 20 percent in *S. occidentalis*. Tinkle (1972) found that there was nearly 50-percent egg mortality in *Sceloporus undulatus*, whereas in one of the best-documented studies, Blair (1960) discovered a range of 69–81% egg mortality in *Sceloporus olivaceus* over a four-year period. Causes of death included drying of eggs, destruction of nests by predators, and failure of young lizards to escape from the nest. Clark (1970) estimated in *Carphophis vermis* a 46-percent egg reduction between ovarian enlargement and hatching due to a combination of resorption before laying and egg death in the nest. He estimated a 67-percent hatch once eggs were laid. Fitch (1963) estimated an egg loss of 50 percent before and during incubation in *Coluber constrictor*.

An estimate of egg survival for *B. tridactylus* was obtained by examination of the April 1977 sample (Fig. 13). In this sample of 95 specimens, there were 33 hatchlings and 21 females with a body length greater than 115 mm. Unfortunately, no collection was made in January 1977, so it is necessary to assume that both clutch size and percent of gravid females were similar for the two years. The mean oviducal egg number per gravid female for the January 1978 sample was 2.2 (Fig. 15). The mean number of hatchlings per sexually mature female in the April 1977 sample was 1.6. Since oviducal egg number is a reliable estimate of the number of eggs actually laid (Tinkle 1961; Ruth 1977), the rate of success for egg hatch was about 73 percent.

Females reach maturity at 115 mm, and there is no evidence based on the examination of testes size that males mature earlier. The April 1977 sample (Fig. 13) therefore can be assumed to consist of 33 hatchlings, 41 adults, and 20 juveniles. Because *B. tridactylus* reproduces only once a year, these 20 juveniles must be the one-year-old size class that hatched the previous April. By January 1978 this juvenile size class was sexually mature, and the hatchlings of April

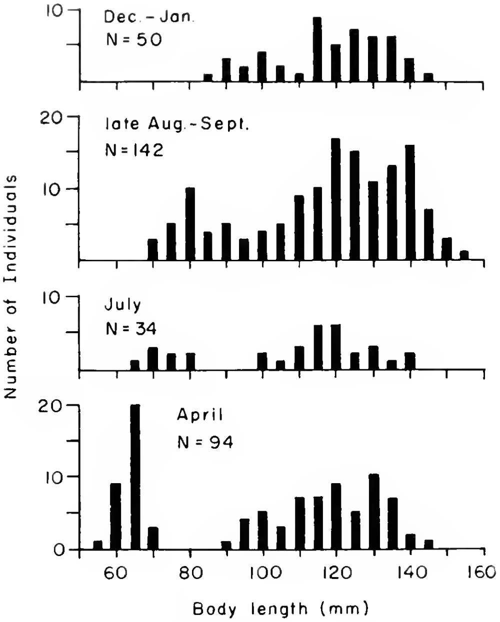

FIGURE 16. Size-frequency histogram of *Bipes tridactylus*. Data are pooled from all samples collected between 1972 and 1978 (Fig. 13).

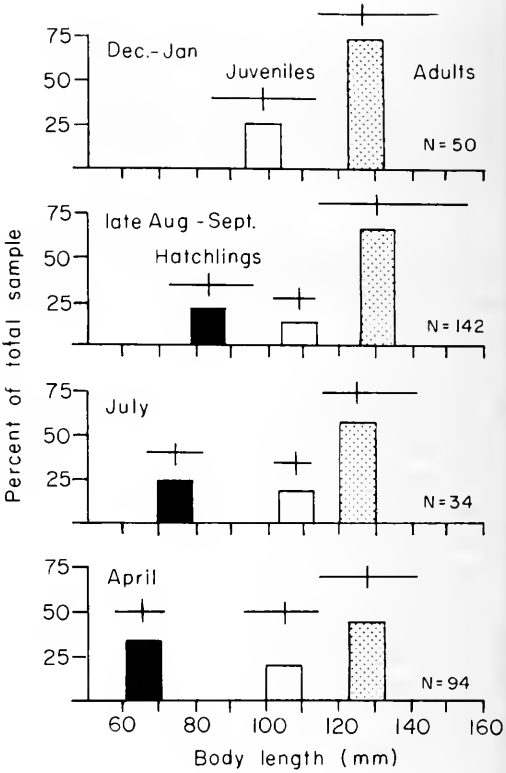

FIGURE 17. *Bipes tridactylus* age classes. Each age class is represented as a percentage of the total sample. Each vertical bar is positioned so that it straddles the mean body length of a given age class. The size range of each age class is shown by the horizontal line above each vertical bar. These data are pooled from the individual samples shown in Figure 13. Hatchlings are the young of the year. Juveniles are the young of the previous year. Adults are two or more years old, except for the December–January sample which contains some adults only 19 months old (see text).

1977 are the new juvenile size class. These data suggest that *B. tridactylus* lay their first clutch at an age of around 21 months. Hatchling growth rate during the first nine months was determined by comparing the mean hatchling size in April 1977 ($\bar{x} = 66.2$, $n = 33$) with the mean juvenile size in January 1978 ($\bar{x} = 102.5$, $n = 10$). The mean hatchling growth rate was 36.3 mm during these nine months.

Additional information on growth rates during the first year was obtained by pooling data for the years from 1972 to 1978 into a single "ideal" year. The data are divided into winter (December to January), spring (April), early summer (July), and late summer (late August to September groups) (Fig. 16). No inter-year variation in this pooled sample can be considered. The contribution of samples from a six-year period may equalize years of greater than normal reproduction and growth with years that may have been less favorable. Pooling data for *B. tridactylus* seems more reasonable than for the other species of *Bipes* for two reasons. First, it is apparent from Figure 13 that *B. tridactylus* reproduces every year, and the contribution of adults to each sample remains relatively constant. Second, climatic conditions are more predictable along coastal Guerrero than in arid Baja California and in the arid Balsas Depression.

A discrete hatchling size class is evident in April and July; however, by late August–September fast-growing hatchlings have "caught up" with slow-growing juveniles from the previous year, and the histogram forms a continuum from juvenile to adult (Fig. 16). Based on data from individual years, the 100-mm point was selected as the break between hatchlings and juveniles for this pooled late August to September sample. Thus, juveniles are specimens between 100 and 115 mm (size at sexual maturity) in body length. In this sample it is possible for a fast-growing hatchling to be erroneously categorized as a juvenile or for a slow-growing juvenile to be categorized as a hatchling. It is assumed that these two possibilities are equally likely and will cancel each other. By December–January only two size classes remain. The juvenile size class (18–19 months old) has now reached the adult size of at least 115 mm, and the females will lay eggs in January at the age of 21 months.

An estimate of hatchling and juvenile survivorship can be obtained from the age structure of *Bipes tridactylus* (Fig. 17). In April, hatchlings make up 35.1% of the sample. The hatchling contribution to the sample decreases to 24.2% in July and 21.0% in late August–September. The apparent increase in hatchling contribution to 26.0% in December may be a sampling error, a miscategorization of slow-growing adults as hatchlings, or a combination of both. Nevertheless, this apparent increase is not great and the effect of hatchling mortality is obvious. An estimate of hatchling mortality during the first year can be obtained by subtracting the percentage of one-year-old individuals in the April sample from the percentage of newborn individuals in the April sample and dividing by the percentage of newborn individuals. In the April sample there were 3 hatchlings (35.1%) and 20 one-year-old juveniles (21.3%). The mortality during the first year is estimated as 39.3%.

Two additional estimates of mortality have been obtained from the July and the late August–September samples. At the time of hatching in April, the ratio was 0.805 hatchling per adult (33/41). If adult mortality is assumed to be small compared to hatchling mortality, the expected number of hatchlings at a later date can be estimated by multiplying the number of adults by 0.805. In the July sample there were 20 adults. The expected number of hatchlings was 16.1 (20 × 0.805), but only 8 were observed, suggesting a 49.7% mortality between April and July. In the late August–September sample of 94 adults, there were 30 hatchlings, compared to 75.7 expected, suggesting 39.6% mortality between April and late August–September. Using this method it is not possible to compare the December–January sample with the April sample because the adult sample in December–January contains an undetermined number of young adults only about 21 months old. These young adults had not yet reproduced and therefore did not contribute to the hatchling class.

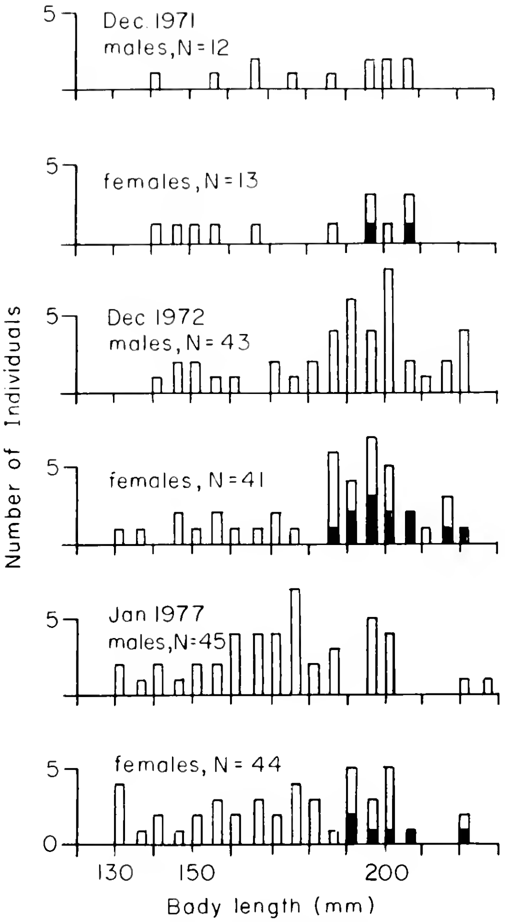

FIGURE 18. Sex ratios and frequencies of gravid *Bipes canaliculatus*. A 50:50 sex ratio is indicated. Only females over 185 mm in body length contain yolked, enlarging ovarian eggs. In a given sample, less than half the adult females were gravid, suggesting that female reproduction may be on a two-year cycle. Each gravid female is represented by a solid rectangle. Hatchlings under 130 mm in body length are not included in the figure.

The estimate of 49.7% mortality between April and July may be high because of sampling error in the small total sample ($n = 34$). The other two independent estimates of mortality are similar and suggest that mortality during the first year is about 40%, and most hatchling mortality occurs soon after hatching, a pattern common to many other reptiles.

Adults make up the largest part of each sample (Fig. 17). The ratio of adults to juveniles ranges from 2.0:1 in April to 5.2:1 in late August–September. Assuming no juvenile or adult

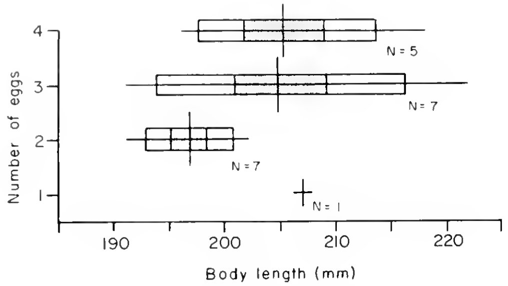

FIGURE 19. Enlarged ovarian egg number of *Bipes canaliculatus*. The egg number ranges from one to four. Each Dice-Lerras diagram represents the size range of females producing a given egg number. Horizontal line is range; vertical line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error. There is no statistically significant relationship between clutch size and body size.

mortality, the adult population (using the April adult–juvenile ratio) must have accumulated from at least a two-year contribution of juveniles. However, there is certainly both juvenile and adult mortality, and unfortunately the data do not allow a precise determination of average adult age.

In summary, female *B. tridactylus* mature at a body length of 115 mm and at an age of around 21 months. Eggs are laid in January and hatch in April. Females reproduce every year. Hatchling mortality during the first year may be about 40%.

### *Bipes canaliculatus*

Large samples of *B. canaliculatus* were collected at various times over a period of several years. Information is available on clutch size, egg-laying season, size of young at hatch, and time to sexual maturity.

Females collected in late December and January contain yolked, enlarging ovarian eggs (Fig. 18). No female smaller than 185 mm body length showed any sign of reproductive activity. Even among the females over 185 mm, fewer than half were gravid. In December 1971, 2 of 8 adult females were gravid (25%); in December 1972, 12 of 29 were gravid (41.4%); and in January 1978, 6 of 17 were gravid (35.3%). As fewer than half the females were gravid in any sample, female reproduction may be on a two-year or longer cycle. There is no statistically significant increase in the number of enlarging ovarian eggs, which ranged from 1 to 4 ($\bar{x}$ = 2.8), with increased body size (Fig. 19). Females collected in April, July, August, and September showed no reproductive activity; thus, eggs are laid after January and before April. Hatching may begin in April; the smallest specimen (93 mm body length) was collected at this time. No samples were obtained in May and June, but samples from July and August contain hatchlings less than 110 mm in body length.

It is not possible to estimate egg mortality because no samples are available from May and June, the months when most hatching must occur. However, large samples were obtained in August or September over a six-year period (Fig. 20), and it is possible to determine the percentage of hatchlings present in the population three months after hatch, which can then be compared to reproductive potential. From an examination of size-class data for each year (Fig. 20), it appears that hatchlings may have reached a maximum body length of 130 mm by August or September.

Using data on reproductive potential obtained in 1971, 1972, and 1978, it is possible to estimate the reproductive potential during other years (Table 3). Since *B. canaliculatus* has a 50:50 sex ratio (Fig. 18), the expected number of eggs in a sample of both sexes will be half the female clutch size. The female clutch size was determined by dividing the number of eggs in a sample by the number of adult females in the sample. The female clutch size was 0.55 eggs per female in 1971, 1.41 in 1972, and 1.12 in 1978. The average clutch size was 1.02 eggs per female or 0.51 eggs per adult (Table 3). The expected number of eggs produced each year was determined by multiplying the average number of eggs per adult (0.51) by the number of adults in the sample. The observed number of young in each sample was then compared to the expected number in order to estimate mortality (Table 3). Because the samples with observed number of hatchlings were collected 3–4 months after hatching, and because estimates of egg production were determined from enlarging ovarian eggs, three factors could have contributed to mortality. First, some of the ovarian eggs may not have been laid. Second, some eggs may not have hatched. Third, some of the juveniles may have died between hatch time and sample time.

The estimate of about 40% hatchling survival at an age of 3–4 months (Table 3) is higher than that found for *B. tridactylus*. Hatchling survival

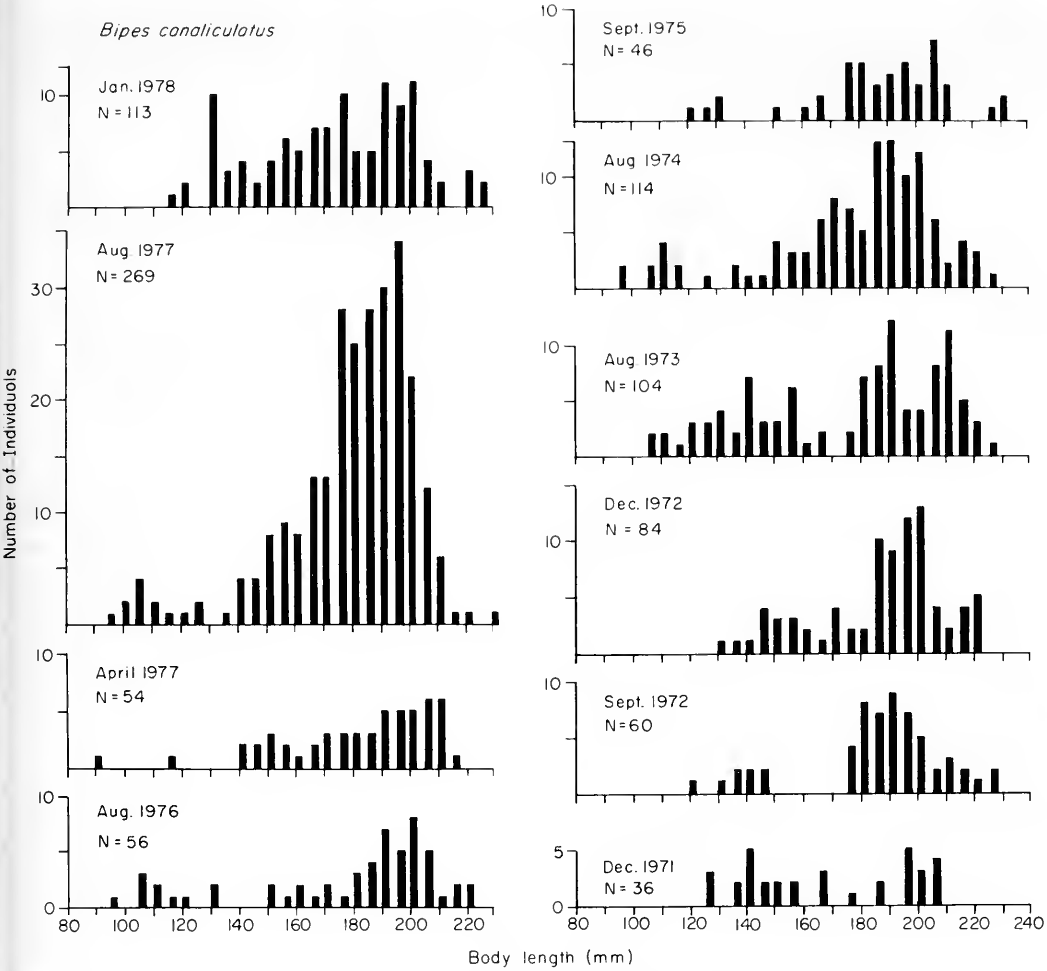

FIGURE 20. Size frequency distributions of all *Bipes canaliculatus* samples.

during the first year has been determined for a number of snakes and lizards. Estimates of less than 40% have been made for: *Sceloporus undulatus*, 18% (Tinkle 1972); *Sceloporus graciosus*, 17.5% (Tinkle 1973); *Uta stansburiana* 8.8–30.3% (Tinkle 1967); *Basiliscus vittatus*, 10% (Hirth 1963); *Ameiva quadrilineata*, 10% (Hirth 1963), and *Diadophis punctatus*, 33% (Fitch 1975). Estimates of greater than 40% hatchling survival during the first year have been made for: *Xantusia vigilis*, 80% (Zweifel and Lowe 1966); and *Carphophis vermis*, 70% (Clark 1970).

The estimate of 40% hatchling survival for *B. canaliculatus* falls within the range reported for other squamate reptiles. It must be emphasized that this figure includes egg mortality and not just mortality from the time of hatching. Estimates of mortality beyond the age of 3–4 months cannot be made from the size-frequency data (Figs. 20, 21). However, data on frequency of tail loss may provide a minimal estimate of mortality in older *B. canaliculatus*. It will be recalled that hatchlings under 130 mm in body length (i.e., young-of-the-year) had a tail-loss frequency of 2.4%, those over 130 mm but less than 180 mm 10.9%, and those over 180 mm 15.6%. Assuming an equal likelihood of being attacked head first and eaten or being attacked tail first and escaping, the percent tail loss in a given size class gives one estimate of mortality due to predation. The increase in percent tail

TABLE 3. MORTALITY ESTIMATES OF HATCHLING *Bipes canaliculatus* COLLECTED IN AUGUST AND SEPTEMBER, THREE TO FOUR MONTHS AFTER HATCHING. Expected number of hatchlings was determined using the average clutch size (1.02 eggs per adult female). Since a 50:50 sex ratio is indicated (Fig. 17), the expected number of hatchlings is half the average clutch size (0.51) multiplied by the number of adults in the sample. The mortality estimate was determined by subtracting the observed number of hatchlings from the expected number of hatchlings and dividing by the observed number of hatchlings.

| | Sample Size | No. of Adults | Observed No. of Hatchlings | Expected No. of Hatchlings | Mortality Estimate | Survivorship |
|---|---|---|---|---|---|---|
| Sep 1972 | 60 | 38 | 8 | 19.4 | 0.587 | 0.413 |
| Aug 1973 | 104 | 56 | 15 | 28.5 | 0.475 | 0.525 |
| Jul–Aug 1974 | 114 | 64 | 11 | 32.6 | 0.662 | 0.338 |
| Sep 1975 | 46 | 28 | 4 | 14.3 | 0.720 | 0.280 |
| Aug 1976 | 56 | 34 | 10 | 17.3 | 0.422 | 0.578 |
| Aug 1977 | 270 | 140 | 13 | 71.4 | 0.812 | 0.188 |
| | | | | Mean | 0.613 | 0.387 |
| | | | 95% Confidence Limits of Mean | | 0.613 ± 0.170 | 0.387 ± 0.170 |

loss between yearlings (under 130 mm) and the rest of the non-adult sample is about 8.5% (10.9% − 2.4%). The increase found in the adult size class is 4.7% (15.6% − 10.9%).

One method of estimating the number of years required to reach sexual maturity is to use the pooled August–September samples obtained over a six-year period (Fig. 21). Only 8.5% of this sample were hatchlings of the year. Adults (over 185 mm) made up 55.3% of the population, and juveniles, which were neither hatchlings of the year nor adults, accounted for the remaining 36.2% of the population. Using these data it would take five years to accumulate the juvenile population from the small annual hatchling contribution allowing for low mortality among hatchlings.

A second method of estimating time to maturity is to use the average hatchling and juvenile contribution to the samples over the six-year period (Table 3, Fig. 22). Hatchling contributions ranged from 5% to 18% ($\bar{x} = 12\%$), juveniles from 21% to 43% ($\bar{x} = 30\%$), and adults from 52% to 63% ($\bar{x} = 58\%$). Even with low mortality, it would take three years to accumulate the juvenile contribution observed in August and September (actually 40 months because hatching occurs about 4 months earlier). By January, the oldest juveniles now 45 months old may reach sexual maturity at a size of 185 mm. It is evident, however, from the large adult contribution found in each sample that most of the adult population is older than four years.

In summary, female *B. canaliculatus* mature at a body length of 185 mm and a minimum age of 45 months. Less than half of the adult female population reproduces each year. The mean clutch size per gravid female is 2.8, but the mean clutch size per adult female is only 1.02. Eggs are laid after January and before April. Mortality between ovarian egg enlargement and hatchling age of three months averaged 61.3% over a six-year period.

### *Bipes biporus*

At least one sample of *B. biporus* was collected during every month of the year except February and November. Samples were obtained over a period of several years during winter (December–January), spring (March–April) and late summer (September) (Fig. 23). Information is available on clutch size, egg-laying season, approximate incubation time, size of young at hatch, growth rate during the first year, and number of years necessary to reach sexual maturity.

Females collected in late June and early July 1972 contained enlarged ovarian or oviducal eggs. Six of 32 females were gravid and had a body length greater than 195 mm (Fig. 24); 9 larger females were not gravid. In a sample of 101 females collected in late June and early July 1979, there were 26 gravid females, all but 2 over 185 mm in body length. There was no sign of reproductive activity in 29 of the 53 females over 185 mm in body length. Their ovaries contained only small follicles less than 1 mm in diameter. The two smaller gravid females were 174 and 184 mm in body length. Eighteen of 20 females in the 170–184-mm size class were not gravid

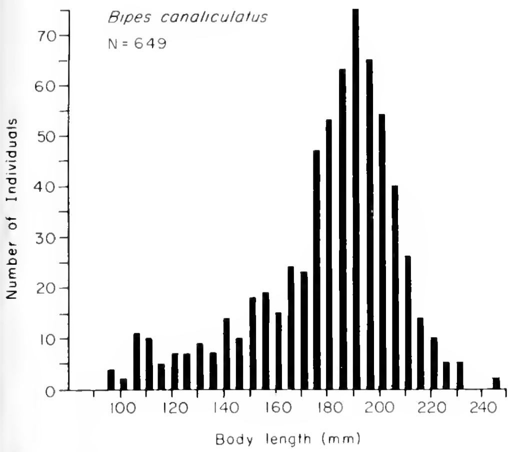

FIGURE 21. Size frequency distribution of *Bipes canaliculatus*. Data pooled from all samples collected in August and September between 1972 and 1978 (Fig. 20). Each specimen has been assigned a size class based on 5-mm increments in body length. Hatchlings of the year are less than 130 mm in body length. Sexually mature females are over 185 mm in body length.

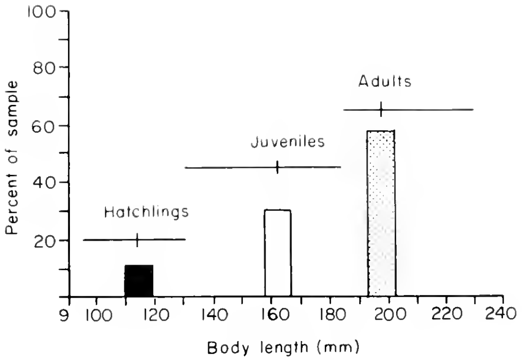

FIGURE 22. *Bipes canaliculatus* age classes. Each age is represented as a percentage of the total sample. Each vertical bar is positioned so that it straddles the mean body length of a given age class. The size range of each age class is shown by the horizontal line above each vertical bar. These data are pooled from individual samples (Fig. 20) collected in August or September during the years 1972–1977. Hatchlings are the young of the year. Juveniles are young that have accumulated over several years. Adults are individuals over 185 mm in body length.

(Fig. 24). Based on these data it appears that most female *B. biporus* mature at about 185 mm in body length and that female reproduction may be on a two-year or longer cycle. No gravid females were found during other months of any year.

Clutch size ranged from one to four with a mode of two (Figs. 25, 26). The mean clutch size per gravid female was 2.2 in 1972 and 2.1 in 1979. Because not all adult females were gravid, the mean clutch size per adult female was 0.76 in 1972 and 1.04 in 1979. Although the 1972 sample is too small for statistical analysis, it is evident from the 1979 sample (Fig. 26) that large females lay more eggs than small females.

Samples contained about twice as many adult females as adult males (Table 4). It is not known whether this difference is due to differential mortality, sampling bias favoring females, or a skewed primary sex ratio. Even among juvenile *B. biporus*, more females were collected than males, although the difference was not statistically significant.

Hatchlings generally first appear in late September. In the sample collected 29–30 September 1972, an obvious hatchling class ranging in size from 90 to 109 mm in body length is present (Fig. 23). Using data on adult sex ratio, clutch size, and number of hatchlings, it is possible to estimate egg mortality for 1972. In this sample of 99 individuals, there were 19 hatchlings and 62 adults with a body length greater than 185 mm. If the adult sex ratio is two females for each male, a random sample of 62 adults should contain 41 females. These 41 females would produce 31 eggs because the clutch size per adult female was 0.76 in 1972. An estimate of about 40% egg and early hatchling mortality preceding the time of sampling is obtained by comparing the observed number of hatchlings (19) with the expected number of eggs (31). August and early September samples for the years 1973, 1974, and 1975 were collected before hatchlings first appeared. A single hatchling (90 mm) was present in the September 1973 sample (Fig. 23). Other small individuals (110–129 mm in length) are hatchlings from the previous year. This same sample illustrates the great size range of yearlings (110–154 mm). If young hatch at about 90 mm, some may grow only about 20 mm and others 60 mm during the first year. Due to the range in body length of yearlings, it is difficult to break the samples into age classes. Except for the September 1972 sample, there is no discrete break between hatchlings and yearlings. In samples collected other years in December to January, a hatchling size class (three months old) is present. However, it is likely that this class actually

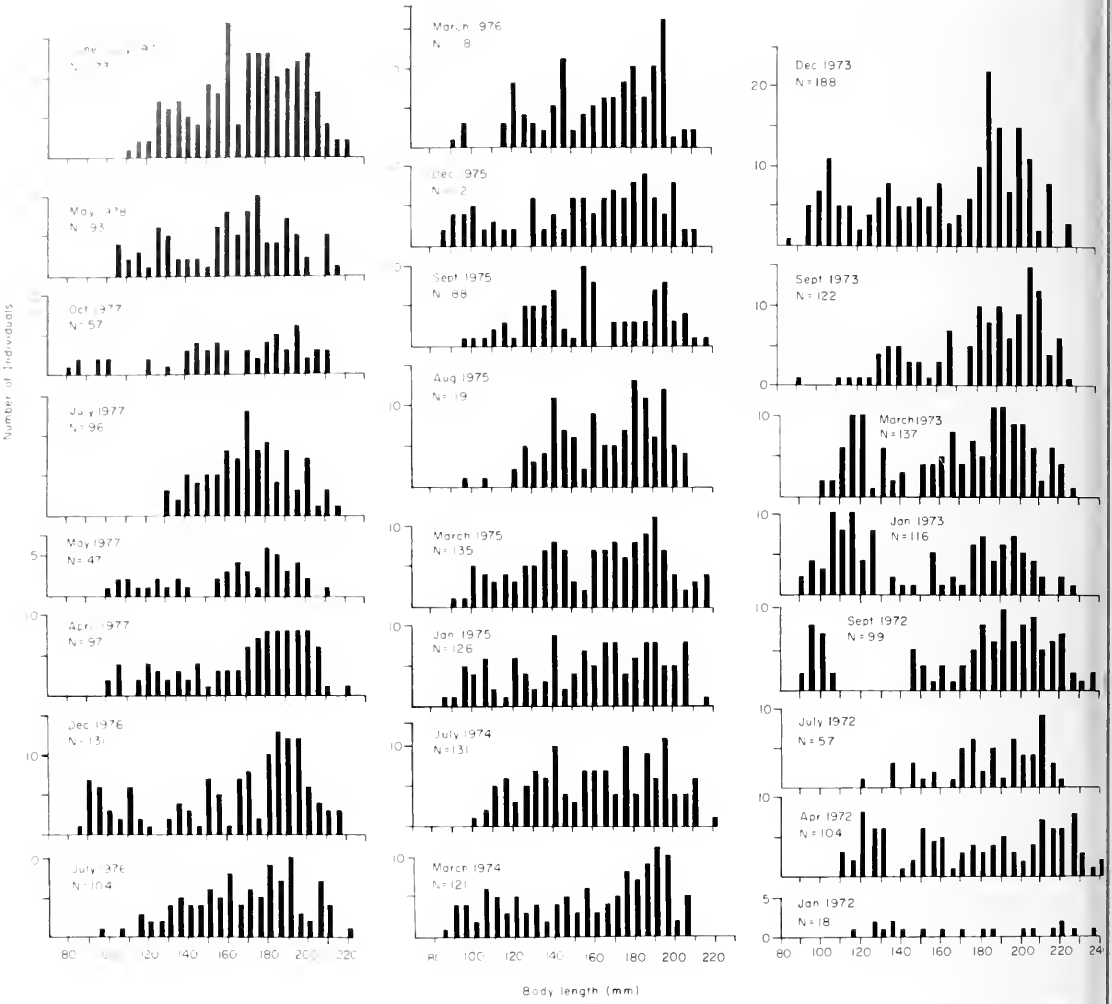

FIGURE 23. Size frequency distributions of all *Bipes biporus* samples.

contains some yearlings. Nevertheless, these December and January samples are the best available to estimate the number of years necessary to reach sexual maturity (Fig. 23).

Except for January 1973, the number of hatchlings per adult ranges from 0.43 to 0.53 (Table 5). The 1.58 hatchlings per adult found in January 1973 may be due to sampling bias favoring the hatchlings. Inasmuch as there had been heavy rainfall during October, November, and December 1972, the ground was wet and temperatures were low when collections were made in January 1973. Many adults may have been deeper underground and were not encountered. Additional evidence for sampling error in January 1973 comes from the clutch-size data for July 1972 (Fig. 24) and the number of hatchlings in the September 1972 sample (Fig. 23). It would not have been possible for 31 adults to produce 49 hatchlings (Table 5).

It is evident (Table 5) that over a four-year period there were somewhat fewer than twice as many juveniles (268) as hatchlings (157) collected. Allowing for low mortality, it would take two years to accumulate the juvenile population observed in December and January (actually 27 months since hatching occurs in September). By the following July some juveniles would be 33 months old and might occasionally yolk up eggs (Fig. 24). However, most juveniles do not ma-

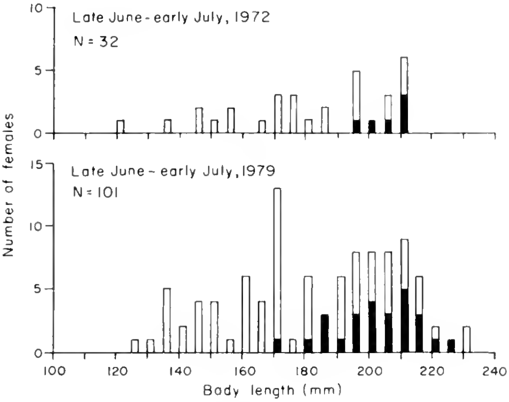

FIGURE 24. Frequencies of gravid *Bipes biporus*. Mature females are usually over 185 mm in body length. Gravid females are represented by solid rectangles.

ture until a year later at an age of about 45 months.

In summary, female *B. biporus* usually mature at a body length of 185 mm and at an age of about 45 months. Occasionally, smaller females may reproduce (none in 1972; 2 of 20 in 1979). Fewer than half the adult females are gravid in a given year. Eggs are laid in July, and hatchlings appear in September.

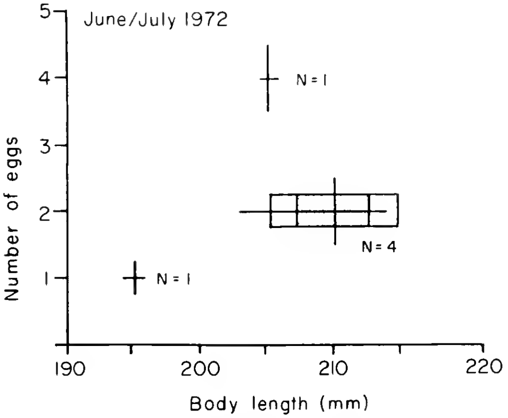

FIGURE 25. Enlarged ovarian and oviducal egg number of *Bipes biporus* collected during late June and early July 1972. The egg number ranges from one to four. No female with three eggs was found in this small sample. The Dice-Lerras diagram represents the size range of females producing two eggs. Horizontal line is range; vertical line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error.

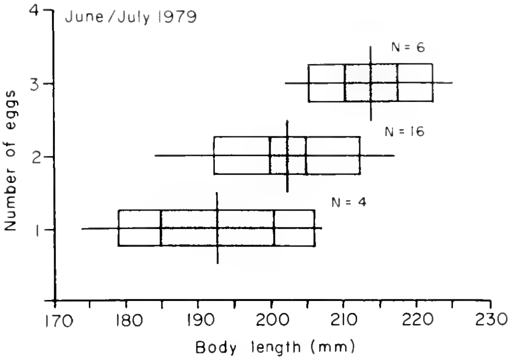

FIGURE 26. Enlarged ovarian and oviducal egg number of *Bipes biporus* collected during late June and early July 1979. Each Dice-Lerras diagram represents the size range of females producing a given egg number. Horizontal line is range; vertical line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error. Females producing three eggs are significantly larger than those producing one or two eggs (Student's $t$-test; $P < .05$).

## Discussion

An analysis of the reproductive traits of *Bipes* places all three species at the K end of an r–K continuum (sensu Pianka 1970b, 1972). These traits include delayed maturity, small clutch size, and in two of the species, non-annual reproduction. It is not possible to compare the life history traits of *Bipes* with other amphisbaenians because no data are available. There is, however, a large body of data available on lizard reproduction (Fitch 1970; Tinkle et al. 1970).

TABLE 4. SEX RATIO OF *Bipes biporus*. The samples have been broken into two size classes: juveniles (under 185 mm in body length) and adults (over 185 mm in body length). Hatchlings (under 130 mm in body length) are not included because of the difficulty in accurate sex determination. The data suggest that there are about twice as many adult females as adult males.

| Date of Sample | 130–185 mm | | >185 mm | |
|---|---|---|---|---|
| | ♂ | ♀ | ♂ | ♀ |
| Jul 1972 | 13 | 14 | 13 | 15 |
| Mar 1974 | 28 | 27 | 12 | 25* |
| May 1977 | 8 | 18* | 5 | 10 |
| May 1978 | 29 | 31 | 6 | 18* |
| Totals | 78 | 90 | 35 | 68* |

* = significant increase in number of females above a 50:50 ratio ($P < .05$, chi-square test).

TABLE 5. BREAKDOWN BY AGE CLASS OF *Bipes biporus* SAMPLES COLLECTED DURING DECEMBER AND JANUARY BETWEEN 1973 AND 1976. Hatchlings are the young of the year based upon apparent breaks in distribution of size classes. Juveniles are individuals one or more years old that have not yet reached sexual maturity. Adults are individuals that are over 185 mm in body length.

| Date | Sample Size | No. of Hatchlings | No. of Juveniles | No. of Adults | No. of Hatchlings per Adult | Rainfall During Previous 12 Months |
|---|---|---|---|---|---|---|
| Jan 1973 | 137 | 49 | 57 | 31 | 1.58 | 475.1 mm |
| Dec 1973 | 188 | 36 | 69 | 83 | 0.43 | 198.9 mm |
| Jan 1975 | 126 | 20 | 61 | 45 | 0.44 | 157.7 mm |
| Dec 1975 | 112 | 24 | 43 | 45 | 0.53 | 84.9 mm |
| Dec 1976 | 131 | 28 | 38 | 65 | 0.43 | 288.7 mm |
| Totals | 694 | 157 | 268 | 269 | 0.58 | |

*Bipes* have an extremely low reproductive potential compared to most lizards.

Within the genus *Bipes*, both *B. canaliculatus* and *B. biporus* have a much lower reproductive potential than *B. tridactylus* (Table 6). Mean clutch size per gravid female is similar for all three species (2.15–2.8 eggs), but *B. tridactylus* females mature at least one year earlier than do the other two species, and all female *B. tridactylus* are gravid each year, while fewer than half the adult female *B. canaliculatus* and *B. biporus* are gravid each year.

Although there are ecological and behavioral differences, all three species live in similar subterranean environments. The stability of the underground certainly tempers the effects of seasonal and annual climatic fluctuations. This point is well illustrated by Table 5. Except for the high number of hatchlings obtained in January 1973, which was most likely due to sampling error (see above), the ratio of hatchlings to adults remained remarkably constant over a four-year period (0.43–0.53). This suggests a similar reproductive success each year even though there was considerable fluctuation in annual rainfall during these years. Although 1975 was a drought year when half the cattle in Baja California died and *Sauromalus* were found dead and dried in crevices, the *Bipes* population appeared to suffer no ill effects.

Egg deposition occurs during the dry season, and hatchlings emerge during or shortly before the onset of summer rains. In coastal Guerrero, where *B. tridactylus* is found, the rainy season starts in May or June. In the Balsas Basin, where *B. canaliculatus* is found, the rainy season starts in June or July; and in the Cape region of Baja California, where *B. biporus* occurs, the rainy season usually begins in August or September.

## Field Observations

All three species of *Bipes* are subterranean. Only 3 out of more than 3800 individuals obtained during this study were found active on the surface. Some *B. biporus* were found under surface objects such as rocks and logs, but most of the *B. biporus* and all of the *B. canaliculatus* and *B. tridactylus* specimens were dug from the ground. Unlike most other reptiles in western Mexico, *Bipes* are active throughout the year

TABLE 6. COMPARATIVE FEMALE LIFE HISTORY TRAITS IN THE GENUS *Bipes*.

| | Approx. Size at Maturity | Approx. Age at Maturity | Length of Reproductive Cycle | Mean Clutch Size per Gravid Female | Mean Clutch Size per Adult Female | Time of Egg Deposition | Time of Hatching |
|---|---|---|---|---|---|---|---|
| *B. tridactylus* | 115 mm | 21 mos | Annual | 2.2 | 2.1 | Jan | Apr |
| *B. canaliculatus* | 185 mm | 45 mos | Biennial | 2.8 | 1.02 | Feb–Mar | Apr–Jun |
| *B. biporus* | *185 mm | *45 mos | Biennial | 2.15 | 1.0 | Jul | Sep |

* In July 1979, two gravid females less than 185 mm in body length were obtained. These individuals could be 33 months old.

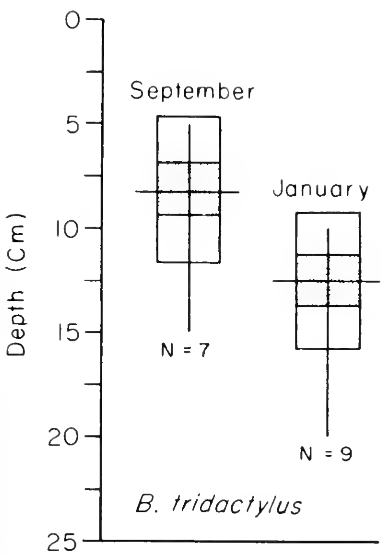

FIGURE 27. Depth beneath surface of ground of *Bipes tridactylus*. The two Dice-Lerras diagrams represent the depths beneath the surface at which individuals were found during the rainy season (September) and during the dry season (January). Vertical line is range; horizontal line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error. Individuals collected in January were significantly deeper than those collected in September (Student's *t*-test; $P < .05$). Both samples were collected between 1600 and 1800 hr.

TABLE 7. DEPTH BENEATH SURFACE OF GROUND OF 208 *B. biporus* AT TIME OF CAPTURE. At all times of the year specimens were most frequently found within a depth of 2.5 cm below the soil crust. Samples were collected between 900 and 1200 hr.

| Depth (cm) | Dec + Jan | Mar + Apr | Jul | Sep | No. Indiv. |
|---|---|---|---|---|---|
| 2.5 | 21 | 54 | 28 | 6 | 109 |
| 5.0 | 8 | 43 | 10 | 4 | 65 |
| 7.5 | — | 14 | 4 | — | 18 |
| 10.0 | — | 10 | 2 | 1 | 13 |
| 12.5 | — | — | — | — | 0 |
| 15.0 | — | 3 | — | — | 3 |
| No. indiv. | 29 | 124 | 44 | 11 | 208 |
| Mean depth (cm) | 3.2 | 4.8 | 3.9 | 4.1 | |

and can be easily collected at any season. There are interspecific differences in the depth at which the species most commonly occur and in their thermoregulatory behavior.

### Depth

The two mainland species are usually deeper in the ground than is *B. biporus*. *Bipes tridactylus* often were encountered between 5 and 20 cm beneath the surface (Fig. 27). Individuals collected during the dry season (January) were significantly deeper ($\bar{x}$ = 12.5 cm) than those collected in September during the rainy season ($\bar{x}$ = 8.2 cm). During the dry season the soil near the surface is dry, but damp at greater depths. During the rainy season the soil is damp throughout, and the invertebrate food supply is likely to be more plentiful near the surface in the humus layer.

Data on depth preference of *B. canaliculatus* are available only for the month of August. The mean depth was 19.8 cm (range 2.5–60 cm). There is little leaf litter or humus on the banks of the Río Balsas at the study site and individuals were usually encountered in association with the roots of trees. Burrow systems extend from near the surface to depths of one meter or more and individuals seem to move randomly about their burrows. Along the shaded banks of the river (Fig. 4), there are only slight temperature differences between shallow and deep soil. On 1 August 1976 at 1400 hr the soil temperature was 28.0 C at a depth of approximately 10 cm, 27.8 C at 20 cm, 27.0 C at 30 cm, 26.4 C at 45 cm, and 29.0 C at 60 cm. The lack of an invertebrate-rich humus layer combined with the thermal uniformity of burrow systems may contribute to the apparent random depth of occurrence of this species.

Most *B. biporus* were collected near the surface at all seasons. Pooled data on 253 individuals obtained during the winter, spring, summer, and fall show a mean depth at time of capture of only 3.6 cm (range 2.5–15 cm). A total of 165 of these animals were found within 2.5 cm of the surface. The burrow systems of the species extend toward the surface and then run just under the soil crust. Because collecting was done by digging in the ground with shovels, individuals deeper than about 20 cm (the length of a shovel blade) were not encountered. This collecting bias, however, does not obscure the point that this species lives mainly in shallow burrow systems. Out of a total of 208 animals, only 13 were found at a depth of 10 cm, and only 3 at 15 cm (Table 7). Over 50% were found within a depth of 2.5 cm of the surface. In contrast, not a single

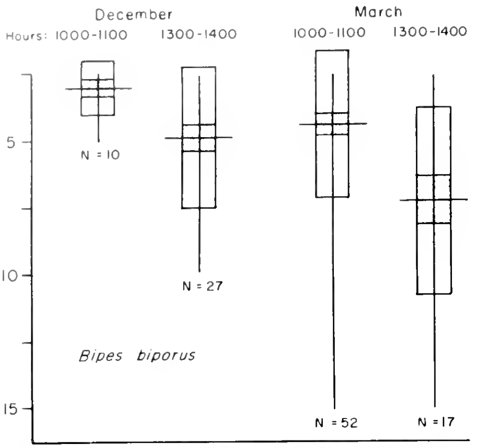

FIGURE 28. Depth beneath surface of ground of *Bipes biporus* at different times of the day. Vertical line is range; horizontal line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error. In both December and March individuals were significantly deeper in the afternoon than in the morning (Student's $t$-test; $P < .05$).

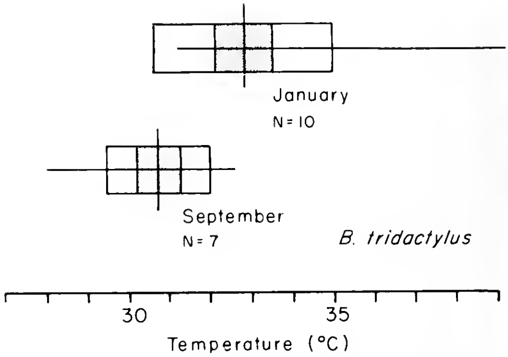

FIGURE 29. Cloacal temperature of *Bipes tridactylus*. The two Dice-Lerras diagrams represent the cloacal temperatures of individuals collected during the dry season (January) and the rainy season (September). Both samples were obtained between 1600 and 1800 hr. Horizontal line is range; vertical line is mean; open rectangle on each side of mean represents one standard error. Individuals collected in January had a significantly higher cloacal temperature than those collected during September (Student's $t$-test; $P < .05$).

*B. tridactylus* and only one *B. canaliculatus* were found at this depth.

Even within the narrow range of depths at which this species was found, there were subtle differences in preferred depth at different times of the day. This slight diurnal vertical movement was probably correlated with behavioral thermoregulation (see below). Due to the narrow range of depths at which this species was active, preferred depth could only be determined statistically when large samples were available from different hours of the day. Although differences were not significant on an hour-by-hour basis, during both December and March, individuals were significantly closer to the surface at 1000 hr than at 1300 hr (Fig. 28). The *Bipes* were "basking" near the surface in the morning, and once they had reached a suitable body temperature and/or the soil had warmed to greater depths, they move over a greater vertical distance.

*Bipes biporus* also showed diurnal shift in horizontal position with respect to shade. This

TABLE 8. POSITION OF *Bipes biporus* WITH RESPECT TO SUNNY OR SHADY LOCATIONS. Data are presented for three seasons: Winter (December), Spring (March and April), and Summer (July and August).

| | Winter | | Spring | | Summer | |
|---|---|---|---|---|---|---|
| Time of Day | No. in Shade | No. in Sun | No. in Shade | No. in Sun | No. in Shade | No. in Sun |
| 0600–0659 | — | — | — | — | 0 | 4* |
| 0700–0759 | — | — | — | — | 4 | 18* |
| 0800–0859 | — | — | — | — | 15 | 30* |
| 0900–0959 | — | — | 2 | 1 | 8 | 11 |
| 1000–1059 | 0 | 7* | 6 | 21* | 1 | 1 |
| 1100–1159 | 0 | 8* | 10 | 32* | — | — |
| 1200–1259 | 4 | 12* | 2 | 14* | — | — |
| 1300–1359 | 4 | 13* | 2 | 8 | — | — |
| 1400–1459 | 12 | 19 | 0 | 1 | — | — |
| 1500–1559 | 0 | 4* | 3 | 2 | — | — |
| 1600–1659 | — | — | 5 | 6 | — | — |

* = significantly higher proportion of individuals found in sunny locations (chi-square test, $P < .05$).

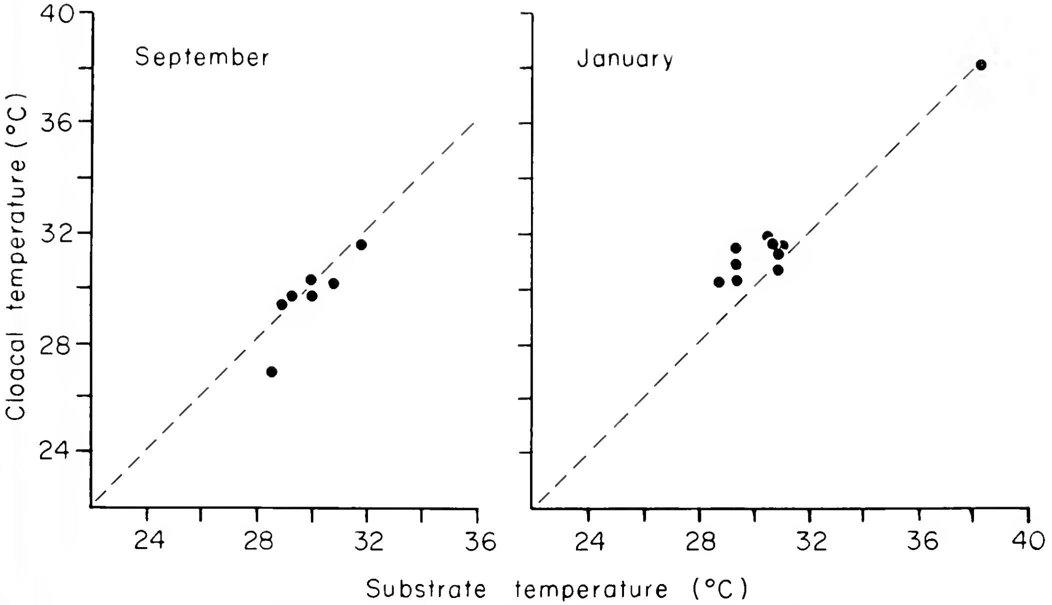

FIGURE 30. The relation of cloacal temperature to substratum temperature in *Bipes tridactylus* during the rainy season (September) and the dry season (January). No individual had a cloacal temperature more than 2.0 C above or 1.6 C below the substratum temperature. Both samples were collected between 1600 and 1800 hr.

species was usually found in the vicinity of a surface object such as a tree, shrub, or fence post. By horizontal movement around surface objects, an individual could position itself to be in either a sunny or shaded location. During most of the one-hour sampling periods, more individuals were found in sunny than in shaded locations (Table 8). This was particularly striking for July and August when samples were obtained very early in the morning. Even with the sun low on the horizon and shadows from surface objects shading much of the surrounding ground, a significantly greater number of *B. biporus* were found in sunny locations (Table 8).

## Temperature

Limited temperature data for *Bipes tridactylus* suggest that this species does not exhibit much thermoregulatory behavior (Fig. 29). Mean cloacal temperatures of individuals collected in January ($\bar{x}$ = 31.8 C) were significantly higher than of those collected in September ($\bar{x}$ = 29.7 C) (Student's *t*-test; $P < .05$). However, mean substratum temperatures at points of capture were also significantly higher in January than in September ($\bar{x}$ = 30.9 C versus 29.1 C). A plot of cloacal temperature against substratum temperature shows that there is little difference between the two (Fig. 30). Individuals collected in January tended to have slightly higher cloacal temperatures than the adjacent substratum, but in no case was the difference more than 2.0 C. Likewise, no individual was found with a cloacal temperature lower than 1.6 C below the substrate temperature.

These data suggest that any thermoregulatory behavior in this species may be limited to slight positional changes. Not only are temperatures higher in January but it will be recalled (Fig. 27) that individuals are found deeper in the ground in January than in September. This species occurs in a subtropical region where soil temperatures are warm year around but warmer during the dry season (January) for three reasons: (1) a lack of cloud cover increases the number of hours that the sun's rays strike the surface of the ground; (2) the surface ground cover of small annual plants is reduced; and (3) ground temperatures are not lowered by evaporative cooling. A retreat deeper into the ground during the dry season may allow this species to avoid high temperatures near the surface and also to find moisture in the deeper soil layer.

Temperature data for *Bipes canaliculatus* are

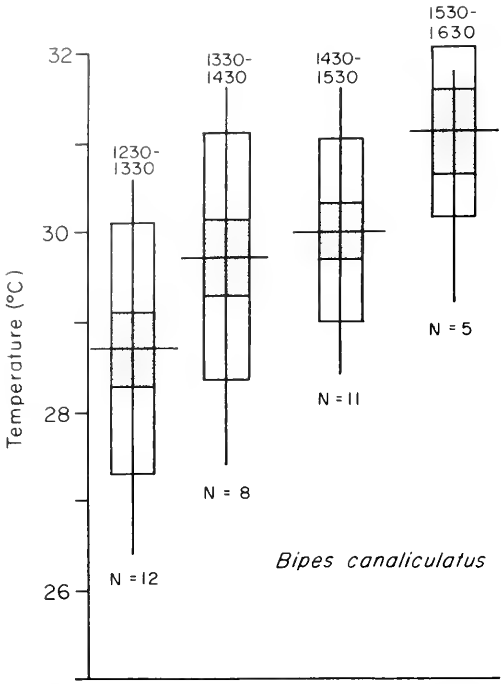

FIGURE 31. Cloacal temperature of *Bipes canaliculatus* showing change with time of day in August. Each Dice-Lerras diagram represents the cloacal temperatures of individuals collected during one-hour time periods between the hours of 1230 and 1630. Vertical line is range; horizontal line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error. Cloacal temperatures of individuals collected between 1530 and 1630 hr are significantly higher than those collected between 1230 and 1330 hr (Student's *t*-test; $P < .05$).

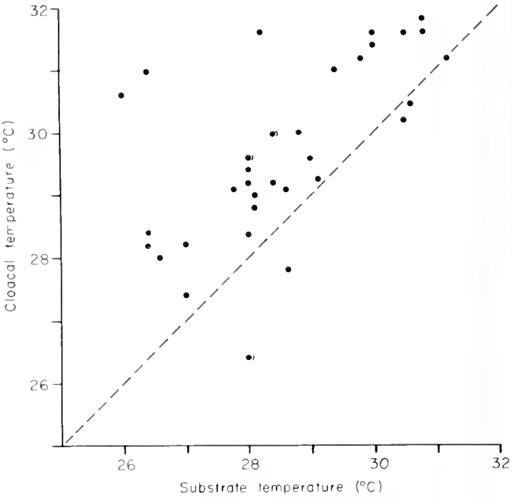

FIGURE 32. The relation of cloacal temperature to substratum temperature in *Bipes canaliculatus*. The plot shows that in most cases cloacal temperature was higher than substrate temperature. A direct relationship would be represented by points falling along the dotted line.

only available for the month of August. Cloacal temperatures were obtained over a four-hour period between 1320 and 1630 hr (Fig. 31). Mean cloacal temperatures increased as the afternoon progressed from a low of 28.7 C for individuals collected between 1230 and 1330 hr to 31.1 C for individuals collected between 1530 and 1630 hr. Most individuals (30 of 36) had a cloacal temperature that was higher than the temperature of the adjacent substratum (Fig. 32).

Data on the soil–depth relations of this species appear to be contradictory to the thermal data for two reasons. First, soil temperatures taken in burrows in shaded areas at depths ranging from 10 to 60 cm fell within a narrow range (26.4–29.0 C). Second, the apparent random location of individuals with respect to depth would predict a close agreement between cloacal and substratum temperature because this species does not seem to "need" to be at any particular place and would be expected to show thermal correspondence with its surroundings. How can individuals be consistently warmer than their substratum, and how do they increase their temperature as the afternoon progresses?

The highest burrow temperature recorded in the shade was 29.0 C. However, there were 11 examples where the substratum temperature in the burrow exactly where a *Bipes* was located was higher (Fig. 32). These soil temperatures may have been taken at locations that had been warmed by morning sun. This does not, however, explain how six individuals (Fig. 32) could have had a cloacal temperature greater than the highest substratum temperature recorded (31.2 C). Although no temperatures were taken just below the surface, one would predict high temperatures in the sun just below the soil crust, and if individuals had been near the surface, they could achieve body temperatures higher than 31.2 C.

The somewhat indirect reasoning presented above suggests that *B. canaliculatus* exhibits behavioral thermoregulation by movement about its burrow system. Thermal data for the morning hours would be most useful.

Temperature data for *Bipes biporus* are avail-

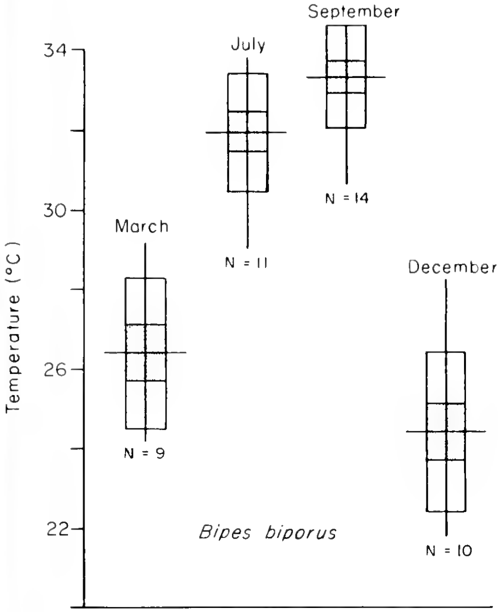

FIGURE 33. Cloacal temperatures of *Bipes biporus* showing a change with season. Individuals were obtained between 1000 and 1100 hr except for the July sample which was obtained between 0900 and 1000 hr. Vertical line is range; horizontal line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error. Mean cloacal temperatures are significantly higher in July and September, the warmer months of the year, than in December and March (Student's *t*-test; $P < .05$).

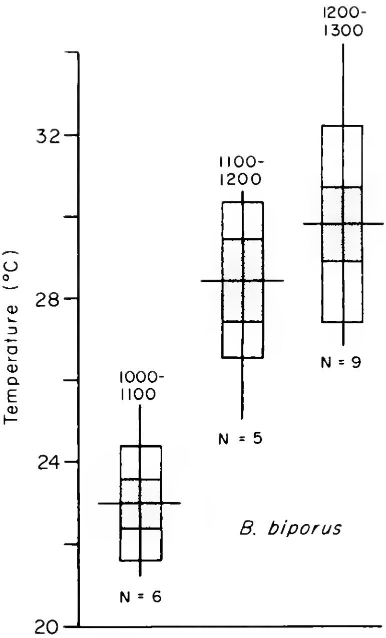

FIGURE 34. Cloacal temperatures of *Bipes biporus* showing a change with time of day in March. The three Dice-Lerras diagrams represent the cloacal temperatures of individuals collected during hourly time intervals between 1000 and 1300 hr. Horizontal line is range; vertical line is mean; open rectangles on each side of mean represent standard deviation; solid rectangle on each side of mean represents one standard error. Individuals have a significantly higher cloacal temperature between 1100 and 1300 hr than between 1000 and 1100 hr (Student's *t*-test; $P < .05$). All individuals were found within 2.5 cm of the soil crust.

able for four times of the year (December, March, July, and September). Morning cloacal temperatures have been compared for individuals obtained between 1000 and 1100 hr in December, March, and September and between 0900 and 1000 hr during July (Fig. 33). Mean cloacal temperatures were significantly higher in July and September, the warmer months of the year, than they were in December and March. At any time of the year, mean cloacal temperatures were higher late in the morning than early in the morning. The mean cloacal temperature of individuals collected during March between 1000 and 1100 hr was 23.0 C, and between 1200 and 1300 hr was 29.8 C (Fig. 34). During July the mean was 26.2 C between 0700 and 0800 hr and 32.1 C between 0900 and 1000 hr (Fig. 35). These data for March and July include only individuals found in burrow systems within 2.5 cm of the surface. The data demonstrate the facts that temperatures in *Bipes* are higher during the warmer months of the year (July and September) than they are during the colder months (December and March), and that cloacal temperatures increase during the course of the day as the surface layer warms. In July, between the hours of 0900 and 1000 soil temperatures within 2.5 cm of the surface ranged from 28.4 to 30.4 C; September, between the hours of 1000 and 1100 from 30.2 to 34.2 C; December, between the hours of 1000 and 1100 from 21.4 to 27.8 C; and March, between the hours of 1000 and 1100 from 23.4 to 29.0 C.

These data make it appear that *B. biporus* does not show behavioral thermoregulation, but instead exists passively in the soil, warming and cooling with substratum changes. However, this is not the case. Other data show that individuals prefer to be in sunny locations and near the surface early in the day (Fig. 28, Table 7). Con-

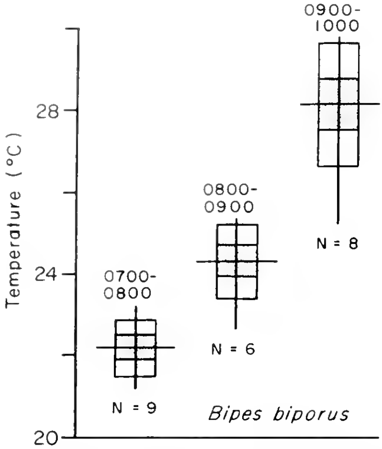

FIGURE 35. Cloacal temperatures of *Bipes biporus* showing a change with time of day in July. The three Dice-Lerras diagrams represent the cloacal temperatures of individuals collected during hourly time intervals between 0700 and 1000 hr. All individuals were found within 2.5 cm of the soil crust. Horizontal line is range; vertical line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error. Individuals have a significantly higher cloacal temperature during each time interval as the morning progresses.

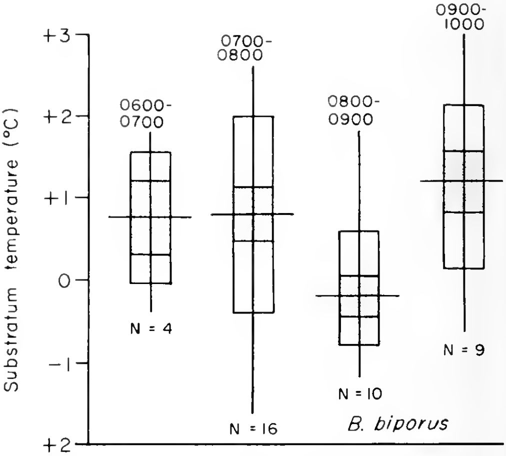

FIGURE 36. Difference between cloacal and substratum temperatures in *Bipes biporus* in relation to time of day. Each Dice-Lerras diagram represents the difference between cloacal temperature and substratum temperature of individuals collected during one-hour time periods between the hours of 0600 and 1000 during a single day, 21 July 1976. Vertical line is range; horizontal line is mean; open rectangle on each side of mean represents one standard deviation; solid rectangle on each side of mean represents one standard error. Mean cloacal temperatures were lower than substratum temperature between the time period 0800 to 0900 hr. During the time periods 0700 to 0800 hr and 0900 to 1000 hr, mean cloacal temperatures not only exceed substratum temperatures but were significantly above the mean cloacal temperature during the 0800-to-0900-hr time period (Student's $t$-test; $P < .05$).

vincing additional data demonstrating behavioral thermoregulation are available as well.

During the morning of 21 July 1976, substratum and cloacal temperatures were obtained for 39 *B. biporus* between 0600 and 1000 hr (Fig. 36). Between 0600 and 0800 hr, individuals had mean cloacal temperatures that were higher than the substratum. Between 0800 and 0900 hr, mean cloacal temperatures were lower than the substratum, and between 0900 and 1000 hr, cloacal temperatures were again higher than the substratum. The question is, why is there a "dip" in temperature between 0800 and 0900 hr? In the early morning *Bipes* move upward in their burrows to near the surface where soil temperatures have cooled during the night. The early morning soil temperature at the surface is over 7 C lower than the temperature at a depth of 20 cm (Table 9). The warm *Bipes* come to the cool surface in anticipation of warming further as the morning sun heats the soil. Thus, in the early morning their cloacal temperatures are higher than the substratum. They do not have to wait long because the sun quickly raises the soil temperature, and by 0800 to 0900 hr (Fig. 36) substratum temperatures slightly exceed cloacal temperatures. Soon the surface substratum temperature is above the preferred *Bipes* temperature, and they either move slightly deeper (Fig. 28) or else move into the shade (Table 8; 8 of 11 individuals were in the shade during the summer between 0900 and 1000 hr). Thus *B. biporus* clearly exhibits behavioral thermoregulation.

## Discussion

Temperature may be the most important physical factor in the ecology of reptiles (Heatwole 1976). Through a combination of the physical characteristics of heat exchange, behavioral activity patterns, and physiological factors, reptiles are able to regulate their body temperatures. Numerous studies, mostly on diurnal lizards, have shown that individual species have a preferred range of body temperatures and are able to seek and maintain these temperatures during their times of activity (Cowles and Bogert 1944; McGinnis and Brown 1966; Ruibal 1961; Heatwole 1976).

The main physical properties of heat exchange that are utilized by reptiles to gain or lose heat are absorption of radiant energy, convection, and conduction. Diurnal surface reptiles may utilize all three physical properties to achieve and maintain a preferred body temperature. Thermal studies have not been conducted on obligatory fossorial reptiles. Species that are never active on the surface must rely primarily on conduction to regulate their body temperature. Strictly fossorial species such as *Bipes* are thigmothermic, and because they derive their body temperatures from the soil in which they live, they have been regarded as having little or no capacity for thermoregulation (Cowles 1962).

It is now known that some fossorial species can thermoregulate if necessary. *Bipes biporus* clearly thermoregulates by vertical and horizontal changes in location during the day. Thermoregulation may be particularly important to this species because it occurs in an area where temperatures are low during the winter. By "basking" near the surface, it is able to reach a sufficiently high temperature to be active throughout the year, even though both air temperatures and deep soil temperatures are low.

The two mainland species, *B. canaliculatus* and *B. tridactylus*, occur further south in a tropical environment with high temperatures throughout the year. In these two species behavioral thermoregulation does not appear critical for year-round activity.

## ACKNOWLEDGMENTS

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This study would not have been possible without the help of the local inhabitants at the study areas. Sr. Mariano Rojas of Tecpan de Galeana, Sr. Fidensio Leya of Mezcala, and Sr. Rudy Velez of La Paz were especially helpful.

The following individuals, perhaps curious to see *Bipes* in the field, each assisted on a single field trip: Samuel Sweet, James Hanken, James Lynch, Robert Stebbins, Nathan Cohen, Stephen Ruth, Ray Huey, Robert Macey, and John Cadle. Although not each individual actually dug up a *Bipes*, they all tried. Three people went on many trips to Mexico. They helped dig, tag, weigh, measure, and preserve far more *Bipes* than they ever imagined they would. Steve Garnick, James Dixon, and Robert Seib provided tremendous help. On one trip, when I had to return home early, Robert Seib went to Mezcala alone and obtained 270 *Bipes canaliculatus* in a single day. This was my most valuable single sample because it allowed me to estimate the age structure for this species.

TABLE 9. SOIL TEMPERATURE (°C) PROFILE AT LA PAZ, BAJA CALIFORNIA SUR, MEXICO, DURING THE MORNING OF 21 JULY 1976.

| Depth (cm) | Sunny Clearing in Open Mesquite Thicket 0745 hr | Sunny Open Field 1000 hr | Deeply Shaded Mesquite Thicket 1000 hr |
|---|---|---|---|
| Surface | 24.8 | 42.8 | 29.4 |
| 2.5 | — | 41.6 | 29.2 |
| 5.0 | 26.6 | 35.0 | 29.0 |
| 10.0 | 29.2 | 32.6 | 28.6 |
| 15.0 | 31.4 | 32.8 | 29.0 |
| 20.0 | 32.2 | 34.0 | 29.6 |
| 25.0 | — | 34.6 | 29.8 |

## RESÚMEN

El género anfisbénido *Bipes* consta de tres especies morfológicamente distinguibles por sus diferencias en tamaño corporal, longitud de la cola, número de anillos y grado de reducción digital. *Bipes biporus* se distribuye en la península de Baja California, *B. tridactylus* en la costa de Guerrero, y *B. canaliculatus* (incluyendo *B. alvarezi* Smith y Smith, considerado aquí como sinónimo) en la cuenca del río Balsas, en Guerrero y Michoacán. Hasta la fecha, estas tres especies habían sido consideradas escasas. Entre 1971 y 1979 varios sitios de estudio fueron visitados en diversas ocasiones y en diferentes estaciones del año. Individuos de *Bipes* fueron fácilmente recolectados por excavación y sobre 3000 de ellos se acumularon al término del trabajo de terreno.

La distribución alopátrida de las tres especies es razonablemente explicable en referencia a los eventos tectónicos ocurridos en el oeste de México en los últimos 20 millones de años. El *Bipes* ancestral habría quedado separado en tres poblaciones debido a la formación de la península de Baja California y al levantamiento de la Sierra Madre del Sur en Guerrero.

Autotomía caudal se produce por un único plano de fractura intravertebral. Como no ocurre regeneración del apéndice, su pérdida es permanente y provee información útil sobre los niveles de predación a que los *Bipes* están sujetos. La frecuencia poblacional de pérdida de cola es baja en *B. biporus* (2.7%) y más alta en las dos especies continentales (10.2% en *B. canaliculatus* y 17.0% en *B. tridactylus*). En las tres especies la incidencia de colas autotomizadas aumenta con la edad de los individuos. Una mayor presión de predación sobre los *Bipes* continentales podría deberse a la presencia de víboras de coral (*Micrurus*), las que están ausentes en Baja California. Estas víboras pueden entrar a los sistemas de túneles excavados por *Bipes* y es conocido que se alimentan de estos anfisbénidos.

Las características de historia de vida difieren en cada especie. *Bipes tridactylus* madura a un tamaño de 115 mm, aproximadamente a la edad de 21 meses. Hembras grávidas presentan un tamaño promedio de puesta de 2.2 huevos y se reproducen anualmente. *Bipes canaliculatus* madura a un tamaño aproximado de 185 mm, con 45 meses de edad. Aunque el tamaño promedio de la puesta es 2.8 huevos por hembra grávida, éste se reduce a 1.0 si se considera que las hembras se reproducen sólo cada dos años. *Bipes biporus* madura aproximadamente con 185 mm, a una edad de 45 meses. La puesta promedio es de 2.2 huevos por hembra grávida, pero como su ciclo es bianual el promedio se reduce a 1.0. La proporción de machos a hembras es 50:50 en *B. tridactylus* y *B. canaliculatus*. Sin embargo, en *B. biporus* las hembras casi doblan en número la cantidad de machos encontrados. Actualmente no es posible decidir si esta diferencia se debe a errores de muestreo, mortalidad diferencial de los sexos, o a una tasa sexual primaria sesgada en favor de las hembras.

Las tres especies son de hábitos subterráneos y viven en sistemas de túneles construídos por ellas mismas. Los *Bipes* continentales se encuentran usualmente a profundidades entre 10 y 20 cm de la superficie del suelo. En cambio, ningún *B. biporus* se encontró a profundidades mayores de 15 cm y más del 50% de los individuos fueron recolectados en túneles muy superficiales, a alrededor de 2.5 cm de profundidad. Estas diferencias en estratificación podrían estar relacionadas con la conducta termorregulatoria de las tres especies. Los dos *Bipes* continentales se distribuyen en areas subtropicales donde las temperaturas del suelo son altas durante todo el año. Probablemente las capas de suelo más superficiales exceden la temperatura preferida por estos anfisbénidos. Por otra parte, *B. biporus* termorregula en forma conductual, desplazándose entre zonas soleadas y sombreadas de acuerdo a su temperatura.

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