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THE HERPETOFAUNA OF KOMODO, WITH NOTES ON ADJACENT AREAS

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THE HERPETOFAUNA OF KOMODO, WITH NOTES ON ADJACENT AREAS

Walter Auffenberg[1]

Synopsis.—The reptiles and amphibians of Komodo are reviewed; their taxonomy, distinguishing features, habitat preferences, parasites, and food habits are discussed. Zoogeography of the Lesser Sunda Islands is reconsidered in the light of new geologic data. A number of the included species have never before been reported from Komodo—some constitute considerable range extensions. New taxa are *Typhlops schmutzi* (n. sp. from Komodo), *Hemiphyllodactylus typus pallidus* (n. ssp. from Komodo), and *Cyrtodactylus laevigatus uniformis* (n. ssp. from Flores). *Leilopisma kadarsani* Darevsky is placed in the synonomy of *Emoia similis* Dunn, and *Sphenomorphus mertensi* Darevsky is placed in *S. emigrans emigrans* (Lidth de Jeude). *Cryptoblepharus boutonii burdeni* (Dunn) is given specific status as *C. burdeni* Dunn.

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INTRODUCTION

During 1969-70, 1971, and 1973 I collected reptiles and amphibians on Komodo and nearby islands in connection with a 17-month study of the Komodo monitor (*Varanus komodoensis*, Auffenberg, in press). This report deals with the material collected on Komodo incidental to that study, though comparative material from other Sunda Islands is often referred to. Earlier reports dealing with the herpetology of Komodo were results of two previous major field studies in the area: the Douglas Burden expedition (Dunn 1927a, 1927 b, Burden 1927) and the joint Indonesian-Soviet Expedition (Darevsky 1964a, 1964b, 1964c, Darevsky and Kadarsan 1964). The present contribution shows that the fauna is considerably more diverse than previously believed.

MATERIALS AND METHODS

Three collections form the basis of this study: those of the Florida State Museum, University of Florida (UF), the American Museum of Natural History (AMNH), and the Museum Zoologicum Bogoriense (Bogor, Java, MZB). Fortunately I was able to see in the wild all but two of the species reported from the island and to study the types of all the endemic forms.

Synonymies in the species accounts include only the original reference, the earliest use of the present name, and all synonymies used in papers dealing with Komodo and nearby islands. The spelling of many place names in Indonesia is remarkably varied, and no gazetteers include all the local names. I have tried to be consistent in using the most approved local spellings.

ACKNOWLEDGEMENTS

Primary support for the investigation of the behavior of *Varanus komodoensis* came from the New York Zoological Society and the Florida State Museum. Critical aid in the field came from various agencies of the Indonesian government. In particular, I owe thanks to the official assistance and cooperation of Hasan Basjarudin Nasution, Directorate of Forestry, and Walman Sinaga, Department of Conservation, Bogor. Without their help it would have been impossible to study the monitors on any of the islands. Otto Soemarwoto, National Academy of Biology, S. Somadikarta, Museum Zoologicum Bogoriense, and especially Sjamsiah Achmad, Indonesian Institute of Sciences, were instrumental in facilitating our research program. I am very grateful for the varied assistance rendered the project by the late Hilmi Oesman, Surabaja Zoological Gardens, and Benjamin Galstaun, Jakarta Zoological Garden.

The field work would have been considerably less successful and pleasant without the able assistance of Putra Sastrawan (Denpasar, Bali), William Holzmark (Sarasota, Florida), Robert Armistead (Gainesville, Florida), Fred G. Thompson and Howard H. Converse (Florida State Museum), and particularly my sons Kurt and Garth. Of utmost importance was the cooperation and interest in the project shown by the Komodo villagers. In the laboratory, I owe many thanks to Richard Franz and Sylvia Scudder (Florida State Museum) without whose help the more tedious parts of the study might have remained incomplete. The suggestions and (in some cases) loans of specimens in their care by Illya Darevsky, S. Kadarsan, G. Zug, E. Williams, H. Oesman, and R. Zweifel are hereby gratefully acknowledged. Finally, this work would not have been possible without the continued interest shown by F. Wayne King, formerly of the New Zoological Society, currently Director of the Florida State Museum.

Those drawings not done by myself (uninitialed) are the work of Nancy R. Halliday and Glen Rogers. Rhoda J. Rybak typed and copystyled the manuscript. I am deeply indebted to Alan Leviton and George Zug, whose critical reviews greatly improved the manuscript.

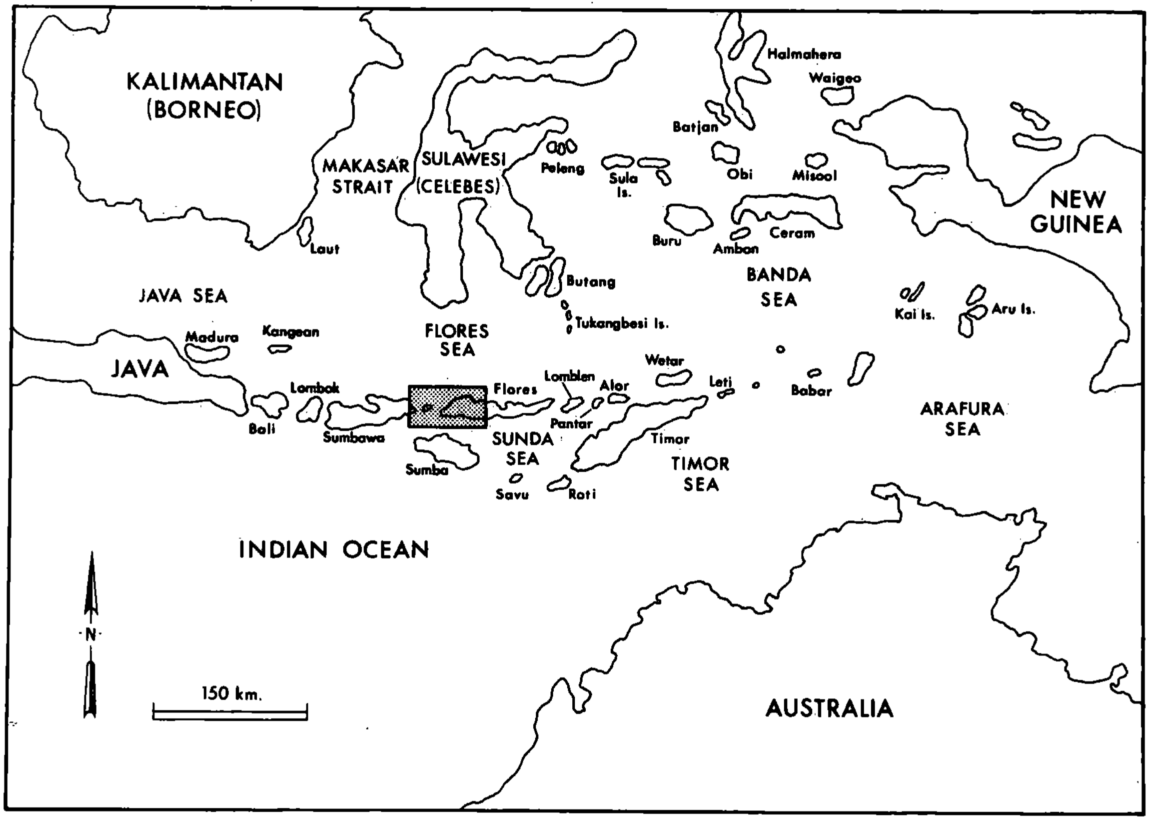


FIGURE 1.—Map showing location of Komodo (in marked rectangle, enlarged as Fig. 2).

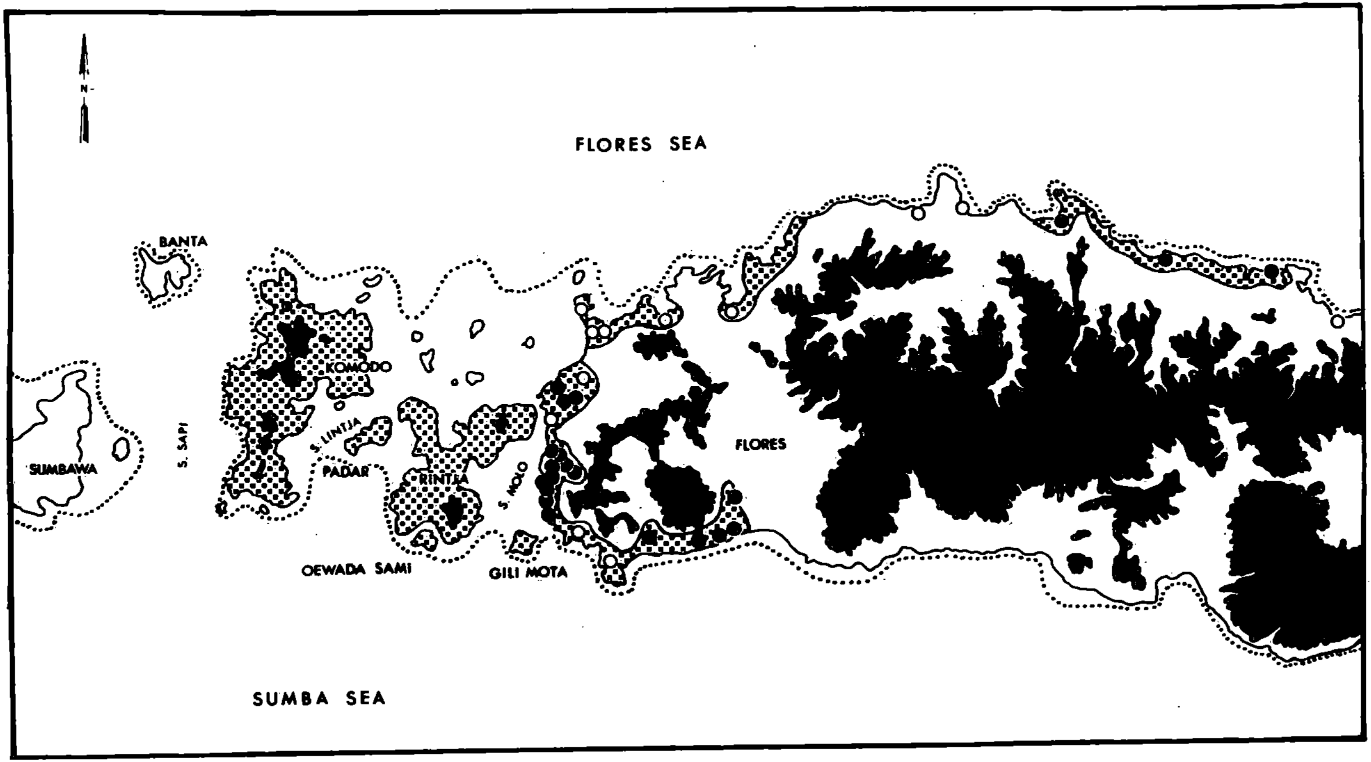


FIGURE 2.—Komodo Island and vicinity. Dotted line represents 100 m contour below sea level; black area indicates land surface above 500 m.

ECOLOGY OF KOMODO

Komodo is a small island (ca 160 km^2) of the Lesser Sunda group between Java and New Guinea (Figs. 1 and 2, 8°S, 119°E). Much of the surface is hilly to mountainous (maximum elevation to 827 m). Komodo localities mentioned in the text are shown on Figure 3.

The general aspect of the island is typical of all arid, uplifted regions, because the mountains have steep angular slopes and alluvial fans. Stream beds and valley floors tend to be rocky with shallow residual or alluvial soils. Rapid runoff leads to deep, nearly vertical-sided gullies. At the same time, vegetation is relatively simple with the low seasonal rainfall producing open, xerophilous communities dominated by the savanna. Long drought and fires deplete the already sparse vegetation and lead to considerable erosion during the short wet season.

EDAPHIC FACTORS

GEOLOGIC.—Although climate is obviously responsible for the altitudinal zonation of Komodo plants, regional zonation is determined largely by geologic factors. The driest habitats are in lowlands where the ground is impermeable and the slopes steep, e.g. the dense coralline limestones near Ntodo Klea and the many igneous hilltops. These areas are often sparsely covered with grass. Under these conditions detritus collects only at the foot of most hills and along intermittent stream courses. The permeable ground of these areas receives and holds runoff from the hills and can support an open forest.

The western and southern parts of Komodo are built on an igneous core comprised largely of fine-grained, slightly basic rocks. Flanking this volcanic mass are lenses of tuffs, sandstones, and conglomerates with intercalated limestones, sandy shales, and clays. The eastern part is composed mainly of steeply tilted beds of coralline limestone; Padar, Rintja, and Flores are very similar. Detailed geological accounts of the area were given by Ehrat (1928a, b), Brouwer (1942a, b), Bemmelen (1949), and Umbgrove (1949).

Soils of the Lesser Sunda Islands have not been studied. They have little or no visible duff during most of the year. Leaf litter collects at the base of some perennial shrubs but generally disappears quickly.

CLIMATIC FACTORS

Because the climate in this part of Indonesia is so poorly known, I collected weather data comprising an almost complete annual cycle at Loho Liang, Komodo. Techniques and additional details are given in Auffenberg (in press).

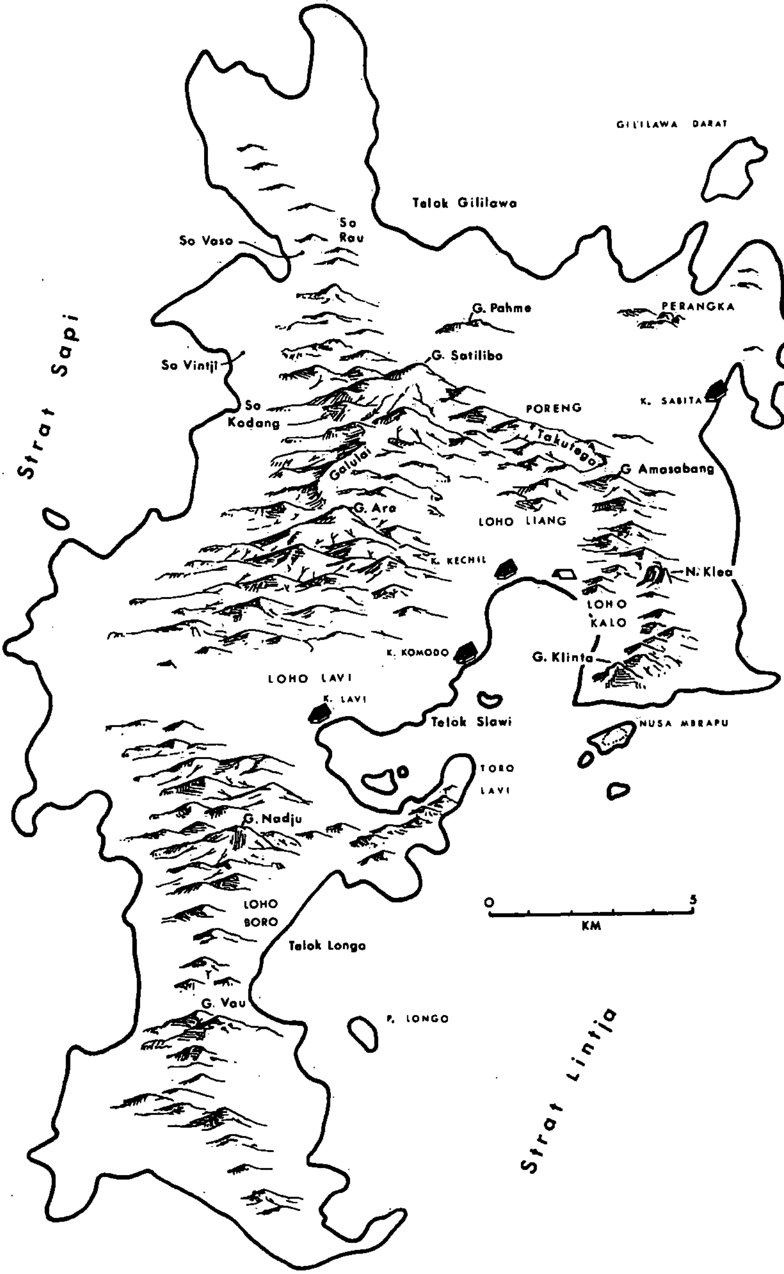


FIGURE 3.—Komodo place names used in text. Symbols used are: houses=villages, tent=base camp.

PRECIPITATION.—Komodo lies in the driest part of Indonesia, with an annual total rainfall of about 50 cm in the lowlands and a minimum of 125 cm in the uplands. The heaviest precipitation occurs during the monsoon (December to March). The low annual average is largely due to the fact that no rain falls on the island during the June monsoon. As a result only two amphibian species occur on the island. One *(Oreophryne jeffersoniana)* is found in moist upland forests; the other *(Kaloula baleata)* is adapted to lowland xeric conditions and spends most of the year in aestivation. Aestivation is also common among most snakes, including the fossorial ones.

GROUND WATER.—Free water is available in pools at all elevations during the rainy season. The largest and longest-lasting are those at high elevations, particularly along stream beds. Free water is rare near the coast, except during the monsoon when small, wild boar wallows often form temporary breeding ponds for *Kaloula baleata* and water holes for large reptiles such as *Varanus komodoensis.*

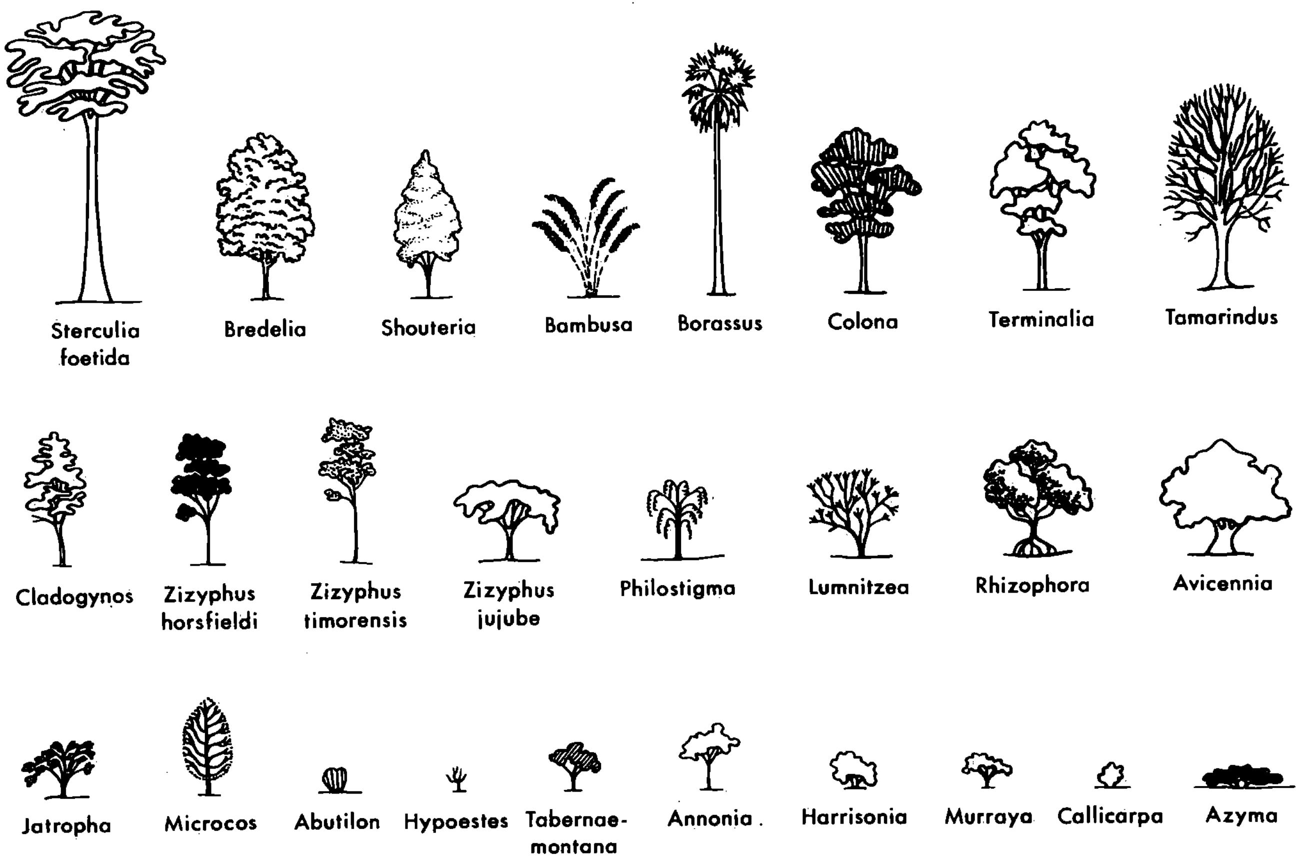
TEMPERATURE.—Maximum air temperature was 43°C, minimum 17°C. Black bulb temperatures varied from 23°C at night and on cloudy days to 54°C after the short rainy season and before the beginning of the dry period. Average annual temperatures were 26.7°C at sea level and 22.0°C at 400 m.

VEGETATIONAL FACTORS

Three major lowland plant formations can be recognized on Komodo and adjacent islands: tropical deciduous (monsoon) forest, savanna, and steppe. In addition, most islands in this area have small fringing mangrove forests. Quasi-cloud forest is generally found in the mountains.

QUASI-CLOUD FOREST.—On Komodo, shade producers are found only in the pinnacle and ridge forests above 500 m. Moist and cool (the local rural folk call the community *tanah dingan,* meaning cool ground), they harbor a relictual flora of many endemic species. Floristically it is characterized by moss-covered rocks, rattan, bamboo groves, and many tree species generally absent at lower elevations *(Terminalia zollingeri, Podocarpus nerifolia, Uvaria rufa, Ficus orupacea, Calophyllum spectabile, Mischocarpus sundaicus, Colona kostermansiana,* and *Glycosmis pentaphylla).* Though this forest's distribution is only 6 km² on Komodo, it is widespread on larger nearby islands. The typical composition of this forest type at its lower limits is illustrated in Figure 4 (G. Wasedoo, Flores).

The reptiles and amphibians most commonly encountered within this forest are listed in Table 1. Species restricted to it are *Sphenomorphus schlegeli, Sphenomorphus striolatus,* and *Oreophryne jeffersoniana.*


Sterculia foetida
Bredelia
Shouteria
Bambusa
Borassus
Colona
Terminalia
Tamarindus
Cladogynos
Zizyphus horsfieldi
Zizyphus timorensis
Zizyphus jujube
Philostigma
Lumnitzea
Rhizophora
Avicennia
Jatropha
Microcos
Abutilon
Hypoestes
Tabernae-montana
Annonia
Harrisonia
Murraya
Callicarpa
Azyma

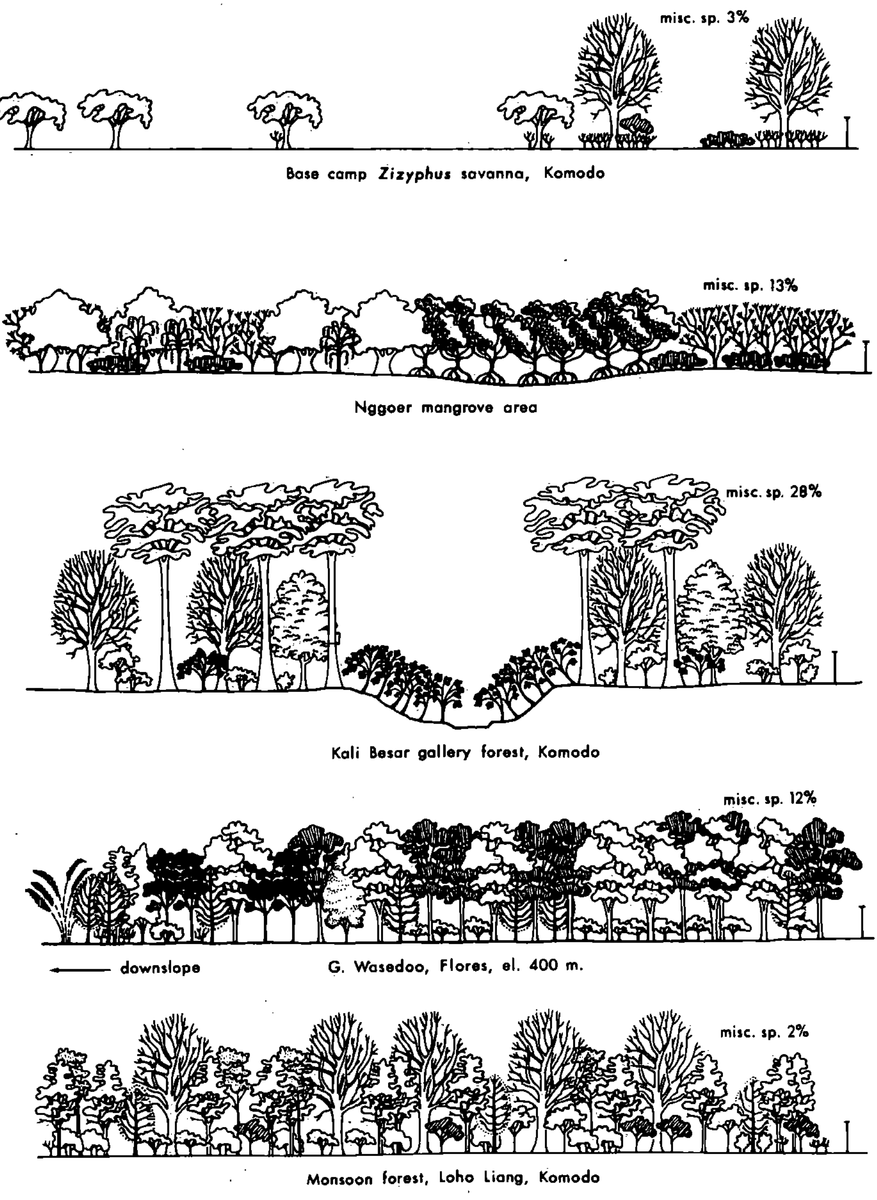


FIGURE 4.—Graphic transects through major forest communities in the study area, showing major larger plants only. The Gunung Wasedoo transect represents the transitional zone to quasi-cloud forest. A 2 m vertical bar is shown on the right side for scale. Identification of symbols is given on the facing page.

TABLE 1.—Ecological distribution of Komodo reptiles and amphibians (A=arboreal, T=terrestrial, F=fossorial, W=aquatic).

Species	Quasi-cloud forest	Monsoon forest	Savanna	Steppe	Mangrove forest	Littoral
FROGS						
Oreophryne jeffersoniana	T					
Kaloula baleata		T	T	T		
REPTILES						
Cyrtodactylus darmandvillei		A,T				
Cyrtodactylus laevigatus		A				
Hemidactylus frenatus		A	A			A
Lepidodactylus lugubris		A	A			
Gekko gecko	A	A	A			
Cosymbotus platyurus		A	A			
Hemiphyllodactylus typus		A				
Gehyra mutila		A	A			A
Varanus komodoensis		A(young,)	AT	T	T	A,T
Draco volans	A	A				
Mabuya multifasciata	T	T				
Sphenomorphus florensis	A,T	A,T				
Sphenomorphus striolatus	A,T					
Sphenomorphus emigrans	A,T	A,T				
Sphenomorphus schlegeli	T					
Emoia similis			A,T	T		

Cryptoblepharus boutonii						T
Cryptoblepharus burdeni						T
Dibamus novaeguineae	F	F				
Typhlina polygrammica	F					
Typhlina bramina		F	F			
Typhlops schmutzi		F				
Elaphe subradiata		A,T	A,T			
Dendrelaphis pictus		A,T	A,T			
Psammodynastes pulverulentus		T				
Chersydrus granulatus					W	
Cylindrophis opisthorhodus		F				
Cerberus rynchops					W	W
Lycodon aulicus		T	T			
Boiga cynodon		A	A			
Trimeresurus albolabris	A	A				
Vipera russelli			T	T		
Naja naja	A,T	A,T	A,T			
Crocodylus porosus					W	W
Chelonia mydas						W(nesting)
Eretmochelys imbricata						W(nesting)

SAVANNA FOREST.—Most of Komodo is covered with this association ($80\ km^2$). Insolation is usually high, especially in the dry season when the leaves have fallen. The understory is comprised mainly of grasses (0.5-4.0 m high); the dominant grasses are *Eulalia leschenaultiana, Heteropogon contortus, Themeda frondosa,* and *T. triandra.* Common trees are *Borassus filiformis, Tamarindus indicus,* and *Schleichera oleosa.*

Two facies of the savanna community are recognizable. One, dominated by the lontar palm *Borassus filiformis,* develops on well drained soils (Fig. 5). The dominant trees of the other are *Zizyphus jujube* and scattered *Tamarindus indicus* (Fig. 6). The soil, sometimes waterlogged for a few weeks in rainy season and often desiccated the rest of year, is primarily a slightly halomorphic, azonal, alluvial type. Savannas of both facies are distributed from sea level to about 500 m.

In general the herpetofauna of the savanna is much more varied than that of the quasi-cloud forest. *Kaloula baleata* is the only frog regularly found there. Typical reptiles include *Emoia similis, Varanus komodoensis,* and *Vipera russelli.* A complete listing is given in Table 1.

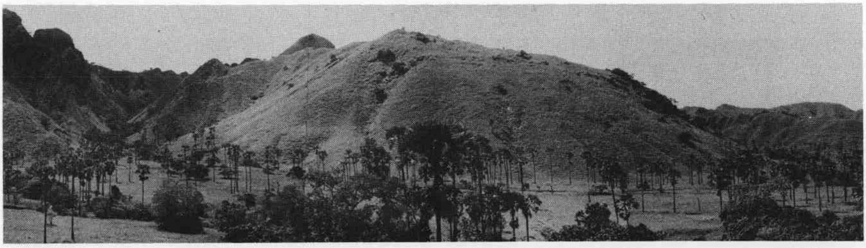


FIGURE 5.—Savana, *Borassus* facies in foreground, Loho Kalo, Komodo; steppe on the background hills.

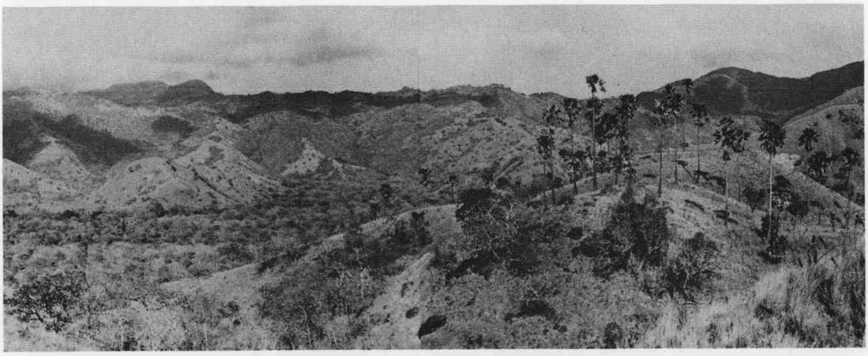


FIGURE 6.—Savanna, *Zizyphus* facies, Loho Kalo, Komodo.

TROPICAL DECIDUOUS (MONSOON) FOREST.—Shown in Figure 7, this association is composed mainly of phreatophytes and some xerophytes. Like the savanna forest, it is largely fire resistant, and many of the trees are almost leafless in the dry season. Some dominant trees, like *Tamarindus indicus,* occur in both associations, but the monsoon forest canopy is higher and more continuous. The crowns commonly touch and the shrub layer may be dense. Dominant trees include *Tamarindus indicus, Sterculia foetida, Zizyphus horsfeldi, Murraya paniculata, Schoutenia ovata, Schleichera oleosa, Cladogynos orientalis,* and *Tabernaemontana floribunda. Tamarindus* and *Sterculia* attain large size and have breast high diameters to 80 cm.

Tropical deciduous forest covers approximately 34 km²—less than half of the total area covered by savanna (80 km²). It is found at all elevations below approximately 500 m, i.e. the most continually dry, hot climate region, locally known as *tanah panas* (hot ground). It may form a gallery along stream courses and often extends in a band-like strip along the base of hills. Typical reptiles include *Varanus komodoensis, Sphenomorphus florensis, Trimeresurus albolabris, Dendrelaphis pictus, Lycodon aulicus,* all typhlopid species, and most of the geckos.

DISTURBED AREAS.—Disturbance is usually by slash and burn methods. Within 8 to 10 years, these plots are usually dominated by *Hypoestes malaccensis* or *Abutilon indicum.* Other common shrubs include *Solanum junghulnii, Callicarpa sappan, Azyma sarmentosa,* and *Microcos paniculata.* The most common trees are *Annonia squamosa and Tamarindus indicus;* the common grasses are mainly *Setaria verticillata, Brachiaria ramosa,* and *Digitaria adscendens.* Common reptile species include *Dendrelaphis pictus* and *Naja naja.*

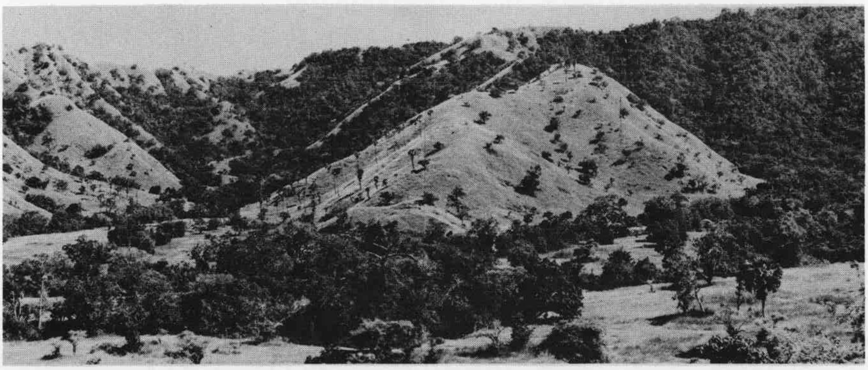


FIGURE 7.—Monsoon forest clothing hill on right and along dry stream beds, Loho Kalo; mixed savanna on drier hillsides.

MANGROVE FORESTS.—Only two mangrove communities are found on Komodo; both are flooded daily by tides. Saline tolerance sorts them out, leading to horizontal zonation along the shoreline.

Rhizophora mucronata usually grows well within the tidal zone, closest to the open water. The tangled roots form impenetrable thickets. On many islands this association forms an almost unbroken fringe along the entire coastline, but on Komodo it is restricted to the east coast near Sabita.

Lumnitzera racemosa is dominant in a few areas behind the *Rhizophora* zone. Though not tall, this species grows very dense, forming large thickets that are occasionally broken by small *Cyperus javanicus* marshes. The mangroves *Ceriops tagal* and *Avicennia alba* are not widespread on Komodo, and the communities of which they are the dominant species are not important habitats. However, they are important on Flores. *Varanus komodoensis* commonly occurs in *Lumnitzera* swamps; less so in *Rhizophora*. Mangrove communities have relatively few reptiles and no amphibians (Table 1). Only the highly aquatic *Cerberus rynchops* and *Chersydrus granulatus* are found there in any numbers. Both are most common in tidal creeks flowing through the regularly flooded forests.

LITTORAL COMMUNITIES.—These communities comprise a hot, dry, sandy or rocky, saline, and windy zone at and immediately behind the beach. Dominant shrubs include *Spinifex littoreus, Crotalaria retusa,* and *Barleria prionitis;* common trees are *Pandanus* sp., *Jatropha curcas,* and *Thespesia populnea.* Relatively few reptiles and no amphibians live here (Table 1), though *Cryptoblepharus boutoni renschi* is commonly encountered. *Cryptoblepharus burdeni* is restricted to rocky coastal areas.

STEPPE.—Tropical grassland or steppe is another important floristic formation (40 km^2), often grading into savanna or forming patches in forested areas. The great variation in occurrence and composition of grassland types has generated a vast literature, especially in respect to their formation and continuance.

Part of the confusion and uncertainty regarding grassland formation in the Lesser Sundas is undoubtedly based on the often repeated error that the steppe communities of these islands are composed largely of alang-alang, *Imperata cylindrica* (Horst 1926, Lallemont 1929, Pfeffer 1959, Kern 1968, *et al.*). Actually, the extensive grass-covered areas within the range of *Varanus komodoensis* are dominated by *Themeda* and *Chrysopogon. Imperata cylindrica* normally occurs on heavy soils, often seasonally waterlogged. On Komodo it is found only in the moist gardens of the main village and in a few small stands in the mountains (Hoogerwerf 1954); it is much more extensive in the larger disturbed parts of western Flores.

The major grassland type in this area, usually dominated by *Themeda* and *Chrysopogon*, covers extensive parts of the islands being considered. Unlike *Imperata* stands, the *Themeda-Chrysopogon* community usually occurs on well drained soils and is particularly extensive in hilly areas (Fig. 5), but it is also common on the valley floor. None of the villagers remembered seeing any change in the character or distribution of this grassland type, whether burned or not. Though this community has relictual steppe and savanna species, no reptiles or amphibians are restricted to it on Komodo.

ECOLOGICAL CORRELATES OF THE KOMODO HERPETOFAUNA.—Of the 38 species of reptiles and amphibians now known from Komodo and small offshore islets, 4 are restricted to quasi-cloud forest, 5 to monsoon forest, none to steppe and savanna (unless they are combined, in which case there are 2), 1 to mangrove, and 1 to littoral situations. The largest number of species is found in monsoon forest (24), then savanna (14), quasi-cloud forest (12), littoral (7, plus 2 nesting species), and finally steppe (4) and mangrove communities (4). A large proportion (51%) of the Komodo fauna is comprised of species at least partly arboreal in habits. The purely terrestrial species constitute only 19% of the total herpetofauna; even the fossorial fauna is nearly as large with 12% total (Table 1). Comparable figures for other areas of high relief, such as the habitats in the State of Michoacan, Mexico (after Duellman 1965), show that, based on the distribution of the 166 Michoacan species, the terrestrial species (39-72% of fauna in each area sampled) are nearly twice as common as the arboreal ones (5-25%). Essentially the same pattern obtains in forested areas of low relief, as in southern Florida where the arboreal herpetofauna makes up only 25% of the total (80 species). The preponderance of arboreality in the Komodo fauna remains unknown, but may be related to the selection processes concerned with waif dispersal.

Inger (1966) listed *Kaloula baleata*, *Rana limnocharis*, *Rana cancrivora*, *Polypedates leucomystax*, *Hemidactylus frenatus*, *Cosymbotus platyurus*, *Mabuya multifasciata*, *Typhlina bramina*, and *Gehyra mutilata* as commensal with man, being found mainly in large man-made clearings, towns, and cultivated land. Of these, only *Kaloula baleata* is widespread on Komodo and is here considered part of the native xeric-adapted community of the island. On Komodo, *Mabuya multifasciata* is apparently restricted to higher elevations and is best considered part of the mesic fauna. Of those listed above, the remaining ones are found only at the coast and could have been transported to Komodo and neighboring islands by man.

Kaloula baleata and *Oreophryne jeffersoniana* are almost entirely terrestrial; the aquatic amphibians (*Rana* species) found on nearby Sumba, Flores, and Sumbawa are absent here. Similarly the simple, xerophilous lowland flora probably also limits the occurrence of arboreal species, such as *Polypedates leucomystax*, which occupies the ecologically similar parts of western Flores, but only in gallery forest along streams. The absence of *Python molurus* on Komodo might be due as much to the presence of the predacious *Varanus komodoensis* as to the general absence of water.

Most of Komodo below 500 m is savanna. Thus, those species confined to lower elevations are either adapted to fire and/or xeric conditions or are closely associated with the activities of man. The small fauna restricted to the area above this elevation is adapted to more mesic conditions and, on Komodo, is comprised of only *Oreophryne jeffersoniana* and *Sphenomorphus schlegeli*. In general, the lowland fauna is considerably more ecologically tolerant, being, in general, distributed over much larger areas. Very few forms are endemic. Furthermore, the ecological tolerance illustrated by this fauna undoubtedly increased the probability for successful interisland dispersal in the past.

SYSTEMATICS

CLASS AMPHIBIA

ORDER SALIENTIA

FAMILY MICROHYLIDAE

Kaloula baleata baleata (MÜLLER)

Figure 8

Bombinator baleata Müller 1836:96 (Type locality: Lewie Gadja, Java).
Kaloula baleata Günther 1858:235.
Callula baleata Günther 1864:436.
?*Bufo biporcatus* Elbert 1912:101.

SPECIMENS EXAMINED.—(23) UF 32580-83, 36164, Denpasar, Bali, 10 m; UF 29247-58, 29260, Loho Liang, Komodo, 5 m; UF 32584, 32586-87, Nggoer, Mangarrai District, Flores, 12 m; UF 32585, Djarek, Mangarrai District, Flores, 120 m.

DESCRIPTION.—Small or moderate-sized frogs, Komodo adults 45-60 mm SVL; stout; head broader than long; short snout; canthus distinct, usually rounded; tympanum usually hidden, ½-¾ diameter of eye; supratympanic fold present; transverse occipital fold in most adults; dorsal skin thick, with large mucous glands, variable in texture; two metatarsal tubercles, inner one well developed, less than length of first toe, compressed; outer one without a sharp edge; finger tips much wider than penultimate segments; no metacarpal tubercles; usually three subarticular tubercles on fourth toe.

Color of posterior surface of thigh mottled; dorsum mottled, brown or purplish-brown, with yellow or red blotches in axilla and on thigh. Males with dark gular pigmentation, rest of venter cream, sometimes mottled with brown (Fig. 8).

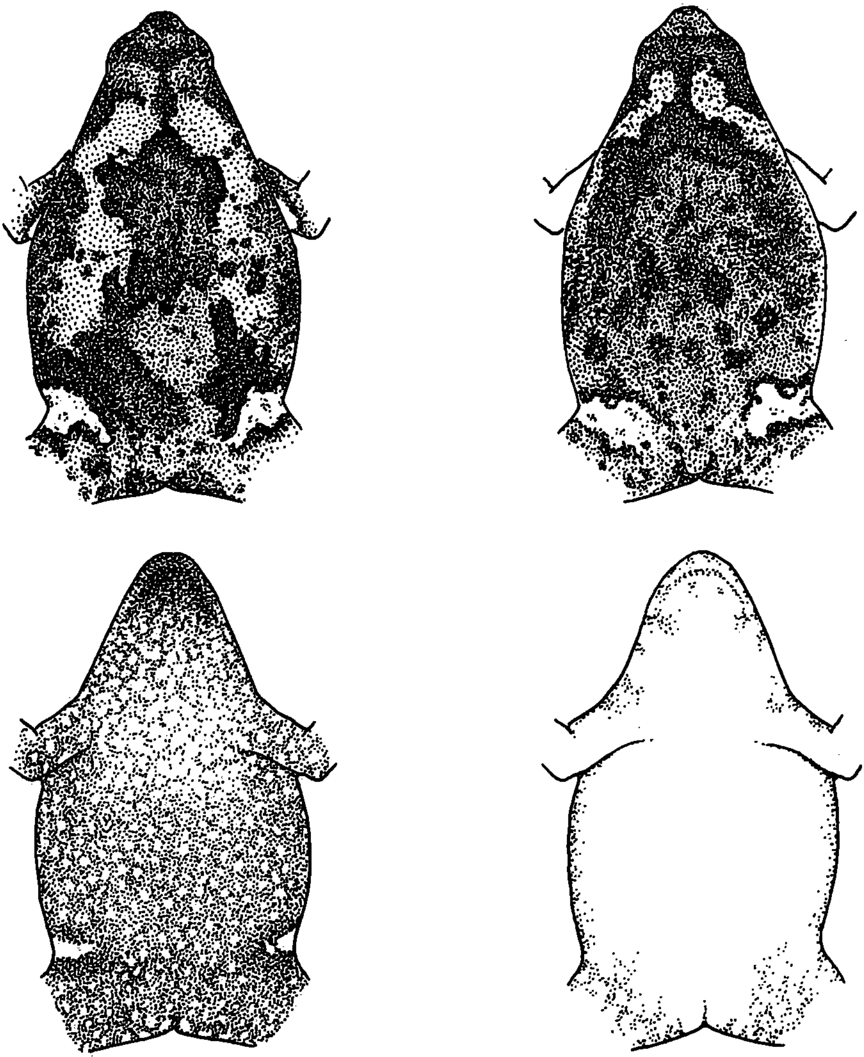


FIGURE 8.—Dorsal (above) and ventral (below) views of *Kaloula baleata baleata*, Loho Liang, Komodo. Left, male (UF 29250); right, female (UF 29252).

DISTRIBUTION AND HABITAT.—A widely distributed form found from the Malay Peninsula and the Philippines southeastward to Flores. In the Komodo area it is known from that island (Dunn 1928), Flores and Sumbawa (Mertens 1930), and Sumba (Kampen and Brongersma 1931; Forcart 1949). Mertens (1930) reported that in the Lesser Sundas it occurs up to 800 m, though all our Komodo and Flores specimens were collected near sea level. Dunn (1928) collected two specimens from Komodo at 650 m. Parker (1934) said the species occurred up to 1525 m.

In savanna habitats on Komodo, the frogs remain in their burrows for much of the last half of the dry season (July to November). During the wet season (December through June) and early part of the dry season the frogs tend to leave their burrows every night, often climbing onto grass tussocks and trees, where they apparently feed largely on ants. We found them on banana, tamarind, and *Zizyphus* trees. Mertens (1929a, 1931) reported seeing them as high as 2.5 m on trees on Bali and Java; Taylor (1921) reported that he found them in the leaf axils of *Pandanus* as high as 7 m, as well as in burrows in the ground. With the first monsoon rain in December, these frogs call from their burrows at night.

REPRODUCTION.—When wild boar wallows become filled with several inches of rain water, individuals quickly gather to reproduce. Breeding choruses on Komodo were recorded from 16 January to 8 March from wild boar wallows near the coast and in pools along intermittent streams as high as 400 m. The voice is a sonorous chuck-chuck-chuck.

Remarks.—Dunn (1928) reported finding fragments of this frog in the stomachs of two *Trimeresurus albolabris*. Mertens' (1930) statement that Dunn reported *K. pulchra* from Komodo is incorrect, for the latter stated that it occurs on Flores; *K. baleata* on Komodo.

FAMILY RANIDAE

Oreophryne jeffersoniana DUNN

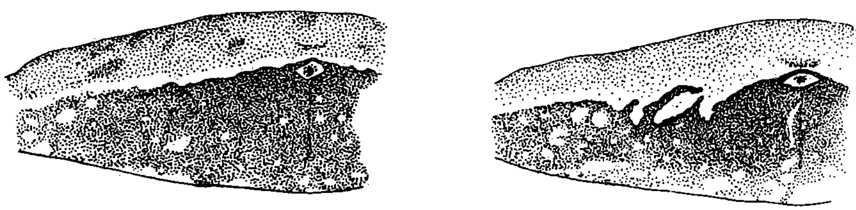
Figure 9

Oreophryne monticola Mertens 1927c:236 (part).
Oreophryne jeffersoniana Dunn 1928:3 (Type locality: Komodo).
Oreophryne darewskyi Mertens 1965:189 (Type locality: Rintja).

SPECIMENS EXAMINED.—(15) AMNH 24530-31 (holotype and paratype), MCZ 14861 (paratype), Komodo; MCZ 35172, Ruteng, Flores, ca 1200 m; UF 40357-60, 1 km E. Djarek, Flores, 60 m; UF 40361-63, 1 km E Nggoer, Flores, 30 m; UF 40364-65, Tjereng, Flores, 800 m; UF 40366-67, Ruteng , Flores, 1200 m; UF 40368, Potjo Dedeng, Nunung, Flores, 1200 m; UF 40670, Loho Lavi, Komodo, 12 m. Also 2 *Oreophryne celebensis* (MCZ 2808, 26091), 10 *O. monticola* (AMNH 23705-6, 24814-15; MCZ 2897, 10193-94, 14862-64) from Lombok and *O. rookmaakeri* (MCZ 15816, paratype), Rana Mesa, Mangarrai District, Flores, 1200 m.

Taxonomic Remarks.—The Komodo material of *O. jeffersoniana* is closely related to at least some populations from nearby islands that currently are regarded as distinct species. These are *O. rookmaakeri* (type locality: Rana Mesa, Mangarrai District, Flores), *O. darewskyi* (Rintja), *O. variabilis* (Celebes), and *O. monticola* (Bali and Lombok). Mertens (1930) recognized this strong resemblance and set all the species (except *O. darewskyi*, which was described later) apart as a distinct group, comprised of isolated, insular populations he believed sufficiently distinct to warrant specific status. Mertens' discovery and description of *O. darewskyi* in 1964 tended to obliterate the distinctiveness of the previously described populations. He, in fact, suggested that future work might show that this group represents a single *Rassenkreis*. The material collected during my study suggests that some of the characters previously believed specifically distinct (1) are ontogenetically variable (hind leg length), (2) vary individually, ontogenetically, and/or sexually (dorsal warts), or (3) show discordant variation within the entire complex (dorsal color and pattern). I find no basis for Merten's distinction of "plump" body for *O. rookmaakeri* and "not so" for *O. darewskyi*.

Other characters, such as the color pattern of the belly and posterior thigh, the relative size of finger dilations, and proportional lengths of the fingers, seem farily constant within populations and in my opinion serve to distinguish two groups, which at this time I prefer to consider as being specifically distinct. The most diagnostic of these characters is the color of the posterior part of the thigh. In *O. jeffersoniana* this surface bears a dark brown horizontal band edged with white above and sharply demarcated from the much lighter ventral surface (Fig. 9, not as evident in old preserved specimens). In *O. monticola* and *O. rookmaakeri* this area is (1) lighter in color and (2) not edged above with white. Furthermore, the SVL for both sexes of *O. jeffersoniana* is less ($\overline{X}$ = 15.1 mm) than in *O. monticola* ($\overline{X}$ = 20.8) or *O. rookmaakeri* (30.0 in the type); the dorsal area and thighs are usually quite warty in



A B

FIGURE 9.—*Oreophryne jeffersoniana* posterior thigh surface. (A) UF 40670, female, Loho Lavi, Komodo; and (B) UF 40365, male, Tjereng, Flores.

the males and females of *O. jeffersoniana*, only in males (and then rarely) of *O. monticola*, and smooth in the type (♀) of *O. rookmaakeri*; the fingers are proportionately shorter in *O. jeffersoniana* with digit 1 usually barely reaching the base of digit 2 and extending up onto digit 2 in the other species; the finger pads are proportionately smaller in *O. jeffersoniana* (Fig. 10) and never found on digit 1, rarely on 2 and 4, whereas they are always on 2 and 4 in the others and often on 1; the ventral body surface and particularly the chin are heavily mottled in *O. jeffersoniana*, less in the others and sometimes uniform white; the dorsal color and pattern (although variable in all three) is generally darker in *O. jeffersoniana*, with fewer examples of longitudinal banding (a common pattern in *O. monticola*); a postorbital dark spot or short stripe is usually present in *O. jeffersoniana* and absent in *O. monticola*; the posterior surface of the humeral portion of the arm is heavily marbled in *O. jeffersoniana* and more or less uniform in the others[1].

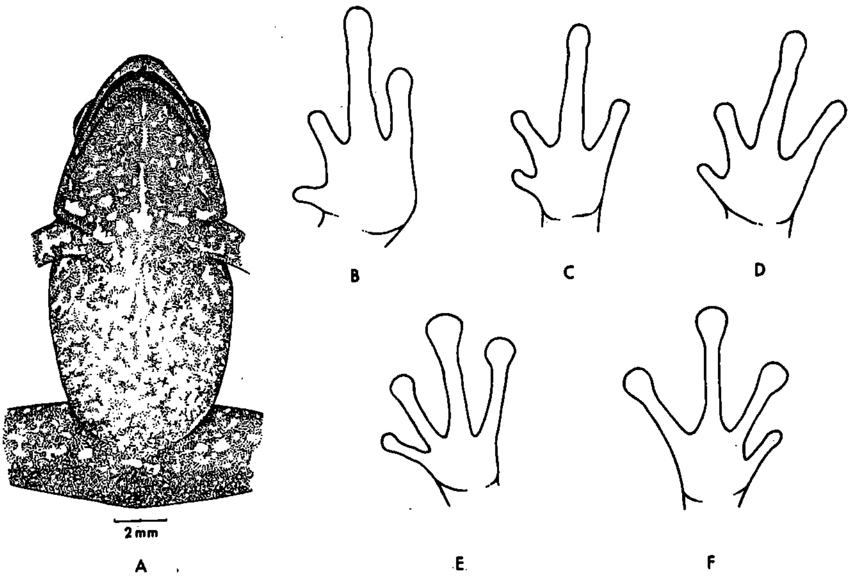


FIGURE 10.—(A) ventral surface *Oreophryne jeffersoniana*, UF 40365, Tjereng, Flores; (B) left front foot, *O, jeffersoniana*, paratype, MCZ 14861, Komodo; (C) left front foot, holotype, *O. darewski*, Senckenberg Mus. ZIL-4126 Rintja; (D) left front foot, *O. jeffersoniana*, UF 40362, Nggoer, Flores; (E) left front foot, *O. rookmaakeri*, paratype, MCZ 15816, Flores; and (F) right front foot, *O. monticola*, MCZ 10193, Lombok.

[1]Mertens (1965) stated that additional material from Bali (= *monticola*, *fide* Mertens 1930) may show that this population is to be considered distinct. He suggested that same possibility for the single Sumbawa specimen (= *jeffersoniana* here and in Mertens 1930).

Thus *O. jeffersoniana* (and its synonym *O. darewskyi*) represent one species group, with *O. monticola* and the closely related *O. rookmaakeri* in the other Sundanese species group of these frogs. My examination of both *O. variabilis* and *O. celebensis* suggest that they are not so closely related to the Lesser Sunda species as had been previously believed.

DESCRIPTION.—A very small frog (SVL 12.0-21.0 mm; $\bar{X}$ = 15.1 mm) with a large, oval, entire tongue; short, rounded snout with rounded canthus; interorbital space broader than the upper eyelid; tympanum feebly distinct, ⅔ diameter of eye; finger and toe discs feebly developed, with first finger much shorter than second and barely reaching base of second when adpressed; toes free, no subarticular tubercles, but very feeble inner metatarsal tubercle; heel reaching posterior border of eye; skin above with few to many small to relatively large warts (few and smaller in young), often with a median line of elongate warts from tip of snout to cloaca and another from eye to more than halfway to groin; belly finely granular; dorsal color tan to gray-brown, with warts often outlined in black; a fine, light middorsal line and/or a darker triangular mark, or two small dark spots on scapular region, or nearly uniform, or spotted; laterally below glandular line usually darker, often brown; chin heavily mottled (50-70% dark) with dark brown to black on dirty white ground color (Mertens' Sumbawa specimen dirty white below); thighs indistinctly marbled or barred above, with brown posterior surface, sharply set off from dorsal color by narrow white line (Fig. 10). Dunn (1928) reported a cartilaginous procoracoid running from base of clavicle to scapula.

DISTRIBUTION AND HABITAT.—Previously known only from Komodo (Dunn 1928) and Sumbawa (Mertens 1930, probably originating from the Tamboro Volcano region); specimens collected during the NYZS expedition show this species also occurs in western Flores. In this paper, the Rintja specimens Mertens (1965) described as a new species, *O. darewskyi*, are considered as belonging to the species *O. jeffersoniana* because of the similarily of color pattern, toe lengths, disc sizes, and adult SVL lengths.

Dunn (1928) described the Komodo habitat as heavily forested rocky peaks, where individuals were found hopping about on the moss-covered rocks and surface debris of the mesic forest floor. Other populations of the same species were described as occurring in similar mesic montane habitats. During this study adults were collected on Flores from beneath stones and rotting piles of vegetation. Juveniles (recently transformed ?) were found hopping about the edges of shallow rocky pools. Adult males were found calling (8 June) in a reedy pool formed by a small hillside spring.

As all previous specimens were taken above 600 m elevation, *O. jeffersoniana* was considered a montane form (Dunn 1928; Mertens 1930, 1964), but our single Komodo specimen and some of those from Flores were taken between 8 and 100 m above sea level in and/or near small springs and seeps at the foot of mountains. The better known *O. monticola* is not known to occur below 600 m, nor is the related *O. rookmaakeri* (900-1200 m, this paper).

REMARKS.—Remains of one specimen of *O. jeffersoniana* were found in the stomach of a *Psammodynastes pulverulentus* taken in a mesic montane forest on Gunung Ara, Komodo.

CLASS REPTILIA

ORDER TESTUDINATA

FAMILY CHELONIIDAE

Chelonia mydas japonica (THUNBERG)

Figure 11

Testudo japonica Thunberg 1789:178 (Type locality: Japan).
Chelone mydas Weber 1890:161.
Chelone agassizii Burden 1927:94.

SPECIMENS EXAMINED.—(7) UF 29263-69, Pulau Longo, off the east coast of Komodo.

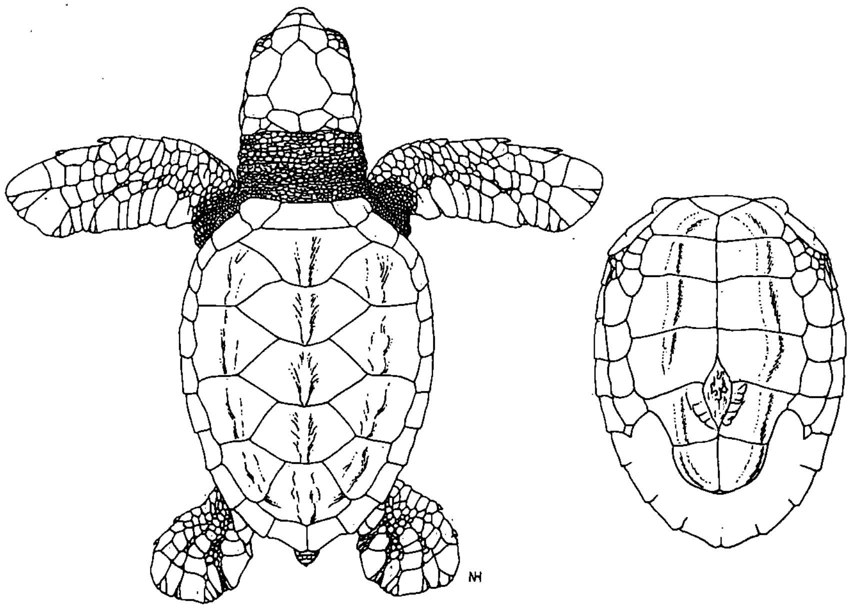


FIGURE 11.—Hatchling *Chelonia mydas japonica*, UF 29263, Pulau Longgo, off Komodo.

REMARKS.—Previously reported in the Komodo area only from Flores and Sumbawa (Mertens 1930). Occasionally found in Telok Slawi and other bays surrounding Komodo, the species is known to nest only on the beaches of Pulau Longo and Padar. My data suggest this species lays eggs at least twice a year in this area, for we have dates of 12 September and 27 November for hatchlings, 7 October and 29 March for egg laying. Nesting thus takes place during both the middle and late dry season, from at least the middle of July through the middle of October, and then again at the end of the wet season in March and April.

Both humans (on Pulau Longo and Padar) and Komodo monitors (on Padar only) commonly raid the nests (see *Eretmochelys imbricata*). Adults are commonly netted and harpooned by Balinese turtle fishermen, who travel many hundreds of miles for this and other species of sea turtles.

Eretomochelys imbricata squamosa (GIRARD)
Figure 12

Testudo imbricata Linné 1766:350.
Eretmochelys imbricata Agassiz 1857:381.
Eretmochelys imbricata squamosa Mertens 1927c:242.

SPECIMENS EXAMINED.—(2) UF 29261, Telok Slawi at Loho Liang beach, Komodo.

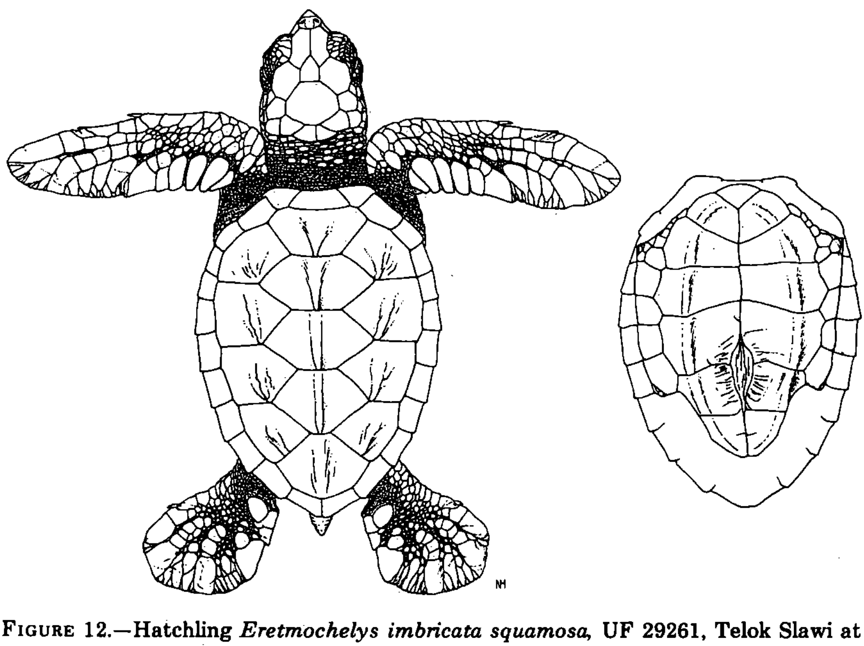


FIGURE 12.—Hatchling *Eretmochelys imbricata squamosa*, UF 29261, Telok Slawi at Loho Liang beach, Komodo.

REMARKS.—Previously reported in the Komodo area from Sumba (Mertens 1928a, Forcart 1949) and Sumbawa and Flores (Mertens 1930). The two Komodo specimens here reported were recently hatched, collected from shallow water off a sandy beach on 12 February. A third hatchling (not preserved) was found dead on the same beach near Nanenepi on 29 April. Remains of an adult were found in the fresh droppings of *Varanus komodoensis* on Pulau Padar on 16 January. These data suggest that in the Komodo area most nesting probably takes place during the monsoon months of January and February. Hatching takes place in the late monsoon months of March and April. *Varanus komodoensis* regularly excavate the nests and eat the eggs of this species on Komodo beaches. Komodo villagers do not eat the flesh, but only the eggs of the turtles. Turtle fishermen from Bali regularly hunt for all species of marine turtles in the bays and backwaters around Komodo. I saw one adult they slaughtered that contained crab remains.

ORDER CROCODYLIA

FAMILY CROCODYLIDAE

Crocodylus porosus SCHNEIDER

Crocodylus porosus Schneider 1801:159 (no type locality designated).

SPECIMENS EXAMINED.—(2) UF 34888, left dentary, Loho Lavi, Komodo; UF 36200, tooth of very large specimen, Loho Lavi, Komodo.

DISTRIBUTION AND HABITAT.—Though widely distributed over much of coastal southeastern Asia, the saltwater crocodile has a spotty distribution in the Sunda Islands. Mertens (1930) reported it from Timor, Lombok, and Flores, Zollinger (1850) from Sumbawa, and Forcart (1949) from Sumba. Darevsky failed to mention it from Komodo, although Broughton (1936) referred to a single small specimen in her account of *Varanus komodoensis* there. While occasionally seen along the northern coast of Flores, it is apparently extirpated on Komodo—chiefly by hide hunting. A large crocodile ate a school teacher in Reo, Flores, in 1967. Darevsky (1964a) reported specimens from eastern Rintja and cited native accounts of them in western Flores. My extensive search in the same part of Flores in 1972 failed to disclose any in appropriate habitats, and local villagers claimed they were all killed by hide hunters several years previously. In the Lesser Sunda Islands *Crocodylus porosus* is usually found in estuaries and embayments, commonly in mangrove swamps. Where not persecuted, they are often seen basking on open sand beaches. On Komodo they have previously been seen in Soro Masalong, the western arm of the large bay on the southeast coast, as well as the eastern mangrove coast from Sabita southward to Tandjung Kunning. Broughton (1936) reported a 2 m specimen eating carrion at one of her baiting stations more than 400 m from the nearest water.

ORDER SQUAMATA
SUBORDER SAURIA
FAMILY GEKKONIDAE
Cyrtodactylus darmandvillei (WEBER)
Figure 13

Gymnodactylus d'armandvillei Weber 1890:160 (Type locality: Sikka, Flores).
Gymnodactylus defossei Dunn 1927a:1 (Type locality: Komodo, el 650 m).
Cyrtodactylus darmandvillei Darevsky 1964a:564.

SPECIMENS EXAMINED.—(6) UF 28913-17, 30172, Kali Besar, Loho Liang, Komodo; UF 32579, Bara, Flores, 200 m.

DESCRIPTION.—Head broad, large; eyes large, but smaller than the distance between the eye and the ear opening; ear opening vertically oval, ⅔ diameter of eye; dorsal surface of body with small scales,

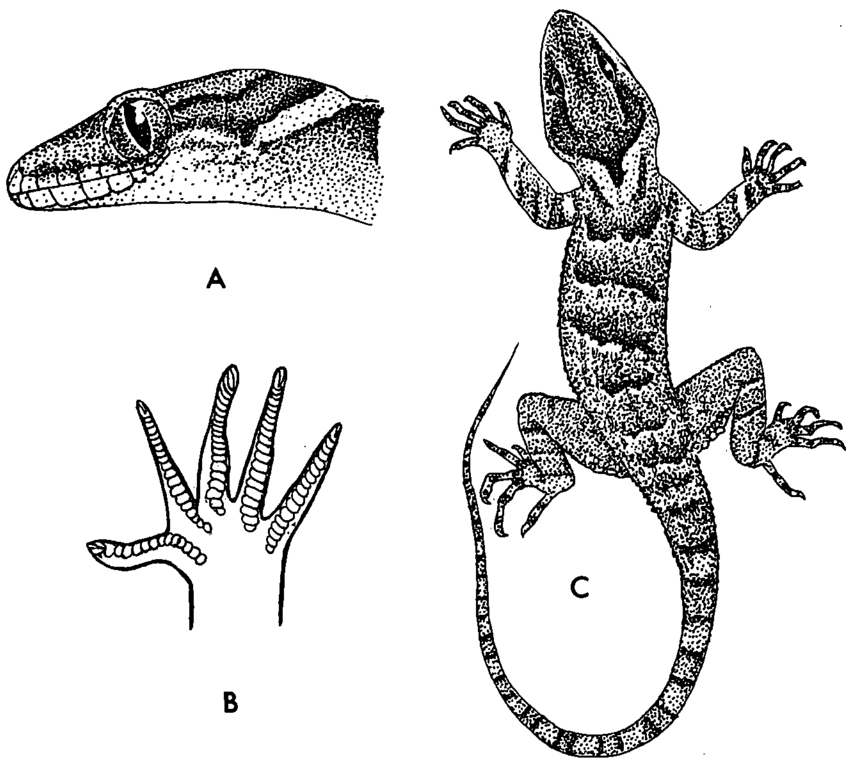


FIGURE 13.—*Crytodactylus darmandvillei*, UF 30172, Komodo. (A) lateral view of head; (B) inferior surface of the left front foot; and (C) dorsal surface.

among which are large, triangular, keeled tubercles, usually longitudinally arranged on top and sides of body and tail; ventral scales small, imbricate; no femoral or preanal pores; tail cylindrical, with enlarged tubercles above, wide scales ventrally.

Ground color grayish-brown with five darker, somewhat wavy crossbands, often lighter, or even absent along middorsal line, none as light as Weber's type from Flores; postocular dark stripe turns medially over ear to form a posteriorly directed V; tail tan to gray, with darker crossbands; juvenile pattern similar but brighter. Adult SVL 86 mm, tail 113 mm; Komodo hatchling SVL 27 mm, tail 35 mm.

Distributuion and Habitat.—It occurs on Flores, Pulau Kalao (off north coast of Flores), Sumbawa (Mertens 1930), and Komodo (Dunn 1927c, Darevsky 1964b), and is probably closely related to *Cyrtodactylus marmoratus* (from Lombok westward). It is found from sea level to 650 m elevation.

Mertens' (1930) Sumbawa specimen was taken on a large tree, and Darevsky (1964a) reported that his specimens were taken under the loose bark of dead trees. Our single specimen from Flores was collected under a large granite boulder on a grassy hillside. Our Komodo specimens were taken at night, when they were very active and often scurried away when the headlight beam first struck them, unlike *Gekko gecko*, which usually became inactive in the bright light. We saw many specimens on the verticle clay banks of the dry creek beds, but they were so active, and the banks were so extensive that we caught very few.

Reproduction.—Darevsky (1964a) reported finding a single egg of this species in a *Varanua komodoensis* burrow; our expedition members found them there commonly, always on the surface and usually near the side walls.

Four males were examined; the two less than 64 mm SVL were immature. In the two mature, October individuals the testes were turgid but still subcylindrical (length 4.5/3.8, 7.2/6.8) and the vasa deferentia were turgid and convoluted. The remaining, immature males had flat, smooth, translucent vasa deferentia and flaccid, laterally compressed testes. Both females (SVL 51.5-52 mm) were immature showing very little follicular development, with follicles less that 1 mm in diameter.

Food.—Spiders and various small insects (mainly termites and beetle larvae) are present in half of the specimens.

Parasites.—Unidentified, in colon of one-third of the specimens.

Cyrtodactylus laevigatus Darevsky

Several specimens of this species collected in western Flores are identical to one another and clearly separable from the available

Komodo material. On this basis they are described below as a new subspecies.

Cyrtodactylus laevigatus laevigatus DAREVSKY
Figure 14

Cyrtodactylus laevigatus Darevsky 1964c:171 (Type locality: Komodo, 600-700 m).

SPECIMENS EXAMINED.—(4) Paratype, Museum Zoologicum Bogoriense 979, Komodo; UF 28910-12, Loho Liang, Komodo, 20 m.

DESCRIPTION.—Head medium, depressed; snout longer than the diameter of the eye, which is less than its distance from the ear; ear opening oval, oblique, about one-fourth the eye diameter. Head and body covered with granular scales, with small flat tubercles (sometimes keeled) beginning at occiput and scattered over back; rostral subtriangular, about twice as broad as high, with a median cleft above; nostril between the rostral, first labial, and three small

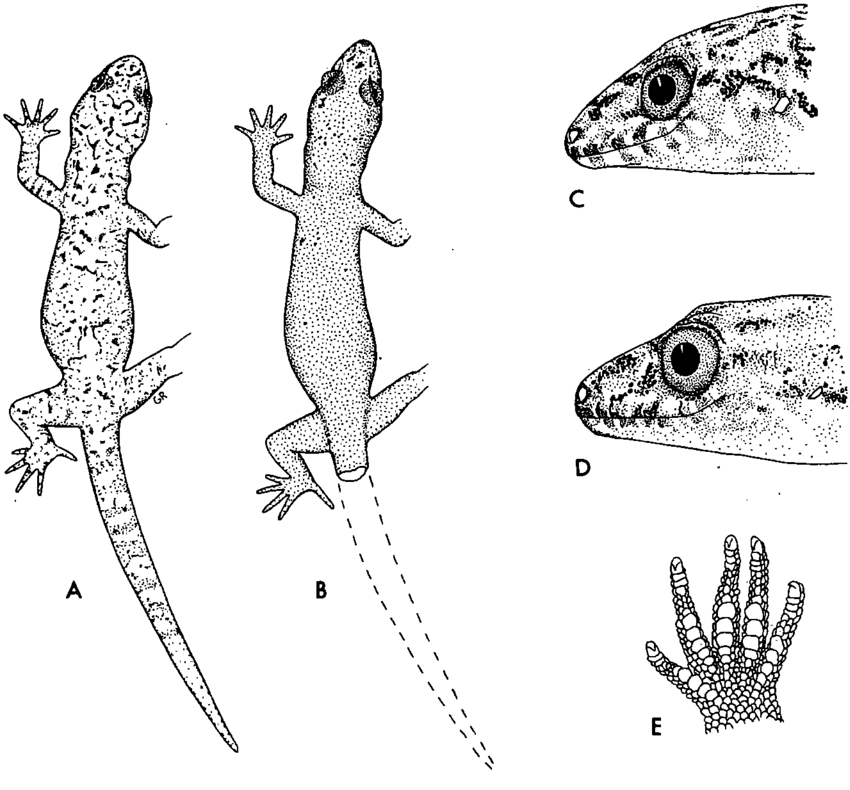


FIGURE 14.—*Cyrtodactylus laevigatus:* (A C and E) *C.l. laevigatus*, UF 28910, Loho Liang, Komodo; (B and D) *C. l. uniformis*, holotype, UF 32596, Nggoer, Flores.

postnasals; 11-13 supralabials, 8-10 infralabials; triangular mental, two pairs of chinshields of which median pair are the largest and touch mental; ventral scales small, smooth, cycloid, imbricate, 32-34 at the middle of the belly; subdigital lamellae strongly dilated only on the basal half, 12-15 under fourth digit. No femoral or preanal pores. Tail round, tapered, covered with small flat scales, larger below, and small tubercles at the base; limbs moderately long, digits depressed at the base, strongly compressed at the end phalanges.

Color tan dorsally with darker irregular spots, often forming short transverse bars that are often interrupted along the vertebral line. Head with small, oblong, irregular brown spots. A dark brown temporal stripe extends from end of snout through eye, over ear, and medially to join first transverse dorsal bar. Infralabials mottled; a dark brown stripe from nostril to upper anterior corner of eye. Larger tubercles of back often whitish. Lower surface whitish. SVL of females 43-44.8 mm, tail 39.3 mm; males 38 mm, 27.5 mm. My counts of 13 and 14 infralabials and 15 and 16 supralabials in this small series, rather than 10-13 and 8-10, respectively, by Darevsky for his series, is undoubtedly due to the fact that both the upper and lower labials become considerably reduced in size at the corners of the mouth, and there is some question as to which scales should be included in the count and which excluded. We counted all the scales to the angle of the mouth and can only presume that Darevsky counted only the enlarged ones.

Distribution and Habitat.—Unfortunately the elevation at which Darevsky's specimens were obtained is questionable. In his species description (1964b), he stated that the type and three paratypes were collected from under stones on the edge of the jungle between 600 and 700 m. However, in another paper (1964a), he reported that the adult specimens were found on tree stumps during the night and the juveniles under stones in dry jungle. Furthermore, the juveniles were said to have been collected at 100 m and the adults at 200 m. Our three specimens were taken during the daytime from under the bark of small, dead *Tamarindus* trees in Loho Liang, approximately 20 m above sea level.

Reproduction.—Both females (UF 28910, 28192) were mature when collected in September 1969. In one, the left ovary contained one large, yolked follicle (6.7 × 5.2 mm) and two small, mainly translucent follicles, of which the largest was 2.8 mm in diameter. The right ovary was more anterior than the left and also contained one large, yolked follicle, approximately 5.6 mm in diameter. The oviducts were large, thick-walled, and considerably convoluted. The second specimen (UF

28912) was similar, with the left ovary posterior containing one large yolked follicle (8.4 × 4.8 mm) and three small, translucent follicles of approximately 2.5 mm in diameter. The right ovary was more anterior and contained one large, yolked follicle (8.9 × 4.5 mm). In addition, three small, transparent follicles, of which the largest was approximately 2.4 mm in diameter, were present. The oviducts were identical to UF 28910. The only male (UF 28911) was collected in late July and was subadult. The testes were less than 1 mm in diameter, very flaccid, and almost translucent. The vasa deferentia were small, flat, and thin-walled.

Eggs and hatchlings are found under loose bark from July through September. There is some evidence that males are mature at the beginning of their second year.

FOOD.—Small beetles (mainly of the family Elateridae) and their larvae.

PARASITES.—Eggs of unknown parasites were found in the intestines of one of the three specimens collected.

Cyrtodactylus laevigatus uniformis **new subspecies**
Figure 14

DIAGNOSIS.—Scutellation as in nominate subspecies, but dorsal color darker, uniform, and not brightly marked with dark brown.

HOLOTYPE.—UF 32596, adult female, Nggoer, Mangarrai District, Flores, 5 m, taken from beneath loose bark of standing tree.

DESCRIPTION OF TYPE.—Head medium, moderately depressed; snout longer than eye diameter, which is less than its distance from the ear; ear opening oval, obligue. Head and body covered with small granular scales, among which are interspersed larger tubercles, keeled above tail, nostril bordered by rostral, first supralabial, and two small postnasals. Supralabials 10 and infralabials 8, mental trangular, one pair of large chin shields, in contact behind mental scale; ventral scales small, smooth, cycloid, imbricate, in 32 rows across belly. no femoral or preanal pores; tail round, tapering with flat scales that are larger ventrally. Limbs moderate. Digits depressed distally, strongly compressed distally. Subdigital lamellae 10.

Generally brownish-gray above with darker brown only on labials, and in faint head markings, as in nominate subspecies. Venter yellowish-white, SVL 47 mm, tail broken.

PARATYPE.—UF 32597, Nggoer, Mangarrai District, Flores; as in holotype, except 14 subdigital lamellae, 11 supralabials, 9 infralabials. The subspecies is named *uniformis* because it lacks any body pattern.

Gekko gecko gecko (Linné)

Lacerta gecko Linné 1758:205 (Type locality: "Indes").
Platydactylus guttatus von Martens 1876:374.
Gecko verticillatus Weber 1890:160.
Gekko gecko Barbour 1912:31.

Specimens Examined.—(29) UF 3307-8, Suwang, Bali; UF 33022, Labuanbadjo, Mangarrai District, Flores; UF 33021, 33023, 30091, 39699, Nggoer, Mangarrai District, Flores; UF 33015-17, Nangelele, Flores; UF 33013-14, 33017, Orang (Baneng), Flores, 610 m; UF 33018, 33019, Pota, Flores, ca 10 m; UF 33020, Bara, Flores, 200 m; UF 28890-97, 28686, 33009-12, Loho Liang, Komodo, 0-30 m.

Distribution and Habitat.—A very widely distributed form, apparently common throughout the Sunda Islands; in the Komodo area previously reported from Lombok, Sumbawa, Pulau Endah (off Flores south coast), Flores, Komodo, Padar, Celebes, and Sumba (see Mertens 1930, Forcart 1949, Darevsky and Kadarsan 1964, and others). Mertens (1930) stated that it does not extend higher than 800 m, which fits with our obversations on Komodo.

It is usually found in isolated trees with large knot-holes and other cavities. On Flores, expedition members found as many as five in one rotten tree. In most mesic places where various ferns and orchids cover the surface, specimens may find refuge in the epiphytic growth; sometimes under loose bark, particularly on dead tamarind trees. Prime habitat on Komodo and western Flores was the savanna biotope, especially that dominated by *Zizyphus jujube* trees. Density of adult specimens in this habitat type at the Base Camp in Loho Liang, Komodo, was calculated as about 72/km^2 (on the basis of both calling individuals and the distribution and number of appropriate dead and dying trees). Mertens (1930) reported it was sometimes found on mangrove trees (species?). Expedition members found it on large hollow specimens of the mangrove *Avicennia alba* on Flores, but never on *Rhizophora mucronata*.

Individual geckos usually began calling near dusk and continued intermittently until at least 0300 hr. Although they eat a great variety of food, our observations at the Base Camp suggest that they eat many *Hemidactylus* and smaller individuals of their own species, sometimes almost the same size as the attacker, so that they may take as much as 30 min to swallow their prey completely.

Hatchlings with a total length of 85-90 mm were observed to attack and swallow small *Hemidactylus frenatus* successfully.

Reproduction.—Examination of nine females, representing several size classes, showed that sexual maturity was attained at a minimum SVL of 115 mm, but most were not mature until about 120 mm. Shelled ova were found in the oviducts during January, June, and July. Freshly laid eggs were found in March, June, August, and

September, suggesting egg laying throughout the year, with the possible exception of the driest season (October to early December). Hatchlings were seen in May and July. A maximum of only two eggs are laid, apparently each separated by several days. Sometimes only one egg is laid, the other oviduct being empty. The number of follicles varied from five to seven (diameter from 1 to 11 mm). As many as two stages of corpora lutea disintegration are usually discernible at any one time (approximately 3.5 and 8.0 mm in diameter). Egg clusters (1-5, $\overline{X}$ = 2.3) are often found under loose bark. Single females apparently return to the same spot to lay their eggs. The new eggs are glued to the wood, next to the old hatched or spoiled eggs.

Of nine males dissected, the smallest mature individual was 134 mm SVL; specimens 112-118 mm are all immature; all over 148 mm are mature with turgid, cylindrical testes. The vasa deferentia were highly convoluted, flat, and thin-walled. Average SVL of six mature females is 132 mm, for six males 145.3 mm.

FOOD.—*Hemidactylus frenatus, Cosymbotes platyurus,* spiders, and miscellaneous insects (mainly beetle larvae and termites).

PARASITES.—The nematodes (after Pinnell and Schmidt 1977) *Pharyngodon kuntzi* and *Rhabdias* spp. were found in the colon, stomach, and small intestines of seven of the eight specimens examined.

Gehyra mutilata (WIEGMANN)
Figure 15

Hemidactylus (Peropus) mutilatus Wiegmann 1834:235 (Type locality: Manila, Philippines).
Peropus mutilata Gray 1845:159.
Gehyra mutilata Boulenger 1885:148.

SPECIMENS EXAMINED.—(9) UF 33051-57, Ruteng, Flores, 1200 m; UF 28888, 28896, Loho Liang, Komodo, 10 m.

REMARKS.—A common gecko, often found in houses and very widely distributed. In the Komodo area, it is known from Flores (Mertens 1931), Sumba (Forcart 1949), Komodo (Dunn 1927c, this paper), and Sumbawa (Mertens 1931). A juvenile (UF 33053) from Ruteng, Flores, has distinct dorsal white spots that are faint in larger individuals from the same locality. The Komodo specimens (UF 28888, 28896) collected from the side of the Base Camp building, bear indistinct, wavy, transverse bands.

Hemidactylus frenatus DUMERIL AND BIBRON
Figure 15

Hemidactylus frenatus Dumeril and Bibron 1836:366 (Type locality: restricted by Loveridge 1947:127 to Java).

SPECIMENS EXAMINED.—(54) UF 33027-29, 33033-35, Bara, Flores, 200 m; UF 32595, 33036-46, Nggoer, Mangarrai District, Flores, 10 m; UF 33030-31, Labuanbadjo, Flores, 10 m; UF 33032, Nunang, Flores, 600 m; UF 28879-87, 28889-95, 28897-99, 28900, 28902-5, 28986-7, all from Loho Liang, Komodo, 0-30 m; UF 33026, Padar Island; UF 33024, Jakarta, Java.

REPRODUCTION.—I examined 18 females in varying stages of maturity. These suggested that females become mature at an SVL of about 44 mm (average 46.3). Follicular development clearly shows only one egg is laid at a time. Females with eggs ready to be laid were captured in July and October. Newly laid eggs (N = 6) have a diameter of 6.4 - 7.9 mm, and usually are found in rotten knot holes or under loose bark on the shaded side of *Tamarindus* trees. Of 19 males examined, 10 were considered mature on the basis of turgid, highly convoluted, and thick-walled testes. The average SVL of mature males is 46.7 mm, and maturity is reached at an SVL length of about 42 mm.

FOOD.—Gecko skin found in several stomachs suggest they regularly eat parts of their shed skins. Food remains in the stomachs were comprised of ants, beetle larvae, spiders, and mainly termites.

PARASITES.—Pharyngodonid nematodes were found in the colon of 8 out of 23 specimens examined. UF 28881 has an unidentified skin parasite on several parts of its neck and body.

REMARKS.—A common lizard over a large part of the tropics, particularly near the coast, commonly transported accidentally on native boats. Darevsky (1964a) reported finding them on Komodo outrigger praus. In the Komodo region the species is found on all the islands. Vertical distribution is from sea level to 500 m (Mertens 1931). In nearby areas it is known from Sumba (Forcart 1949). Mertens (1930) stressed the wide range in coloration of individuals from the night to daylight conditions. Maximum SVL on Komodo is 54.3 mm.

Prey of *Gekko gecko*.

Hemidactylus garnoti DUMERIL AND BIBRON
Figure 15

Hemidactylus garnoti Dumeril and Bibron 1836:368.

SPECIMENS EXAMINED.—(1) UF 32571, Djarek, Mangarrai District, Flores, 200 m.

REMARKS.—This species is often a commensal of man, and the single specimen reported here was collected from the wall of a village house. It has previously been reported from Flores and Sumbawa by Mertens (1930). We found none on Komodo.

Cosymbotes platyurus (SCHNEIDER)
Figure 15

Stellio platyurus Schneider 1792:20 (Type locality: not designated).
Hemidactylus (Stellio) platyurus Wiegmann (1834:238.
Cosymbotus platyurus Stejneger 1907:178.

Platyurus platyurus Smith 1935:102.

SPECIMENS EXAMINED.—(16) UF 28901, 28906-09, Loho Liang, Komodo, 0-32 m; UF 33048-50, 33086-87, Denpasar, Bali; UF 33047, Jakarta, Java; UF 32588, 32590-93, Nggoer, Flores, 12 m; UF 32589, Labuanbadjo, Flores.

DESCRIPTION.—Snout longer than the distance between the eye and the ear opening, 1½ times the diameter of the eye; ear opening small, oval, oblique. Rostral trapezoidal, with median cleft above, nostril borders rostral, first supralabial, and 3 postnasals; 9-11 supralabials and 7-8 infralabials; mental large; two pair of chin shields, of which the median pair largest, in contact with each other. Body somewhat depressed, covered above with uniform small granules. A small flap of skin extends from axilla to groin, and another along posterior edge of hindlimb (particularly in adults). Ventral scales cycloid, imbricate, smooth. Males with an uninterrupted series of 34-36 femoral pores. Tail depressed, with a sharply denticulated lateral fringe of scales; uniform dorsally granular scales and ventrally with a median series of transversely dilated plates. Limbs moderate, depressed; digits strongly dilated, partially webbed, 7-9 lamellae under the fourth toe. Gray to grayish-brown above, marked with irregular spots or stripes dorsally, darker gray, brown, or black; generally a dark stripe from eye to shoulder. White ventrally. Young much more brightly colored. SVL about 60 mm in adults, tail 65 mm.

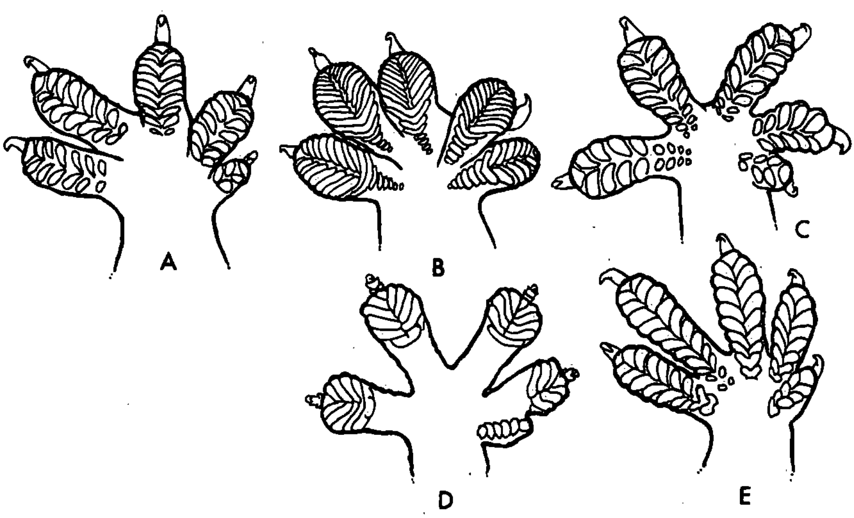


FIGURE 15.—Lower surfaces of right front feet of: (A) *Cosymbotes platyurus* (UF 28907); (B) *Gehyra mutilata* (UF 33055); (C) *Hemidactylus frenatus* (UF 33027); (D) *Hemiphyllodactylus typus pallidus*, holotype (UF 28985); and (E) *Hemidactylus garnoti* (UF 32571).

DISTRIBUTION AND HABITAT.—Widely distributed in Southeast Asia and extending throughout the archipelago. It is often the most common lizard in both urban and agrarian habitats. Komodo and Flores specimens were taken from large trees near sea level. Mertens (1931) reported that it is not found above 700 m. Although he failed to find it in Bali, it is common near sea level in several places along the southeast coast. It is one of several similar-sounding geckos that regularly call in the early evening; the sound produced is "tchack-tchack-tchack."

REPRODUCTION.—Two eggs (7.2-822 mm diameter) are usually laid in moist, rotten wood; my records are for January and March. Average SVL of mature females (N = 8) is 52 mm (49-55); average SVL mature males (N = 5) is 51 mm (48-54).

FOOD.—Spiders and winged and wingless ants.

PARASITES.—Pharyngodonid nematodes were found in the colon of 2 out of 10 specimens examined.

REMARKS.—Sometimes eaten by *Gekko gecko.*

Hemiphyllodactylus typus BLEEKER
Figures 15, 16

Hemiphyllodactylus typus Bleeker 1860:327 (Type locality: Gunung Parang, Java).
Spathodactylus mutilatus Gunther 1872:594.
Spathoscalabotes mutilatus Boulenger 1885:157.

Previously known only from Sumbawa westward, this rare little gecko is reported from Komodo for the first time. The distinctive color and lack of pattern suggests this population be recognized as a separate subspecies (Fig. 16).

Hemiphyllodactylus typus pallidus **new subspecies**

DIAGNOSIS.—Adults differ from those of the nominate form in lacking the dark brown markings on the side of the head and dorsum; juveniles faintly marked.

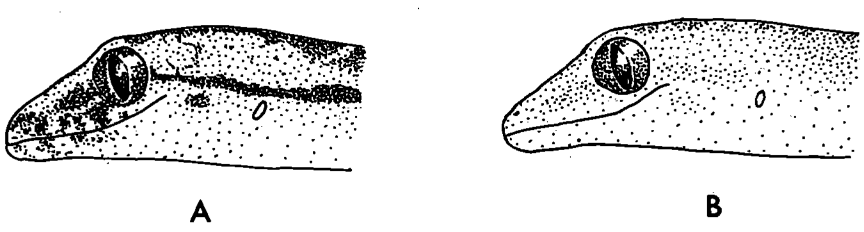


FIGURE 16.—(A) *Hemiphylodactylus typus typus* (*fide* deRooij 1915); and (B); holotype, *H.t. pallidus* (UF 28985).

HOLOTYPE.—UF 28985, adult female, collected October 1969 from beneath dry, fallen leaves in gallery forest along Vai Nggulung, Loho Liang, Komodo, 30 m.

DESCRIPTION OF TYPE.—Digits slender, cylindrical at base, the penultimate joint ending in a strong dilation with two series of oblique lamellae below, separated by a median groove; the inner toe of both back and front feet rudimentary, clawless; the other digits with a free, clawed terminal phalanx projecting considerably beyond the dilated part. Four pairs of lamellae under all normal toes. Pupil vertical. Head longer than broad; snout as long as the distance between eye and ear opening, 1½ times the diameter of the eye; ear opening very small, oval, oblique. Distinct, thickened glandular patch on either side of neck above and in front of insertion of forelimbs. Rostral broad, nearly pentagonal; nostril bordered by the rostral, the first labial, a supranasal, and two small posterior nasals; 11 supra- and infralabials; mental small, triangular; no chin shields. Limbs slender; mental tail cyclindrical. Body long and slender, covered with small granular scales, those on the snout and limbs somewhat enlarged, those on the tail tubercular. Ventral scales larger, smooth, imbricate. No preanal pores.

Light tan above, almost uniformly and finely stippled with dark brown over entire body, tail, and head, very slightly darker from nostril through and behind eye; uniform white below. SVL 32 mm, tail 26 mm.

PARATYPE.—UF 28878, juvenile male, SVL 21 mm, tail 15 mm, from gallery forest along Kali Besar, Loho Liang, Komodo, 20 m. Scalation as in type, except 10 preanal pores on escutcheon of slightly enlarged scales arranged in a shallow V. Ground color light tan, with few faint brown mottlings dorsally, forming a V-shaped stripe on top of snout, very faint stripe from nostril through eye to above ear opening; nine narrow, broken transverse bars, darkest over both hind and front legs; tail faintly ringed; infralabials mottled; chin and venter white anteriorly, becoming finely stippled posteriorly onto base of tail.

TAXONOMIC REMARKS.—Apparently closely related to the nominate form on the basis of identical scalation and similar, but greatly subdued coloration.

DISTRIBUTION AND HABITAT.—The nominate subspecies is known from Sumatra, Simalur, Nias, Borneo, Java, Bali, and Sumbawa, at elevations of 500 to 1300 m. *Hemiphyllodactylus typus pallidus* is known only from Komodo, where it was taken near sea level from beneath leaves in gallery forest. Both it and the nominate form are evidently not common wherever they occur (Mertens 1930).

FOOD.—Presumably small miscellaneous insects.

Lepidodactylus lugubris intermedius (DAREVSKY)
Figure 17

Lepidodactylus intermedius Darevsky 1964c:13 (Type locality: Komodo).
Lepidodactylus lugubris Kluge 1968:338.

SPECIMENS EXAMINED.—(1) Paratype, Museum Zoologicum Bogoriense 978, Komodo; none found during the 1969-70 NYZS expedition.

DESCRIPTION.—Based on type series (after Darevsky 1964c). Snout longer than distance between eye and ear opening, 1½ to 2 times diameter of eye. Forehead concave. Ear opening small, round, straight back from angle of mouth. Head scales granular, largest on snout. Rostral four-sided, broad. Nostril between rostral, first labial, and three nasals; 10-11 supralabials, 8-10 infralabials. Mental small, narrow, about as large as adjacent infralabial; chin shields small, in 3-4 transverse rows. Body and throat with minute granules; ventral scales larger, flat, juxtaposed. Femoral and preanal pores 24, in a long angular series. Tail cylindrical, without sharp lateral edge, covered with small equal scales in feebly expressed groups of 9-10 transverse rows. Limbs moderate; digits with rudimentary webs, inner digit well developed, without claw, middle finger with 9 and middle toe with 11-12 subdigital lamellae.

Light gray above with 7 transverse, undulating, narrow, dark brown transverse bands, darker bands on tail; no contrasting dark streak through eye (though faint in Darevsky's [1964c] Figure 2); lower surfaces greenish-white. SVL 39 mm, tail 35 mm.

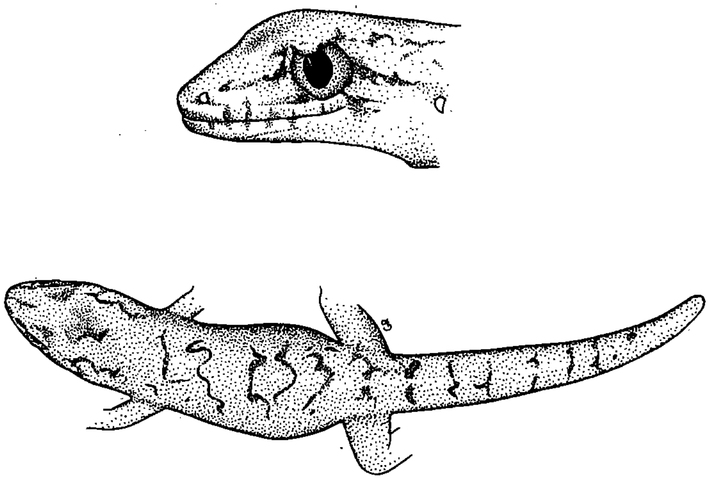


FIGURE 17.—*Lepidodactylus lugubris intermedius*, (*fide* Darevsky 1964b); Komodo.

REMARKS.—I cannot explain how I failed to find this lizard on Komodo, except that it is apparently rare and thus was simply missed by chance alone. Darevsky placed it close to and intermediate between *Lepidodactylus lugubris* and *L. lombocensis*, but it seems part of a geographic cline in certain scale characters (number of femoral pores, labials, and chin shields generally reduced to eastward, and number of subdigital lamellae increased in the same direction). Kluge (1968) correctly suggested relegation of several named species, including this one, to the synonomy of *L. lugubris*. The characters of *L. intermedius* suggest it should be recognized as a geographic race of *lugubris*.

Apparently occasionally eaten by *Dendrelaphis pictus* (Darevsky 1964c).

DISTRIBUTION AND HABITAT.—Known only from Komodo and Rintja, where specimens were collected from under the loose bark of dead tamarind trees (Darevsky 1964c).

FAMILY SCINCIDAE

Cryptoblepharus

In his monographic treatment Mertens (1931) concluded that the 36 populations of *Cryptoblepharus boutonii* he recognized should all be considered geographical races of one another. Of these, 31 occurred on islands. *Cryptoblepharus boutonii* thus became one of the most widespread of all lizard species in the world, having a discontinuous distribution from the east coast of Africa to Hawaii. On the basis of information now available from both Komodo and Padar (and suggested for other islands, such as Timor) it is highly likely that Mertens' interpretation of a single species is perhaps oversimplified. In fact, Mertens himself suggested that the various populations of *Cryptoblepharus boutonii* represent incipient species, and that some may be much more differentiated than others. Data provided here suggest that the two populations in the Komodo area, *C. burdeni* and *C. renschi*, are distinct at the species level.

Dunn (1927c) described *C. burdeni* as a new and distinctive nonstriped subspecies of *Cryptoblepharus boutonii* based on three specimens collected from rocks at the tideline on the east coast of Padar. No *Cryptoblepharus* were found on Komodo. Until this time, no additional specimens of this interesting form were found. Darevsky (1946b) reported the presence of a vividly striped, tree-dwelling *Cryptobelpharus* on Padar, referred to *C. b. renschi* (type locality Sumba). He also reported the same form from Komodo for the first time, but failed to find *C. burdeni* on Padar. During the New York Zoological

Society study, both forms were found on both islands, and each was restricted to a specific habitat type.

Cryptoblepharus boutonii renschi (MERTENS)
Figure 18

Cryptoblepharus boutonii renschi Mertens 1928a:20 (Type locality: northeastern Sumba, Kambaniru, near Waingapu).
Ablepharus boutonii renschi Mertens 1931:154.

SPECIMENS EXAMINED.—(19) UF 29921-25, east coast of Padar, 10 m; UF 29919-20, Loho Boro, near Loho Lavi, Komodo, 3 m; UF 29918, Vai Nggulung, Loho Liang, Komodo, 30 m; UF 29960-61, 29963-64; 28856-59, 28867, 28872, all from near Base Camp, Loho Liang, Komodo, 3-25 m; UF 28871, near Kampung Komodo, Komodo, 20 m.

DESCRIPTION.—A somewhat small, flat- and pointed-headed subspecies of *Cryptoblepharus boutonii* with a markedly striped black and white pattern, composed of five bluish-white to white or cream (rarely light brown) bands and six black to brownish-black bands. Median dorsal stripe, as well as the dark parietal bands, begins on point of snout; maxillary band begins in subtympanal region, somewhat as in *C. b. keiensis*, extending to hindlimb. Sometimes light band begins from white or cream supralabials running posteriorly to ear opening. Belly bluish-white; palmar surfaces white. (Newly hatched individuals have the same color and pattern as the adults [Mertens 1931; UF 29919, 28858, 28860, 28864].) Midbody scales in 24-28 rows in Komodo-Padar series ($\overline{X}$ = 26.0), 22-25 (usually 24) rows on Sumba, according to Mertens (1930); 20-28 in other races. Both middle scale rows larger than those on either side. Lower eyelid immovable, transparent, covering the eye. Nostril in a nasal scale; postnasal well developed in only one of specimens examined. Usually 4 supraciliaries, 5 in three specimens, 3 in four specimens, 2 in four, and 3 on one side and 4 on the other in remaining ones. All have 4 supralabials in front of subocular; anterior loreal as long or longer than high. Lamellar scales of hind digit IV varies from 18 to 24. Size small, SVL about 50 mm, tail about 60 mm. Hind leg reaches to ankle of appressed front leg in males and to axilla in females.

TAXONOMIC REMARKS.—*C. b. renschi* is most similar to the Kei Islands subspecies *(keiensis)*. In the latter (as well as certain pattern phases of *C. b. intermedius*) the parietal bands on the head extend forward only to the supraocular region; in *C. b. renschi* they always extend to the very tip of the snout. *C. b. keiensis* also differs from *C. b. renschi* in having (1) stripes more greenish than silver-white; (2) somewhat less contrasting dark longitudinal stripes; and (3) up to 22 middorsal scale rows, whereas in *C. b. renschi* the largest number of scale rows is 28. However, Mertens (1931) believed that these two subspecies are very closely related to one another. The differences are apparently bridged by the subspecies *C. b. intermedius* (Mertens 1931).

Darevsky (1964a) reported that their 3 specimens from Komodo and 10 from Padar were typical of the subspecies, but with a tendency for increased scale rows when compared to specimens of the same race from Sumba. Our material suggests the same (see description above). No significant difference is evident in the middorsal scale rows of specimens from Padar ($\overline{X}$ = 25.8) and Komodo ($\overline{X}$ = 26.1). Two probably closely related subspecies are found near Komodo—*C. b. sumbawanus* on the eastern half of Sumbawa (*C. b. balinensis* is apparently found in the western half of the island [Mertens 1936]) and *C. b. leschenault* on Flores and other islands eastward.

Distribution and Habitat.—Various localities on Sumba (Forcart 1949), Padar, Komodo, and Pulau Longo (off Komodo). It probably also occurs in western Flores, for in 1971 I failed to capture a specimen seen in a coastal savanna habitat near Nggoer, Mangarrai District. It was certainly a member of this subspecies.

All the specimens reported, including those taken by Darevsky and Kadarsan, were taken in savanna habitats, often on trees or under their bark. With the exception of Forcart's remark (1949) that he found specimens in dry leaves, all other references imply that this subspecies

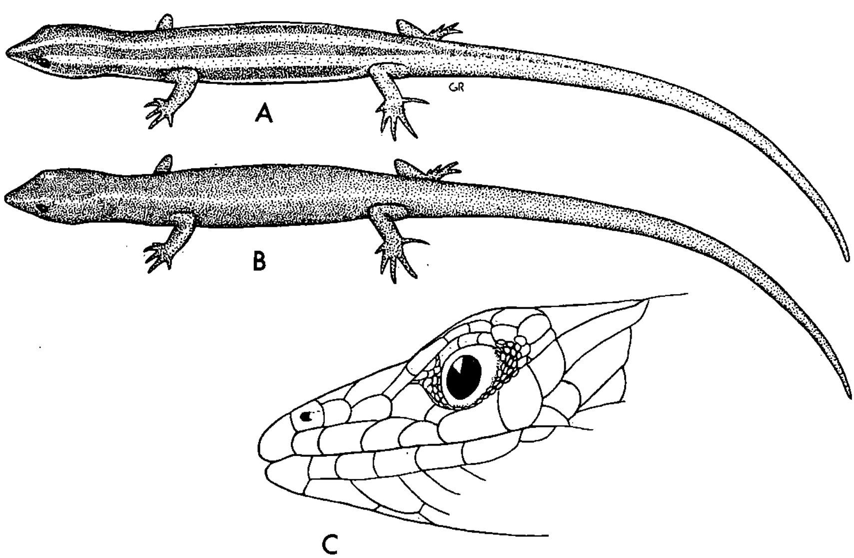


Figure 18.—(A) *Cryptoblepahrus boutoni renschi*, Loho Liang, Komodo (UF) 29918); and (B and C) *C. burdeni*, Gunung Klinta, Komodo (UF 30043).

is normally found on standing trees (Mertens 1927a, 1930, Darevsky 1964a). My observations on both Padar and Komodo show that on these islands it is always found below 100 m, usually on the trunks of the shrubby savanna tree *Zizyphus jujube* and usually close to the sea.

REPRODUCTION.—Newly hatched young have been reported for July (this study and Mertens 1931), August (this study and Darevsky and Kadarsan 1964), and October (this study). When hatched they have an SVL of 17 mm and are approximately 32 mm at the same time the following year.

FOOD.—Spiders and very small insects, most of which are termites and beetles.

PARASITES.—None found in specimens examined.

Cryptoblepharus burdeni (DUNN)
Figure 18

Cryptoblepharus boutonii burdeni Dunn 1927c:11 (east coast of Padar).
Ablepharus boutonii burdeni Mertens 1930:162.

SPECIMENS EXAMINED.—(55) UF 28967-73, west coast of Padar, 20-30 m; UF 29394-401, Tanjung Kuning, Komodo, 0-2 m; UF 30040-46, base of Gunung Klinta, Komodo, 0-2 m; UF 29903-17, Loho Boro, nr Loho Lavi, Komodo, 0-3 m; UF 29867, 29877-86, Pulau Longo, off Komodo, 0-4 m; UF 29887-902, Kampung Sabita, Komodo, 0-2 m.

DESCRIPTION.—Scutellation as in *Cryptoblepharus boutonii*, except anterior loreal as high as or higher than long and with more midbody scale rows. Komodo sample (N = 48) mean 30.9, Padar sample (N = 7) mean 30.6; overall range for total (N = 55) 29-34($\bar{X}$ = 30.8). Subdigital lamellae of 4th hind toe 20-24.

Color and pattern of *C. burdeni* quite different from that of *C. boutonii*. No light stripes nor evidence of them. Entire upper surface metallic dark brown to nearly black, with scattered, irregular lighter flecks. Some individuals nearly uniform brassy brown with slightly darker edge to each scale, sometimes forming faint interrupted longitudinal lines. Ventral surface always an almost uniform bluish-gray to gray; palmar surfaces very dark, soles lighter. SVL of large specimens about 50 mm, tail about 60 mm. Males with hind legs reaching to ankle or middle of forearm of appressed front leg, to axilla in females.

DISTRIBUTION AND HABITAT.—We obtained specimens only from the rocky shores of Padar and Komodo, but we saw others on nearby islets and rocky headlands of extreme western Flores. The habitat is very similar to that of the New Zealand black shore skink *(Leiolopisma suteri)* as described by Towns (1975), although the habits of the two lizards are very different. In the original description of *Cryptoblepharus burdeni*, Dunn (1927c) stated: "These lizards were discovered by Mr. Burden on rocks of the tide line on the east coast of Padar. Later I observed them there in great number, playing about on the wet rocks. . . . On a wave cut bench of rock, beset with small pools and alive with *Periophthalmus* and crabs of various kinds and wet by the waves of the rising tide, these tiny lizards scuttled about unconcerned about their larger neighbors. When I tried to catch some with my hands they ran into water of pools and two were caught there, clinging under water to the rocks." Mertens (1964) pointed out that this species and *C. littoralis* are apparently the most intertidal of all *Cryptoblepharus* species. Some races of *Cryptoblepharus boutonii*, particularly *bitaeniatus*, occur in similar habitats. Concerning this subspecies in East Africa, Loveridge (1920) stated: "This little lizard has adapted to a marine life; it is a remarkable sight to see it running over the rocks, which a moment before were washed by waves; for company it has the peculiar fish *Periophthalmus* and crabs of many species. It flies before the incoming wave and presumably manages to avoid a wetting. It seeks refuge when pursued in the many crevices of the rocks."

Our specimens were collected in similar situations on both Padar and Komodo, scurrying over rocks standing in the water, as well as on rocky cliffs immediately adjacent to the high tideline. None of the specimens was found over 20 m from the water's edge, and never in any place lacking small sea cliffs and rock jumbles at the shore.

TAXONOMIC REMARKS.—Mertens (1964) pointed out several instances of the occurrence of two subspecies of *Cryptoblepharus boutonii* on the same island. He reported both *C. b. balinensis* and *C. b. cursor* on Bali and Lombok. Miller (*in* Brongersma 1934) reported both *C. b. schlegelianus* and *C. b. leschenault* on the north coast of Samoa were due to accidental introduction by man of one of the forms, as he believed the extensive trans-Pacific distribution of *C. b. poecilopleurus* may have been similarly produced; or by waif dispersal. Even more confusing was his finding in Queensland, Australia, of *C. b. virgatus* and *C. b. littoralis* within meters of one another but in different habitats (the latter is now considered a separate species [Cogger 1975]). Also there was the problem of both *C. b. renschi* (reported by Darevsky 1964a) and *C. b. burdeni* (reported by Dunn 1927c) on Padar, both of which are now known from Komodo as well. That transport of one subspecies (*renschi*?) by humans is possible in both insular situations is suggested by the range of the land snail *Rachis punctata*, which is found in Africa, the west coast of India, and Padar—a range very largely influenced by man (Djajasasmita 1972). Many native boats visit Komodo and some stop at Padar for the easily obtainable fresh water there, and *C. b. renschi* may have been accidentally introduced into both islands from Sumba. Such an explanation will probably not, however, explain the presence of both forms in coastal western Flores, or the proximity of two or more subspecies in coastal Queensland (Mertens 1964), parts of New Guinea (George Zug, in litt.), or Australia (Ronald Crombie, in litt.). The entire matter of the relationships of all these populations is far from clear. Even Mertens (1933, 1934a, 1964) was not sure of their status but elected to consider them as a *Rassenkreis* highly modified by man and/or waif dispersal.

At least one of the populations formerly considered a subspecies is now designated a species *(C. littoralis)*. The similarity of this taxon to *C. burdeni* in both appearance and habitat suggested I examine material of *littoralis* to try to determine what relationship, if any, they have to one another. Two paratypes (AMNH 80071-2, Etty Bay by Innisfail, Queensland) and seven additional specimens (UMMZ 132581-2, Cape Tribulation N. Mossman, Queensland; 132583, four specimens from Magnetic Island, Alma Bay, Queensland; 132584, South Moule Island, Whitsunday Passage, Queensland) show low intrapopulational variation and are very unlike *C. burdeni.*

The presence of two highly differentiated populations of *Cryptoblepharus* on both Komodo and Padar, the lack of any indication of intergradation between them, and the fact that both forms were taken within several meters of one another in at least one locality on Komodo (Loho Boro), each in its own environment, strongly suggest that *Cryptoblepharus boutonii burdeni* Dunn is distinctive from *C. boutonii* at the species level and assignable to specific status. Additional material

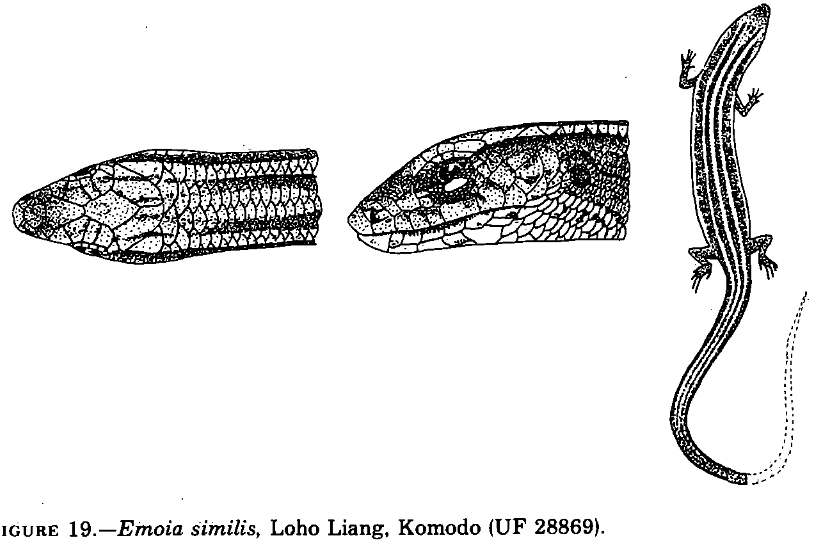


FIGURE 19.—*Emoia similis*, Loho Liang, Komodo (UF 28869).

of *Cryptoblepharus* specimens from East Indian islands will undoubtedly change some of the current views regarding relationships of the populations found there and the distribution of recognized taxa.

REPRODUCTION.—Females lay only one oval egg at a time (10.3-11.3 × 3.2-4.4 mm) during the wet season (recorded for December 16, though yolk deposition in other specimens collected in the same month suggests eggs are laid in January and February as well). I examined 13 females that showed sexual maturity occurs at an SVL of about 37 mm (avg 42.5 mm). We examined 14 males. Mature specimens with thick-walled, convoluted vasa deferentia and well developed, turgid testes were at least 38 mm SVL ($\bar{X}$ = 40 mm).

FOOD.—Almost all dissected specimens contained remains of small insects, most of which were tiny beetles.

PARASITES.—None was recognized in any of the specimens examined.

Emoia similis DUNN

Emoia similis Dunn 1927c:10.
Leiolopisma kadarsani Darevsky 1964b:84.
Leiolopisma kadarsani padariensis Darevsky 1964b:86
Leiolopisma sembalunica rintjana Darevsky 1964b:86.

SPECIMENS EXAMINED.—(13) Holotype AMNH 31977, Komodo; UF 28862, 29965-66, 28868-70, 28873-74, 28877, all from Loho Liang, Komodo, 0-30 m; UF 28875-76, Ntodo Liseng, Komodo, 450 m; UF 28805, macerated, from stomach of *Lycodon aulicus*, Loho Liang, Komodo.

DESCRIPTION. Head medium length. Lower eyelid with undivided transparent disc. Ear opening nearly round, smaller than eye, without any enlarged lobules. Nostril in nasal, bordered above by supranasals. Frontonasal wider than long, bordering rostral anteriorly and frontal posteriorly. Frontal shorter than the single frontoparietal and in contact with 2 supraoculars, 4 supraoculars, no interparietal, usually 2 nuchals, 7 supralabials. Midbody scale rows, all smooth, 26-28 ($\bar{X}$ = 27.3). Dorsal scales somewhat larger than ventral members. Preanals slightly enlarged. Limbs slightly reduced, not meeting when appressed against the body (overlapping in hatchlings). Distance between fore- and hindlimbs 1.5 to 1.8 times the distance between tip of snout and base of forelimbs; 4th digit of hindlimb longer than 3rd, with 18-23 subdigital lamellae.

Color brownish-black, brown, or brownish-gray above, with 5 silvery-white longitudinal stripes (sometimes paravertebral and dorsolateral stripes are cream or yellow). Each stripe passes through the border of two adjacent rows of scales. Vertebral stripe usually begins near snout, extending posteriorly over head, becoming clearly defined in most specimens at occiput, where it is often bordered by a fine dark edge. Stripe extends posteriorly onto base of tail, which is largely an almost uniform bluish-gray. The paravertebral stripes extend from above eye posteriorly to anterior third of tail. Dorsolateral stripes often indistinct. extending from behind ear opening to insertion of hind limb. Abdomen, throat, and chin grayish-white to white. Maximum length 112 mm; SVL/tail 1/1.2 to 1/1.5 ($\overline{X}$ = 1/1.3).

TAXONOMIC REMARKS.—According to the literature no specimens of *Emoia similis* have been collected since the two original individuals obtained by Dunn, now in the AMNH (one has subsequently been skeletonized). Darevsky collected none during his trip to Komodo, and the matter was thus rather confusing; particularly as Darevsky (1964b) described *Leiolopisma kadarsani* from Komodo and a subspecies from nearby. Dunn's (1927c) description of *E. similis* was very short and provided few characters with which to compare it to other scincids. The assignment of the two Komodo specimens to *Emoia* was made on the basis of the presence of supranasal scales. My examination of the type showed it does possess these scales. Furthermore, during 1969-70 I collected the 12 specimens reported here, and they agree with the type in every major detail, including the presence of supranasals (Fig. 19). What is odd is that Darevsky's 15 specimens of identical appearance and from the same locality are said to lack them. Figure 5 of Darevsky's description (1964b) shows an almost completely divided nasal above the nostril. The posterior part of the cleft is sometimes difficult to see, and investigation of the material deposited in the Bogor Museum shows that it is present in the type series of *L. kadarsani.* Therefore, I place *Leilopisma kadarsani* in the synonymy of *Emoia similis* Dunn.

Leiolopisma kadarsani padariensis Darevsky was described on the basis of its having a wider dorsal stripe than the nominate subspecies (particularly near the head) and a slightly less patterned head. Otherwise the two forms are apparently identical. Of the 13 specimens available from Komodo all but two have a dorsal stripe about one scale wide behind the head. UF 28869 and 28870 have wider stripes, that of the former being two scales wide, as in *L. k. padariensis*, and the latter intermediate between the usual Komodo condition and UF 28869 and the three types of *L. k. padariensis.* I am tentatively placing *Leiolopisma kadarsani padariensis* in the synonymy of *Emoia similis.* The occurrence of the subspecific characters in at least some Komodo specimens and that only a few individuals are presently available from Padar suggest that the best present course is not to recognize the Padar population nomenclatorially until more specimens become available. In the event that the subspecific characters are found to be valid, the Padar population should be called *Emoia similis padariensis* (Darevsky).

Mertens (1927a) described *Leiolopisma sembalunicum* on the basis of one specimen from Lombok; none has been found since. Though the skin around the nasal area was scarred, Mertens placed it in *Leiolopisma* on other grounds. *Emoia* was disregarded on the ground that the specimen's legs were far too short. However, their lengths seem equivalent to those of *Emoia similis*. Furthermore, all remaining characters can be matched in these specimens as well, so it is highly likely that *Leiolopisma sembalunicum* Mertens may be a synonym of *Emoia similis*. By the same reasoning, the type series of *Leiolopisma sembalunica rintjana* Darevsky should be reinvestigated, for the figure provided (Fig. 6 of Darevsky 1964b) shows what might be interpreted as supranasals.

DISTRIBUTION AND HABITAT.—Definitely known from Komodo, Padar, and Rintja. Future work may show that it is found as far westward as Lombok.

Darevsky (1964b) stated that this small lizard was common in the grass on the edge of bamboo thickets at altitudes of 500-600 m. Dunn (1927c) found them among stones on grassy slopes at a similar elevation. Our specimens were collected in *Zizyphus* savanna from sea level to about 30 m, usually in the grass or clambering about on the trunks of *Tamarindus* or *Zizyphus* trees.

REPRODUCTION.—I examined 11 females for reproductive data. Of these seven were immature, as judged by the thin-walled, smooth oviducts and lack of extensive follicular development. Of the mature specimens two were gravid; UF 28873 had two large oval-shelled ova (9.7 × 3.7) in the right oviduct and none in the left (January). UF 28868 had one ovum in both the right and left oviducts (December). Interestingly, the former had only one corpus luteum on the right ovary, maintaining both ova, whereas the latter had one corpus luteum on each ovary, corresponding to the single ovum in each oviduct.

The single nongravid female had one follicle on each ovary that showed extensive yolk deposition, whereas the other follicles (4 on left ovary, 2 on right) were small and translucent, exhibiting little if any yolk deposition. The oviducts of the three adult females were all thick-walled and highly convoluted.

In all but two of 10 males examined, the left testes were slightly posterior to the right. In the remaining two both testes were approximately equidistant from the head. Two individuals were juveniles. The testes of adult males collected November through February were turgid and cylindrical to subcylindrical, and the vasa deferentia were thick-walled and extremely convoluted. The right testis was missing on one specimen.

FOOD.—Spiders and miscellaneous insects were found in nearly all the specimens examined, including one small moth, particularly beetle larvae and small grasshoppers.

PARASITES.—None found in specimens examined.

REMARKS.—Occasionally eaten by *Lycodon aulicus*.

Mabuya multifasciata multifasciata (KUHL)
Figure 20

Scincus multifasciatus Kuhl 1820:126 (Type locality: [?] Java).
Mabuia multifasciata Weber 1890:160.
Mabuya multifasciata multifasciata Mertens 1930:257.

SPECIMENS EXAMINED.—(1) UF 30030, Poreng, Komodo, 550 m.

DESCRIPTION.—Snout short, obtuse; lower eyelid scaly; ear opening round to oval (vertical to horizontal) with 3 to 6 sharp lobules on the anterior edge of the opening ($\bar{X}$ = 4.3) (rarely missing in specimens from other areas). Nostril in a nasal scale; postnasal and supranasal scales present; frontonasal twice as broad as long; prefrontal always in contact. Frontal as long as frontoparietals and interparietal together or shorter, in contact with the second of the two anterior supraoculars; 4 supraoculars, second largest. Frontoparietals larger than the interparietal; parietals separated; a pair of nuchals; supralabial 5 largest and below the eye. Body with 29-33 scale rows on Komodo (29-34 in other parts of range), each scale with 3 keels, except those over the pelvic region, which often have 2. Limbs strong, hindlimbs do not reach the axilla. Fourth hind toe longest, with 14-18 nonkeeled subdigital lamellae on Komodo (14-21 elsewhere and sometimes weakly keeled). Largest Komodo specimen SVL 82 mm, tail 124 mm, much larger specimens available elsewhere.

Color of adult females brown or olive-brown above, scales with blackish lateral borders, sometimes forming longitudinal lines in large specimens. Flanks dark brown or black, with light, black-edged spots.

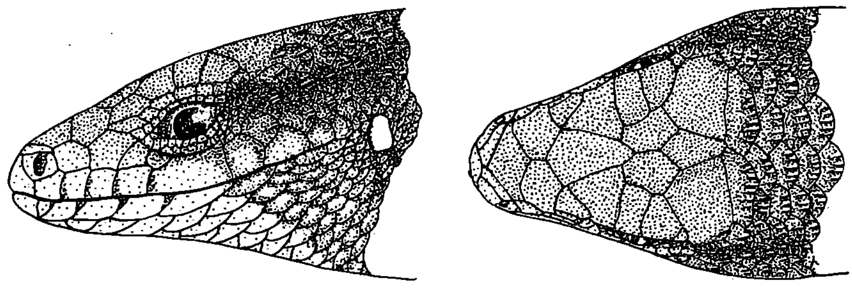


FIGURE 20.—*Mabuya multifasciata multifasciata*, Poreng, Komodo (UF 30030).

Ventrally green to yellow, throat bluish-white; side of head gray to olive-brown; supralabials white, with dusky sutures. Males are similarly colored, except that they are provided with a broad yellowish-green or yellowish-white band from just above the insertion of forelimbs posteriorly to slightly over half way to hindlimbs. Venter and throat darker, often dark gray to blue-green laterally.

TAXONOMIC REMARKS.—*Mabuya multifasciata balinensis* was described by Mertens (1927a) on the basis of a contact between the first supralabial and the frontal. Mertens (1930) found the contact missing throughout the remaining part of the archipelago from which he had specimens. The Komodo and Flores material now available confirms his findings. The remaining diagnostic character of *balinensis* concerns the coloration of males, which have a reddish-brown streak on the top of the snout of large males, and a yellow rather than reddish lateral strip. Unfortunately, no large males are available from Komodo, but adult males from extreme western Flores have a bright red lateral stripe, as in the nominate subspecies. Younger individuals are provided with a gold-colored stripe.

DISTRIBUTION AND HABITAT.—The subspecies *M. m. multifasciatus* is found on Lombok, Sumbawa, Komodo, Rintja, Sumba (Forcart 1949), and Flores. In many areas it is the commonest of lizards. However, on Komodo, Rintja, and western Flores, it is restricted to quasi-cloud forests in mountainous areas and in streamside gallery forests. In more humid zones it is widely distributed. Its altitudinal range is from sea level to at least 1200 m. On Komodo it occurs from 500 to 650 m.

REPRODUCTION.—On Komodo hatchlings were recorded in July and August. Gravid females were collected in July. Two to four round eggs ($\bar{X}$ = 11.5 mm diameter) are laid under stones and in rotten wood. Minimum SVL of 13 mature females is 85 mm, $\bar{X}$ SVL of mature females is 92.5 mm. Ten mature males have a mean SVL of 93 mm and an overall range of 79-111 mm.

Sphenomorphus (Sphenomorphus) emigrans emigrans (LIDTH DE JEUDE)

Figure 21

Lygosoma emigrans Lidth de Jeude 1895:125 (Type locality: Sumba).
Lygosoma everetti Boulenger 1897:504 (Type locality:Sumba).
Sphenomorphus emigrans emigrans Mertens 1928a:230.
Lygosoma (Sphenomorphus) emigrans Smith 1927:220.
Lygosoma (Sphenomorphus) emigrans emigrans Forcart 1949:372.
Sphenomorphus mertensi Darevsky 1964b:81.

SPECIMENS EXAMINED.—(23) UF 28821, 28823-35, 28837, 28839-40, 28960, 28962-66, all from Loho Liang, Komodo, 0-30 m.

DESCRIPTION.—Head obtuse anteriorly; lower eyelid scaly, with 2-4 central scales markedly enlarged, forming a slightly distinct, semitransparent palpebral disc; ear opening oval to nearly round, with three slightly distinct scale lobules anteriorly; nostril in a nasal scale, no supranasal; frontonasal wider than long; prefrontals separated by fronto-frontonasal contact; 5 supraoculars, with second (sometimes third) being the largest; parietals in contact with each other posterior to a single frontoparietal; 7 supralabials; scales of midbody 26-30 ($\bar{X}$ = 27.7); 2 slightly enlarged preanals; tail somewhat thickened along its entire length, long tail (body/tail: 1/1.1-1/1.4); adult SVL 50-65 mm, tail 70-95 mm; limbs short, hindlimb somewhat shorter than distance from tip of snout to base of forelimbs; distance between limbs 1.5 times distance between snout and base of forelimbs; fourth digit of hindlimbs larger than third, with 20-24 subdigital lamellar scales ($\bar{X}$ = 22.4).

Color yellowish-brown above, in which most scales are provided with a brown spot, sometimes aligned longitudinally to produce a short stripe, especially in anterior half of body and sometimes on tail.

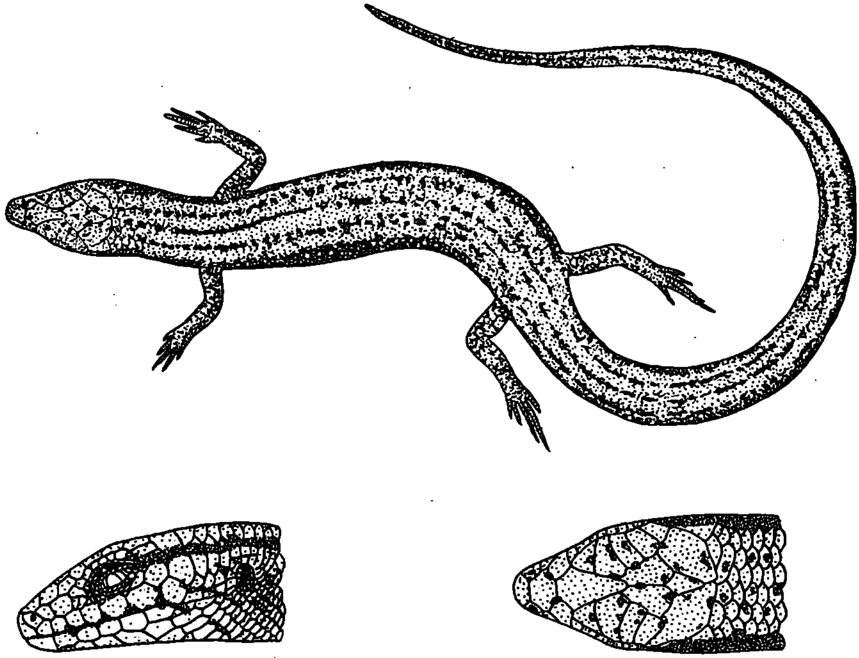


FIGURE 21.—*Sphenomorphus emigrans emigrans*, Loho Liang, Komodo (UF 28851).

A wide dark brown stripe passes from nostril over canthus and eye through temporal area to over hindlimb, sometimes faintly edged with cream above and below. Sides of body below temporal stripes densely covered by small speckles and spots, gradually disappearing toward abdomen. White to cream below. Infralabials variously speckled with brown.

TAXONOMIC REMARKS.—Darevsky (1964b) described *Sphenomorphus mertensi* from Padar without comparing his type material with specimens of *S. emigrans*, of which it clearly is a synonym. No single or combination of characters will separate *S. mertensi* from *S. emigrans*. The distinctly striped *S. e. wetariensis* Mertens has a restricted range from islands north of the Flores coast to Wetar. Mertens (1930) believed the New Guinea material may belong to an undescribed subspecies closely related to *S. e. wetariensis*.

DISTRIBUTION AND HABITAT.—*Sphenomorphus emigrans* was previously unknown from Komodo, though it was reported from several localities on Sumba (Forcart 1949), Wetar, Samao, Pulau Sukur, Teun, Pulau Besar (Gr. Bastaard, north of Flores), and Astrolabe Bay on New Guinea. Curiously, it has not been reported from Flores itself, although it occurs on almost all the islands surrounding it. However, I expect it occurs in at least the westernmost part of the island because of similar habitat. All the Komodo specimens were found under debris and among the leaves on the floor of deciduous monsoon forest. Many were taken from can traps buried along a drift fence. None was found above 30 m or far from the sea.

REPRODUCTION.—Average SVL of 10 mature females is 55.0 mm (range 47-61), for 5 mature males 55.7 mm (42-62). The sex ratio of the total sample (N = 23) is almost exactly 2:1 in favor of females. No gravid females or eggs were found, but follicular development suggests that one egg is laid each year, probably during the wet season, for specimens collected July through October show no major growth of ova, whereas those collected in November have proportionately much larger yolked ova. Unfortunately, none was collected during the monsoon months of December through February.

FOOD.—Small insects, particularly bupestid beetles and their larvae, and ants. Scorpions are also frequently taken. Skink scales found in one stomach suggest that this species occasionally eats its own shed skin—a habit apparently not common among scincids.

PARASITES.—The nematodes *Parapharyngodon maplestonei* and *Pharyngodon kuntzi* were common in the colon.

Sphenomorphus (Sphenomorphus) florensis florensis (Weber)

Lygosoma florense Weber 1890:173 (Type locality: Maumeri, Flores)
Sphenomorphus florensis Barbour 1912:29.
Sphenomorphus florensis florensis Dunn 1927c:5.
Sphenomorphus florensis nitidus Dunn 1927c:5 (Type locality: Komodo, 1200 ft).
Lygosoma (Sphenomorphus) florense Smith 1927:219.

Specimens Examined.—(72) UF 29926-30, 29938-51, all from Nggoer, Mangarrai District, Flores, 0-10 m; Holotype *S. f. nitidus*, AMNH 32068, 650 m, Paratypes AMNH 32055-67, 32070, 32101-4, 0-650 m, Komodo; UF 28819-20, 28822, 28826, 28836, 28838, 28841-54, 28861, Loho Liang, Komodo, 0-30 m; UF 33067-68, 33070-72, Nunung, Mangarrai District, Flores, 700 m; UF 33064, Nisar, Mangarrai District Flores, 200 m; UF 33065-66, Ruteng, Flores, 1200 m; UF 32601-3, Padar.

Description.—Head medium length, snout somewhat shortened; lower eyelid scaly; ear opening oval, smaller than orbit, with 4-7 anterior lobules (usually 6) in Komodo specimens (fewer in some other areas, see Mertens 1930); nostril in a nasal scale, no supranasals; frontonasal slightly broader than long; frontal almost as long as frontoparietal and interparietal together, in contact with 4 anterior supraoculars; 6 to 7 supraoculars, first larger than the second; parietals in contact; no nuchals; supralabials 7, 6 and 7 largest, under

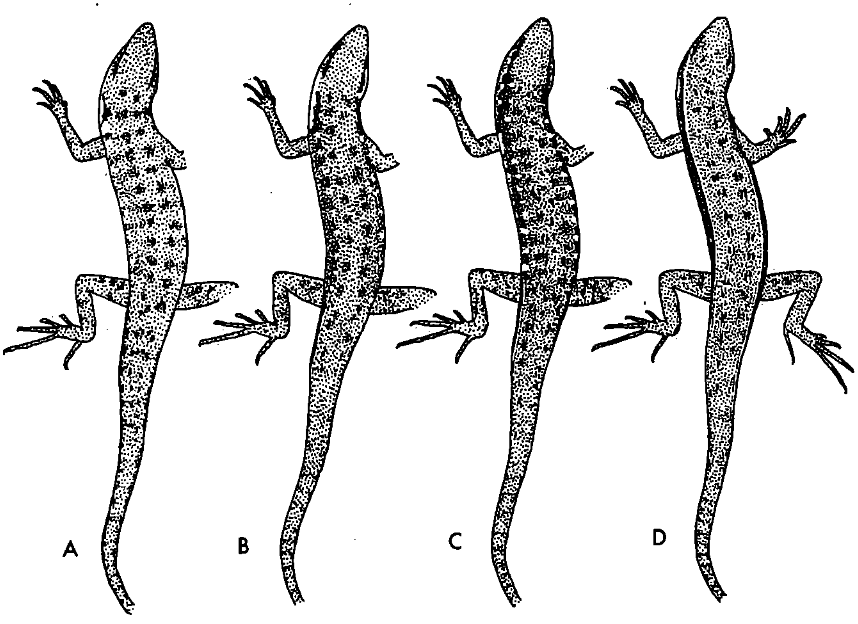


Figure 22.—*Sphenomorphus florensis florensis*, all from Komodo. (A) (UF 28846) SVL 49 mm; (B) (UF 28844) SVL 53 mm; and (C) (UF 28851) SVL 50 mm; (D) (UF 28849) SVL 53 mm.

eyes; scales smooth, largest dorsally, 44-47 in number on Komodo ($\bar{X}$ = 45.9) (43-50 over entire range); length from tip of snout to insertion of forelimb is 1⅓ times the length between appressed limbs; two preanals enlarged; fourth hind toe longest, with 24-29 ($\bar{X}$ = 27.7) smooth (rarely feebly keeled) subdigital lamellae.

Ground color light brown with metallic luster, sometimes with narrow lighter middorsal stripe about one scale wide; dorsally with small brownish spots, sometimes arranged in paravertebral rows, indistinct in large adults, most distinct in young where they sometimes nearly form crossbands; dark brown speckles on legs and dorsal surface of tail; dark lateral stripe beginning behind eye and extending over ear and limb insertions onto sides of tail for ⅓ to ½ of its length. Dark brown stripe widest in middle of body, but often disrupted by white spots along lower edge. Often edged with a narrow white to cream line or white spots above or short vertical bars extending onto dark side stripe. Subcanthal stripe from eye to nostril less evident in Komodo specimens than those from lowland Flores. Subocular dark stripe and supralabial sulcal vertical bars dusky, not intense in most Komodo specimens. Venter, throat, and chin greenish-yellow to yellow-white.

TAXONOMIC REMARKS.—Komodo is the type locality of *Sphenomorphus florensis nitidus*, which Dunn (1927c) described on the basis of several color and pattern characters. After a thorough comparison with topotypic material of *S. f. florensis*, Mertens (1930) placed *S. f. nitidus* in the nominate subspecies, and I agree. All the characters of *S. f. nitidus* are duplicated in specimens from both Flores and Sumbawa. The head of *S. f. florensis* adult males is said to be red-tinged, whereas that of *S. f. nitidus* is not. Mertens stated that only the *S. f. florensis* from eastern Flores were so colored. The male specimens we collected in July are brassy brown on the top of the head, as in most adults, but the chin and throat, as well as the side of the neck and front legs, all have a reddish tinge. This fades into yellow on the chest just in front of and between the forelimbs. The colors are probably sexually correlated, for we did not see them in the few females collected. Furthermore, they may be seasonal. Though Weber (1890) mentioned black flecks on the chin of Flores specimens, Mertens (1930) found none on any of his material, nor did we on our specimens from west Flores or Komodo, but the darker individuals from Ruteng, Flores, have flecks on the infralabials.

DISTRIBUTION AND HABITAT.—*Sphenomorphus f. florensis* has been reported from Sumbawa, Sumba (Forcart 1949), Komodo, Padar, Rintja, Flores, Pulau Besar, Adonare, Alor, Samao, and Timor; *S. f. bar-*

bouri from Wetar, and *S. f. weberi* from Damma. On Komodo it is distributed from sea level to 650 m; on Flores we collected it as high as 1200 m. Throughout its range it is usually found in drier areas. Mertens (1930) reported it from small rocky islets off Sumbawa and in the arid zones of southeastern Flores (particularly *Corypha* and *Pandanus* forests) as well as the moist mountain top forests in both Sumbawa and Flores. It is commonest in open places in monsoon forest, particularly along the dry sandy creek beds. Here it is quite abundant and can be found scurrying about, even at night. It climbs well and on Komodo was often seen in trees to a height of 10 m. Both the New York Zoological Society and the Burden Expeditions found it in the quasi-rain forests of Komodo at about 500 m elevation, but always in open areas, quite often in ecotonal areas.

REPRODUCTION.—The sex ratio is essentially equal (♂♂ 1:1.3 ♀♀). In both males and females maturity occurs at an SVL of about 58 mm (average in females 62.3 mm, males 63.5 mm). Eggs are probably laid during the wet season, for in UF 28961, collected in November, the right ovary contained large, yellow follicles showing advanced yolk development (3.0 mm d.); all others were white and less than 1 mm in diameter. The left ovary had five follicles: one large (3.4 mm d.) and yolked, two with slight yolk deposition (1.5 mm d.), and two very small and translucent. The oviducts were thick-walled and extremely convoluted.

FOOD.—Food remains were found in 75% of the specimens examined. Beetle larvae were most numerous; termites, ants, and grasshoppers were infrequent, spiders more common.

PARASITES.—Endoparasitemia is low, with a colonic oxyuroid (*Thelandros* sp.) found in only 1 of 22 specimens examined.

REMARKS.—One specimen was found in the stomach of a *Lycodon aulicus*. Individuals were frequently seen abroad at night.

Sphenomorphus (Sphenomorphus) striolatus (WEBER)
Figure 23

Lygosoma striolatus Weber 1890:161 (Type locality: Reo, Flores).
Sphenomorphus striolatus Barbour 1912:185.

SPECIMENS EXAMINED.—(65) AMNH 32071, 32076-85, 32090-93, Komodo, 650 m; UF 29931, 32573-78, all from Nggoer, Mangarrai District, Flores, 10 m; UF 33075, Ruteng, Flores, 1200 m; UF 28925-32, Gunung Satilibo, Komodo, 600 m; UF 28933-46, Galulai, Komodo, 500 m; UF 28947-59, Mborombampang, Komodo, el 350 m; UF 28974-83, Gunung Vau, Komodo, 500 m.

DESCRIPTION.—Head moderately short, particularly the snout; lower eyelid scaly; ear opening oval, smaller than orbit, with no lobules; nostril in a nasal scale, no supransals; frontonasal much broader than long; frontal about as long as frontoparietals and interparietal together; 6 to 7 supraoculars, the first longer than the second; parietals in contact; nuchals weakly developed or absent; 5th and 6th supralabials largest and under eye; scales at midbody in Komodo specimens 28-42 ($\bar{X}$ = 40.5), 36-45 over entire range; length from tip of snout to insertion of front leg is about 1⅛ to 1¼ times the distance between the appressed legs; fourth toe largest, with 23-26 keeled subdigital lamellae.

Color not noticeably sexually dimorphic. Metallic brassy brown to greenish-yellow middorsal stripe about two scales wide. A paravertebral row of dark brown to black long spots or dashes, sometimes with cream or white spots in between, dark spots continuing onto tail, though faded. Sides with irregular dark stripes comprised of a brown or black spot on each scale, sometimes broken by narrow irregular stripes, dashes, or spots of cream, tan, or brown. Dark stripe from nostril to eye. Supralabials and infralabials edged ventrally and dorsally with brown or usually black, often extending dorsally along supralabial sulci. Legs speckled with brown or black. Postorbital stripe variable. Ventral surface uniform cream to white. Hatchlings and juveniles colored and patterned as adults.

Distribution and Habitat.—Known only from Komodo, Rintja, Flores, and Damma. Generally widely distributed in quasi-rain forests in the mountains to at least 1200 m elevation, but also at low elevations in moist gallery forests along rivers, such as at Reo and Nggoer, Flores.

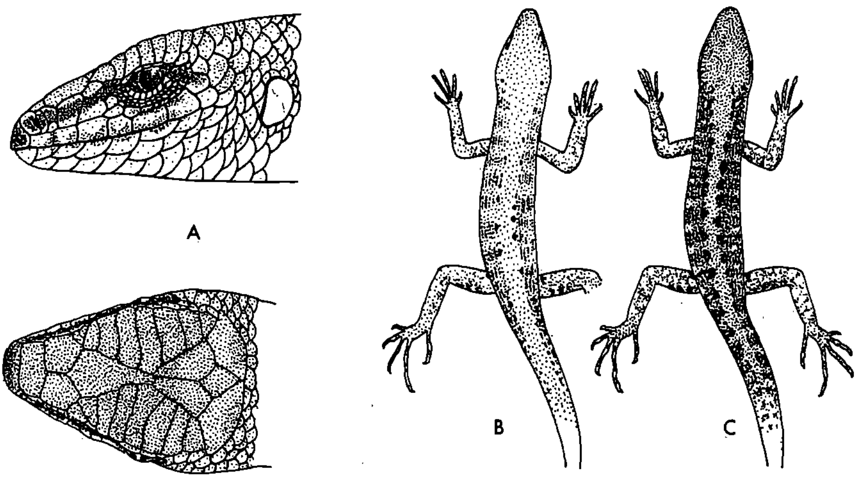


Figure 23.—*Sphenomorphus striolatus striolatus;* (A and B) Nggoer, Flores (UF 32574); and (C) Ruteng, Flores (UF 33075).

REPRODUCTION.—The sex ratio (N = 35) is probably equal (♂♂ 1:1.2♀♀). I examined 18 females for reproductive data; 11 had one shelled egg in the oviduct (11.1-13.4 x 4.5-5.7 mm). The shell was completely deposited, being white and granular. The associated ovaries each had one corpus luteum; disc-shaped, yellow, and an indented center. In all females I examined the oviducts were broad and convoluted (except UF 28948) and very thick-walled and mature (except UF 28942 and 28929). In UF 28942 and 28929 the oviducts were thinner-walled, though each contained shelled ova. The number of follicles varied from 2 to 7 ($\bar{X}$ = 5.3); follicular size from less than 1 to 4.0 mm. Apparently only one egg is laid at a time, 2-7 annually, most of which are laid in the monsoon season, December to February. Average size of 18 mature females is 55 mm, of 15 males 49 mm.

FOOD.—Food remains were found in 90% of the specimens collected. Beetle larvae were most common, but ants, termites, grasshoppers, spiders, adult beetles, and scorpions were also found. The beetle larvae represented several types that are most commonly found deep in rotten wood and suggest considerable digging activity by the lizards.

PARASITES.—Endoparasitemia is low, with the nematode *Trichoskrjabinia secundus* found in only 35 specimens.

Sphenomorphus (Homolepida) schlegeli (DUNN)
Figure 24

Homolepida schlegeli Dunn 1927c:8 (Type locality: Komodo; 650 m).
Omolepida schlegeli Mertens 1930:272.
Sphenomorphus schlegeli Darevsky 1964a:569.
Sphenomorphus oxycephalus Darevsky 1964b:83 (Type locality: Rintja).

SPECIMENS EXAMINED.—(4) Holotype, AMNH 31994; UF 28983-84, Gunung Ara, Komodo, 500 m; UF 28989, gallery forest along Kali Besar, Loho Liang, Komodo, 200 m.

DESCRIPTION.—Snout longer than *S. temmincki;* lower eyelid scaly; ear opening large, round to slightly oval, nearly same size as eye, no scaly lobules; nostril in a nasal; no supranasal; frontonasal wider than long; prefrontals in contact; frontal about as long as frontoparietals and half of interparietal, in contact with first two supraoculars; 5 supraoculars, third largest; parietals in contact behind the interparietal; no nuchals; 5 supralabials; suboculars present; midbody scale rows 22-24, smooth paravertebral rows slightly enlarged; preanals slightly enlarged; limbs very short, small; fourth hindlimb digit longest, with 9 (1 specimen) to 10 subdigital lamellae.

Brownish-gray above with bronze tinge. Two narrow white to cream dorsolateral stripes from last supraocular or over ear opening posteriorly onto base of tail, bordered above by a narrow dark row of spots anteriorly. Sides dark brown, darkest below light dorsolateral stripe and fading to yellow-gray on venter. Throat and chin immaculate to spotted with brown. Tail variable, from almost uniform light brown to marked with a spotted or much darker dorsolateral stripe extending about one half tail length. Body/tail lengths: 22/24, 33/29+, 31/35.

TAXONOMIC REMARKS.—*Sphenomorphus oxycephalus* Darevsky is synonymized with *S. schlegeli* (Dunn) because the stated characters of the type clearly fall within the variation of the specimens of *S. schlegeli* now available from Komodo. The considerably narrow head of the type mentioned by Darevsky (1964b) is obviously due to the fact that the specimen was allowed to dry out, as is clearly shown in the photograph provided in a companion paper by Darevsky (1964a).

Dunn (1927c) placed this species close to the Papuan *S. crassicauda* and *S. forbesi.* In my opinion it seems much closer to the former. Either *schlegeli* or close relatives are logically expected in mountainous tracts of Flores and other more eastern islands of the Lesser Sundas. This group (including *S. unilineatum,* West Irian) is apparently restricted to the New Guinea-Nusa Tenggara section of the Lesser Sundas. The *S. temmincki* group (including *S. parvum*) is much more widely distributed, being found from Sumatra to near Timor. *S. alfredi*

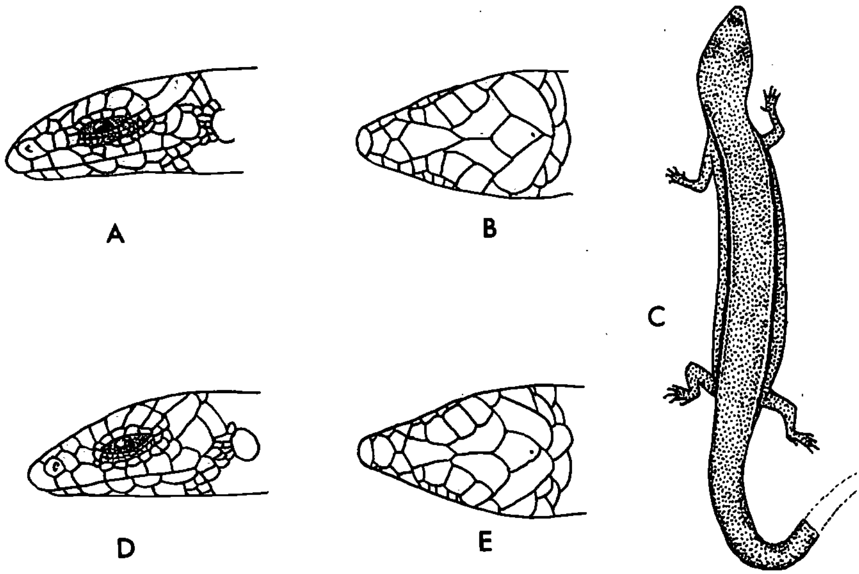


FIGURE 24.—(A and C) *Sphenomorphus schlegeli,* Gunung Ara, Komodo (UF 28983) (B) *S. schlegeli,* holotype (AMNH 31994); and (D and E) *S. oxyrhopus,* holotype (Zool. Inst. Sci., Leningrad, 17598).

and *S. hallieri* comprise a separate subgroup of the subgenus *Homolepida*, restricted to Borneo.

DISTRIBUTION AND HABITAT.—Most quasi-rain forests of Komodo and Rintja, at elevations generally above 500 m.

REPRODUCTION.—Both females examined had 3 follicles in both their right and left ovaries (> 1-1.5 mm). Their oviducts were flat, thin-walled, and only slightly convoluted, suggesting egg laying does not occur during the dry season (specimens collected in August).

Food.—No food remains were found.

PARASITES.—No parasites were found in the two female specimens dissected.

REMARKS.—Until this study only the type was known; collected in "heavy forest, interspersed with great rock masses which forms the elevated center of Komodo." One specimen was taken from the stomach of an adult *Psammodynastes pulverulentus*.

FAMILY AGAMIDAE

Draco volans reticulatus (GÜNTHER)

Figure 25

Draco reticulatus (Günther) 1864:125 (Type locality: Philippines).
Draco volans Roux 1911:496.
Draco reticularis Elbert 1912:329.
Draco timorensis Rooij 1915:75 (part).
Draco volans reticulatus Mertens 1930:249.

SPECIMENS EXAMINED.—(7) UF 28918-24, Loho Kiang, Komodo, 10m.

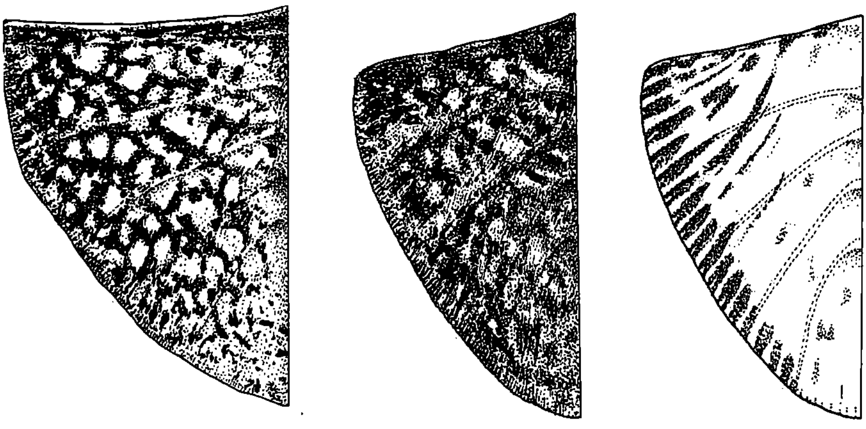


FIGURE 25.—Flight membrane of *Draco reticulatus*. (A) dorsal surface of adult female (UF 28924); (B) same, of adult male (UF 28921); and (C) ventral surface of adult male (UF 28921), all from Komodo.

DISTRIBUTION AND HABITAT.—Previously known from most of the Lesser Sunda Islands: Celebes, Flores, and Sumbawa (Mertens 1930); Sumba (Forcart 1949); and Komodo (Darevsky 1964a, who also saw it on Rintja). Though originally taken in the Philippines, its exact locality was unknown, and it has not been taken there since. *Draco v. volans* extends westward to Thailand on the mainland.

It is a much commoner lizard than the number of captured specimens indicate; many more could have been captured had a serious attempt been made to do so. Mertens (1930) stated that it is more common at higher altitudes, but our experiences suggest it is abundant in any rather mesic, forested area. The gallery forests along both Vai Nggulung and Kali Besar in Loho Liang, Komodo, as well as the coconut plantation near Kampung Komodo, had good populations as dense as those in the higher mountain forests. I agree with Mertens (1929b) that this lizard is most often encountered on large nearly leafless trees in open forests.

REPRODUCTION.—Of the three females examined, only one (UF 28924), collected in February, was gravid. Each oviduct contained two partially shelled, oval ova (14.5-16.9 x 4.1-7.5 mm) ready to be laid, so that the total egg complement would have been four. In addition, the left ovary had two corpora lutea, two large yolked follicles (suggesting multiple clutches), and nine very small translucent follicles. The right ovary had one large yolked follicle, one small translucent follicle, and no visible corpora lutea.

FOOD.—Dissected specimens contained only ants.

REMARKS.—Only one species of *Draco* inhabits the Lesser Sunda Islands chain; it is extremely variable in both color and many of its scale characters (Mertens 1930). As in most individuals of this species, the scales near the vertebral line of the Komodo specimens are somewhat irregular. They also lack the keeled paravertebral scales that are sometimes found in Flores specimens but are missing in those from Sumbawa and Lombok. The dorsal color of the gliding membrane is reticulated with black, brown, and white; those of the males are generally darker than those of the females (Fig. 25). The ventral membrane is uniform white, but some specimens have a few black flecks or streaks, in males particularly near the outer edge (Fig. 25). Dewlap lemon yellow in males.

FAMILY DIBAMIDAE

Dibamus novaeguinea (DUMERIL AND BIBRON)

Dibamus novae-guineae Dumeril and Bibron 1839:834.

SPECIMENS EXAMINED.—(5) UF 33074, female, Vai Nggulung, Loho Liang, Komodo, 300 m; UF 33073, male, Kali Besar, Loho Liang, Komodo, 160 m; UF 29460, 29449, two males, Loho Lavi, Komodo, 30 m; UF 33488, female, 1 km S Nunung, Flores, 75 m.

DISTRIBUTION AND HABITAT.—This distinct legless lizard has a wide distribution—from the Nicobar Islands and the Malay peninsula through the Sundas to New Guinea. In the Komodo area it has been reported from Flores (Smith 1927), Sumbawa (Mertens 1930), Sumba (Forcart 1949), and Komodo (Darevsky 1964a). The usual habitat is under stones in moist forests, generally above 400 m. Our specimens from below this elevation were taken from beneath stones in the gallery forests that extend downward as moist, cooler tongues of the quasi-rain forests on the highest slopes. Darevsky apparently collected his two specimens on the central ridge of Komodo above 500 m. UF 33074 was found drowned after a flash flood.

REMARKS.—Mertens (1930) stated that both his specimens (Flores and Sumbawa) had 22 midbody scale rows, whereas those from Lombok had 20-24 rows, suggesting significant geogaphic variation. Two of the Komodo males have 24 rows and the third male and the female 22 rows. One male (SVL 129 mm, tail 21 mm) is a uniform brownish-purple above and below, with only the enlarged head scales and perianal region lighter; another (92 mm/18 mm) is similar but with lighter spots on the belly, and the third (86 mm/13 mm) is provided with a few random spots over the body and a light band near the middle of the body. The female (132 mm/16 mm) is similar, except that the belly is mottled with lighter color, and two broad bands of the same lighter shade encircle the anterior half of the body.

I can add nothing new regarding this species' reproductive and feeding habits.

FAMILY VARANIDAE

Varanus komodoensis OUWENS

Figures 26-33

Varanus komodoensis Ouwens 1912:1 (Type locality: Komodo).
Placovaranus komodoensis Fejevary 1927:284 (substitute name).

SPECIMENS EXAMINED.—(164) UF 29000-1, skins and skeletons, coast at Nggoer, Mangarrai District, Flores (under permit); UF 28221, right mandible found on surface, Gunung Ara, Komodo; UF 28220, skeleton, tagged #27W in life, killed by monitor #19W on 16 November 1969, Loho Liang, Komodo; UF 28219 skeleton, tagged #18W in life, killed by monitor #19W on 3 April 1970, Loho Liang, Komodo; UF 28227, parts of skeleton from monitor fecal pellets, Ntodo Klea, Komodo; UF 28228, from fecal pellet remains, Loho Liang, Komodo; MZB 582, 6 full term embryos, eggs laid in Surabaja Zoo; MZB (no number), 2 embryos, same date; MZB 926-28, 946, 980-81, Loho Liang, Komodo; MZB 929, Mburo, Flores; plus 127 live specimens examined on Komodo, Padar, and Flores during this study.

DESCRIPTION.—A very large (max. total length ca 3 m, $\bar{X}$ = 1.70 m, $\bar{X}$ SVL = 74.5 cm, see Fig. 26), heavy monitor when adult (max. field weight 54 kg, $\bar{X}$ = 8.6 kg, N = 50, see Fig. 27); males slightly larger

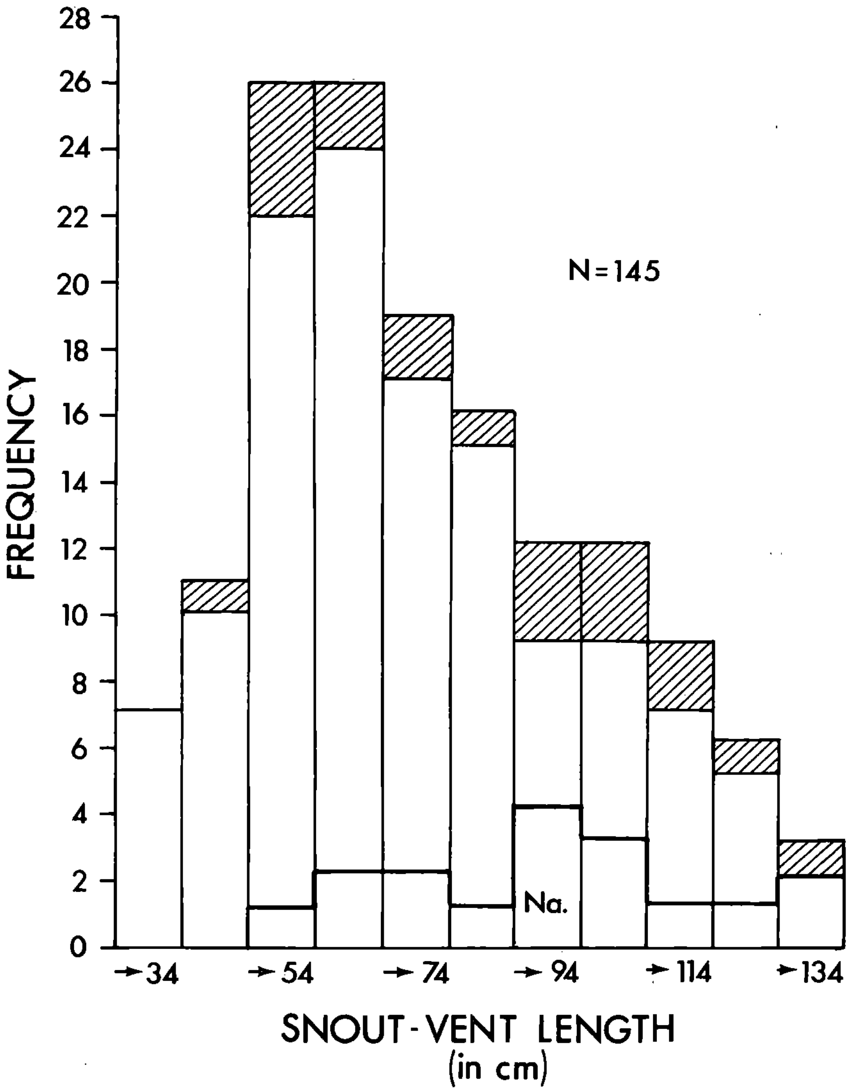


FIGURE 26.—Comparative lengths of *Varanus komodoensis* specimens from Nggoer, Flores (shaded) and Loho Liang, Komodo (clear). Smaller histogram delineated by darker line represents the Nanenepi, Komodo. The latter is mangrove habitat, in which primarily the larger animals occur (see Auffenberg, in press, for details).

than females ($\bar{X}$ total length 10 largest males 2.26 m, 10 largest females 1.76 m); total length of 29 hatchlings 25.3-55.5 cm ($\bar{X}$ = 30.4 cm), weight 80.3 gm. Snout broad, truncated (Fig. 28). Statements by Lederer (1942) and various animal dealers that females have proportionately narrower heads are incorrect (Fig. 29). Round narial openings located near end of snout; tail relatively short and heavy in adults, proportionately larger in young (Fig. 30); cross-section of tail base round in adults, more compressed in young. Teeth considerably compressed

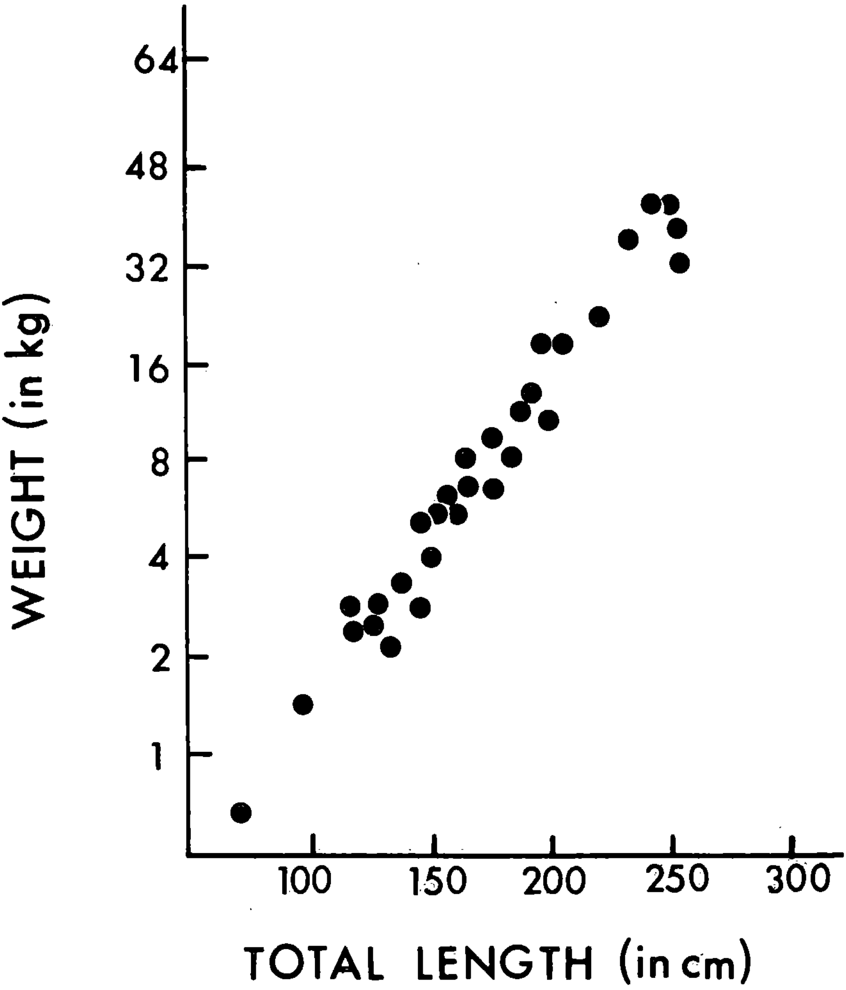


FIGURE 27.—Length-weight relationship in *Varanus komodoensis*, all from Loho Liang, Komoda.

laterally, with serrated posterior edges on at least maxillary and dentary series (Burden 1928, Auffenberg, in press); premaxillary teeth 7; maxillary 13, dentary 12. Males distinguished by a pair of small precloacal pores (Fig. 31), in spite of the suggestion by Mertens (1930) that this character is probably not sexually diagnostic (see Auffenberg, in press, for details).

TABLE 2.—Scale variation in *Varanus komodoensis* from Loho Liang, Komodo (N=50).

Scales	Range	$\bar{X}$	S.D.
Infranasal	4	4	
Interoculars	5-9	6.7	± 0.9
Internasals	6-10	8.2	± 1.4
Mouth-mouth	48-51	49.3	± 1.8
Midbody	170-176	173.8	± 0.4
Ventrals	80-110	92.6	± 7.4
4th toe lamellae	7-8	7.3	± 0.2

Scale data of 50 *Varanus komodoensis* from Komodo are given in Table 2. Upper head scales rounded and slightly raised, largest on snout and smallest in temporal region; supraoculars not differentiated, generally smaller than temporals; interparietal only slightly enlarged; nape scales relatively large, generally conical; dorsal scales smaller than those of neck, but larger than lateral body members, being long and strongly keeled; lower leg dorsal scales weakly keeled; ventrals elongated, varying from weakly keeled to smooth; all caudals strongly keeled, dorsal ones smallest; complete caudal rings only in basal third of tail; two median dorsal tail scale rows slightly enlarged, producing a low double keel; inner surface of proximal part of fourth toe provided with a row of conical lamellae, similar to those of *Varanus varius.*

Apical pits (?) on most scales, as in other species (Smith 1935), those anterior to vent and on thighs are larger and appear different than those in other parts of body; cranial scale organs described in Auffenberg (in press).

Color and pattern of three different-sized Komodo individuals (in life) are as follows: In a hatchling (SVL 19.2 cm, tail 27.1 cm, Fig. 32) head brownish-black dorsally with a few light yellow scattered spots; iris light brown; neck ground color black with transverse darker bands approximately 150° to horizontal when viewed from side; body bands comprised of faint yellow spots, often forming ocelli medioposteriorly and alternating with transverse rows of yellowish-tan or tan spots, becoming ochre with yellowish centers mediodorsally. Body ground color black with transverse rows of dark brown ocelli (10-12 across the back) is a series of small yellow dots, usually in a single row. The tail has 19 yellow bands on a grayish background; the last third is gray laterally, yellow both dorsally and ventrally (reddish-brown medially near its base); tail base gray laterally, interrupted by the bases of the yellow transverse bands. Underside of hindlimbs light rust with small gray dots. Anterior to the insertion of the hindlimbs belly yellowish with rust-brown reticulations forming alternating wide and narrow bands. Central; depressed area of the precloacal scale rosette brown. Soles of hind feet pinkish-white, those of the front feet clear yellow. Behind insertion of forelimbs on the ventral surface, the dorsal ocelli bands pass over the chest and break into three transverse bars, each

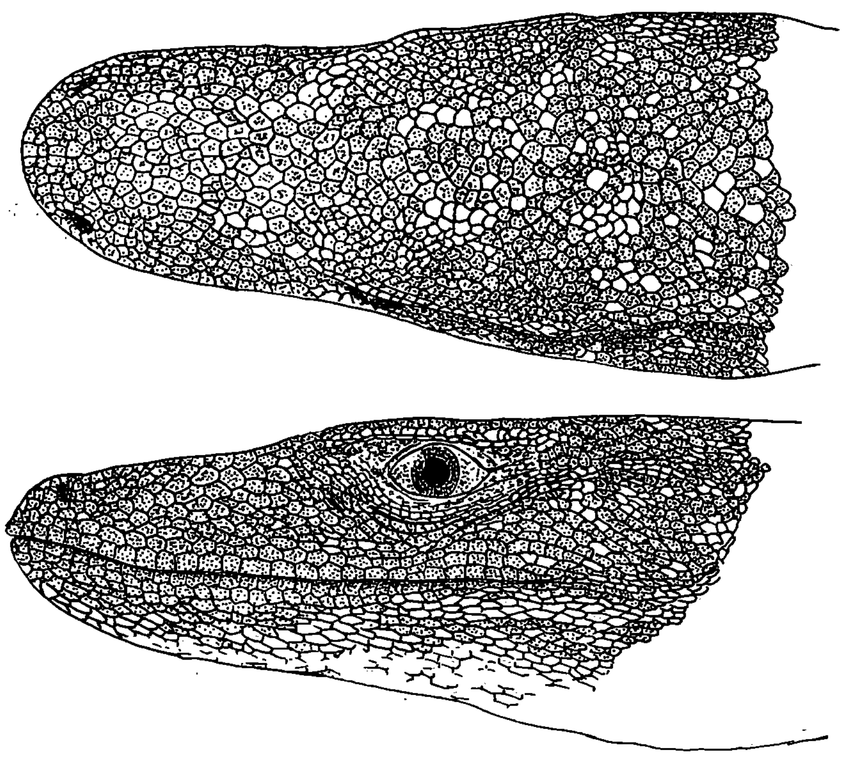


FIGURE 28.—Head of adult *Varanus komodoensis* (UF 29001), Nggoer, Flores.

with two anterior projections. A black linear patch above insertion of forelimbs. Dorsally thighs of hindlimbs black with transverse rows of larger yellow spots alternating with rows of minute dark yellow dots. Lower part of hindlimb black, changing to dark brown on foot with scattered yellow dots and darker edges. Both fore- and hindlimbs have yellow bands at each toe joint. Dorsal surface of front limb black with transverse bands of small yellow dots. Claws black. A gray circle with a yellowish-white center on side of head in front of the tympanum. Yellow patches above and below eye. Three vertical yellow bars on a brownish-black background between eye and nostril. Following jaw angle from immediately behind tympanum to throat slightly pinkish-white. Most of throat yellow with a tinge of ochre sprinkled with black dots. Chin whitish-yellow with greenish-black spots.

The following description is based on 18W, a young male, body length 69.1 cm, tail 84.8 cm. Dorsally head largely black with scattered yellow spots. Nuchal area black with many scales having yellow bases; a few entirely yellow. Hind- and forelimbs black above with small scattered yellow spots. Forefeet entirely black above, hindfeet with a few yellow spots. Body dorsally black with base of some scales

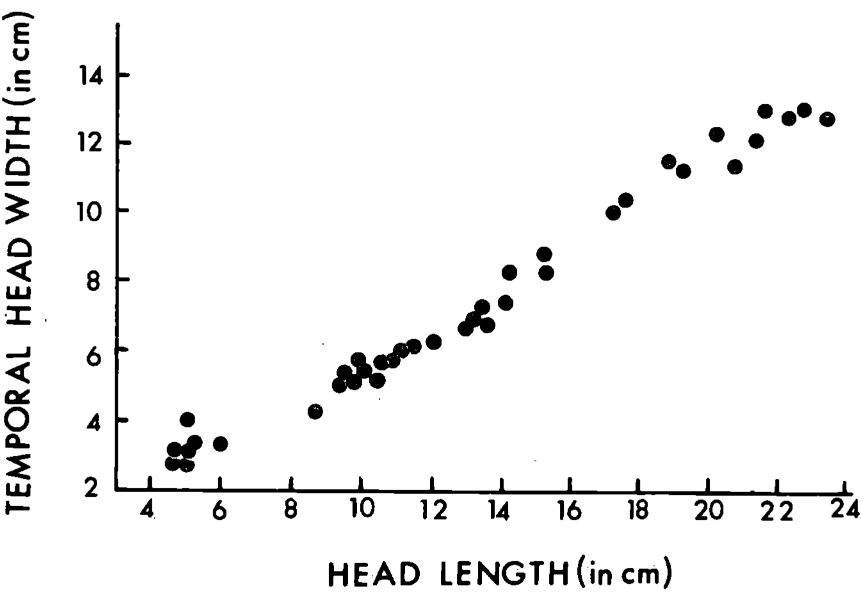


FIGURE 29.—Head width-length relationships of *Varanus komodensis*, all from Loho Liang, Komodo.

reddish-brown and small yellow spots aligned in bands, larger and more numerous laterally. Posterodorsally body and tail base more rust-colored with both black and yellow spots; changing at more compressed middle of tail to yellow-green with brown and black spots; last 2 cm brilliant yellow-green. Most of tail ventral surface yellow with a short medial black stripe. Below tail base three fairly distinct smoky-gray partial bands extending medially, but not to midline which is yellow with a few black scales. Color ventrally near hindlimbs and under thighs yellow to grayish-yellow; soles of hindfeet brilliant

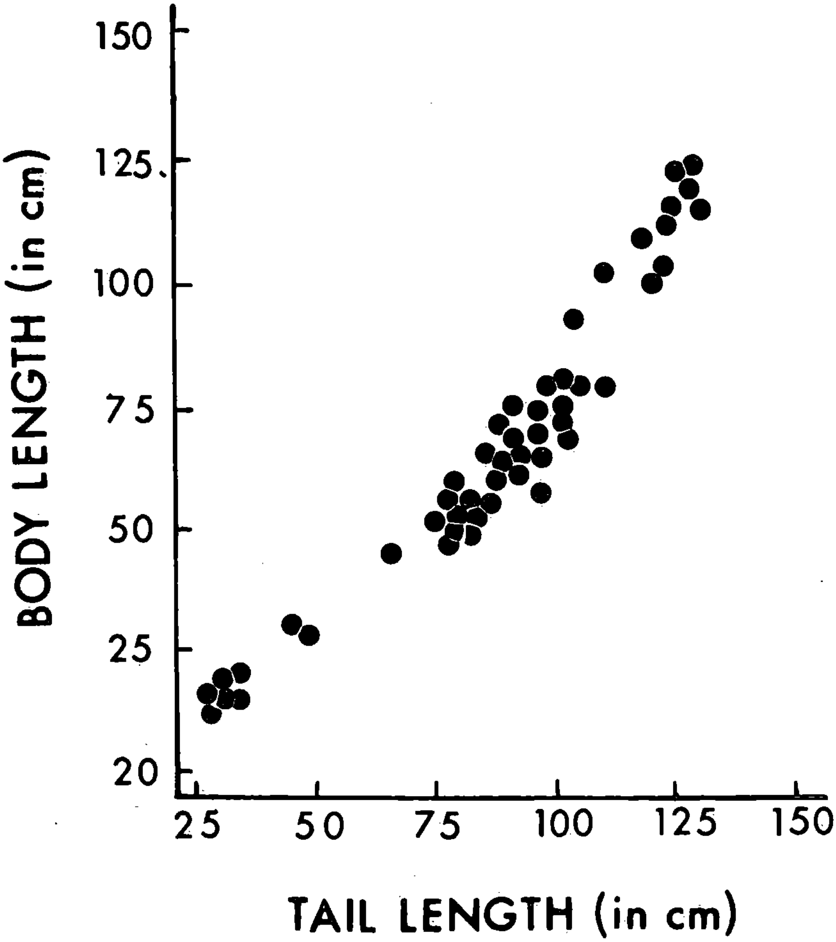


FIGURE 30.—Body-tail length relationships in *Varanus komodoensis*, all from Loho Liang, Komodo.

yellow. Ventrolaterally body more rust-colored, becoming yellowish ventrally with a scattering of black scales under forelimbs. Three grayish-black shallow V's with apices pointed anteriorly on chest. Neck base below speckled with black and yellow, black anteriorly. On chin and anterior part of throat the black spots form narrow longitudinal rows, largest being outer one immediately below lower lip. Between these, scales clear yellow. A greenish-yellow crescent with smoky-gray spots present along chin border. Laterally head grayish-black, intense black temporally. Below and in front of nostrils a large yellowish-gray blotch. Eyelids bright yellow. Sides of lower jaw below mouth black to grayish-black with a few yellow spots.

The following description is based on 26W, body length 64.0 cm, tail 86.4 cm. Head entirely black. Above, neck black, with yellow-green interstitial skin. Back with black to brownish-black scales, with orange, ochre, or sometimes yellow interstitial skin. Below, neck gray to yellow. Dark chest bars still evident. Belly medially yellow, ventrolaterally with light orange countershading. Both front and hind legs black with small yellow spots. Tail dark gray, lighter toward tip, with yellowish-gray bands still evident.

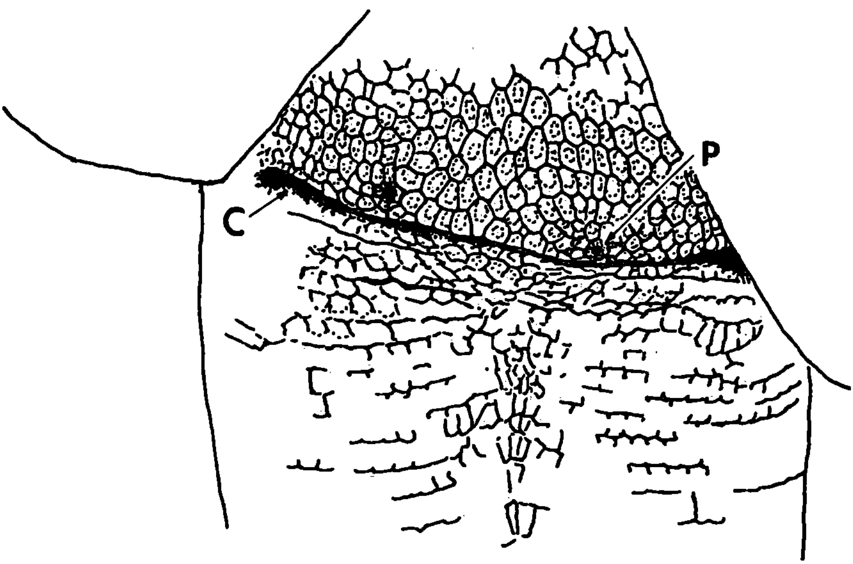


FIGURE 31.—Scalation surrounding cloaca (=C) showing the two precloacal pores found in male *V. komodoensis* (=P).

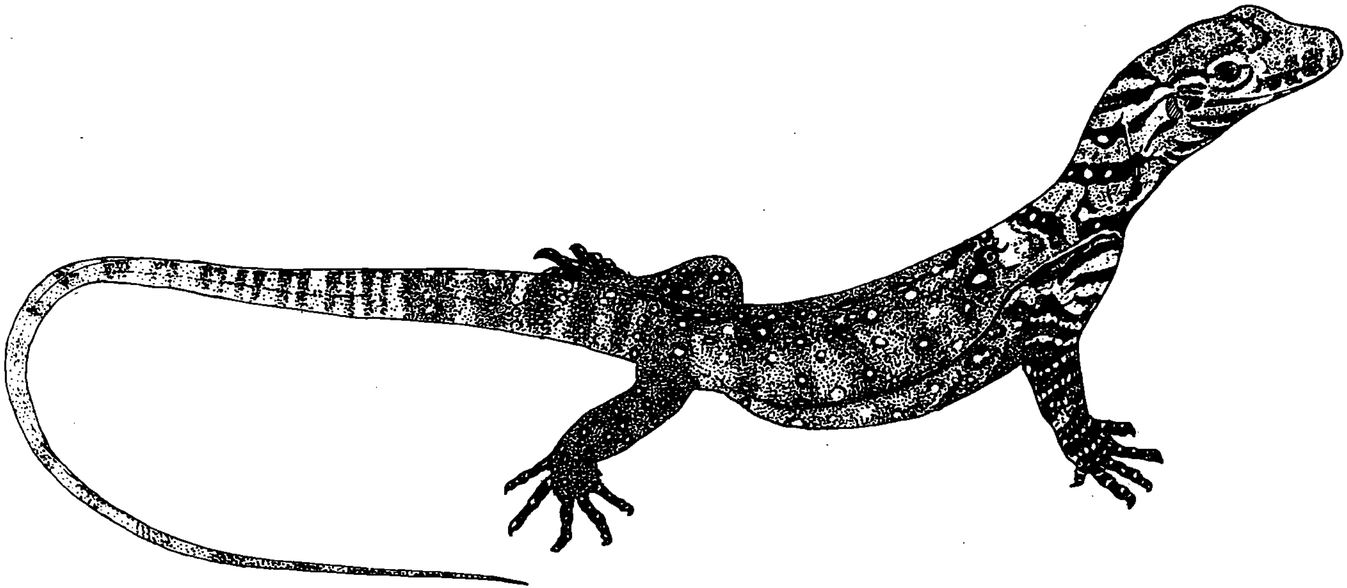


FIGURE 32.— Hatchling *V. komodoensis*, Loho Liang, Komodo (composite from photos and field sketches).

When *Varanus komodoensis* attain 2 m, they are almost uniformly brown or grayish-brown dorsally on body, legs, and tail. Chest bars light gray to absent. Interstitial skin of back rusty. Tail bands completely absent. Belly gray with faint speckling. Particularly old individuals with yellowish-green, pink, or even lavender irregular spots on snout. Tongue pale yellow in individuals of all sizes. Iris always brown.

DISTRIBUTION AND HABITAT.—Known only from Komodo, Padar, Rintja, the western end of Flores, and the small islets of Gili Moto and Oewada Sami (Fig. 33).

It is most abundant in ecotonal situations between savanna and monsoon forests but is common in both, occasionally in steppe and mangrove forests. It does not normally occur in the quasi-rain forest community, which usually begins at an elevation of about 500 m. Young are largely arboreal during their first year of life and often climb high trees in search of shelter or food. The adults are largely terrestrial and rarely climb. They occasionally enter brackish or sea water. Shelter for the young is found under loose bark and in hollow trees. Adults may construct burrows up to 3 m long (usually much shorter) along vertical banks of stream beds or beneath boulders and fallen trees. The burrows are sometimes distinctly clustered. Individuals spend the night sleeping in high grass, dense thickets of bush and saplings, under overhanging shrubs or in the burrows. Large adults use specific thermoregulatory sites, usually on hillsides, that overlook valleys or coastal areas.

REPRODUCTION.—Data from Brongersma (1932), Lederer (1942), Hisada (1966), Galstaun (1973), Auffenberg (in press), and Prato (MS) constitute the basis for the following conclusions. From 1-30 eggs ($\overline{X}$ = 11.3) are laid in a nest(s) excavated in the soil. Females may lay up to three clutches/year from April to September (usually June-August) and interclutch time varies from 1-8 days ($\overline{X}$ = 2.5). Incubation period varies from 2½-8 months, probably dependent on both temperature and soil moisture. Eggs vary in weight from 55-210g ($\overline{X}$ = 124.7), and their size from 59-115 mm ($\overline{X}$ = 86.5) x 42-66 mm ($\overline{X}$ = 55.5). The young normally appear in April through May, and there is some evidence that they remain together in small groups for several months. Adult males have been known to eat the eggs, and there is a report that some females may return to the nest and open it about the time that the young hatch (Pfeffer 1959). Males and females apparently become mature in the 5th to 7th year, at a length of approximately 1.5 m.

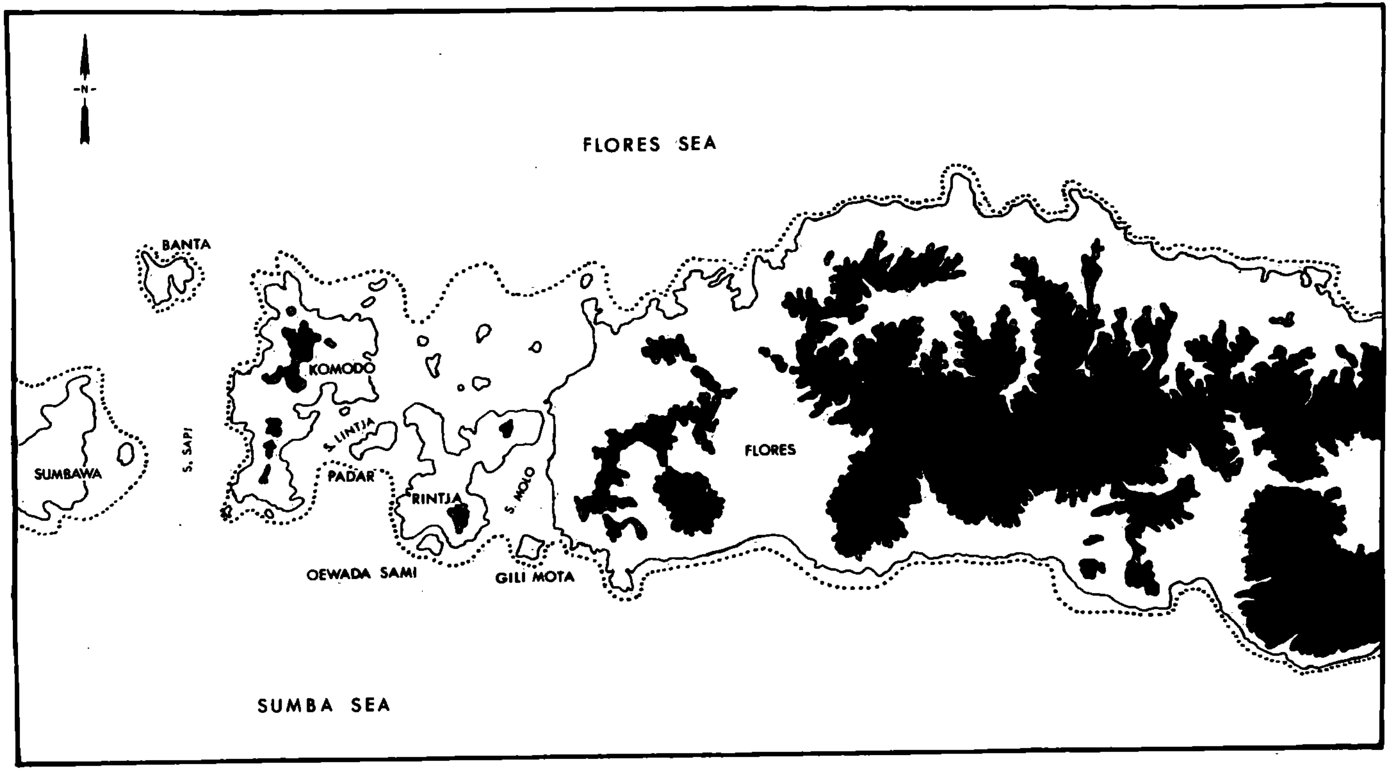


FIGURE 33.—Known distribution of *V. komodoensis* (stippled area). On Flores Island the hollow dots represent native reports and solid ones actual sightings or other proof of occurrence.

FOOD.—Highly opportunistic, this species feeds upon a wide variety of prey (Table 3). While arboreal, the young feed chiefly upon smaller lizards, insects, birds and their eggs; medium-sized individuals eat mainly rodents and larger native birds (such as *Megapodius freycineti*, Lincoln 1974; Auffenberg, in press). These are all captured by active pursuit and/or search. Medium to large adults frequently feed on carrion, though the largest individuals also prey on wild boar and deer, which they usually catch from ambush along game trails.

TABLE 3.—Prey represented in *Varanus komodoensis* fecal pellets (N=4267) collected on Komodo.

Prey eaten	Number occurrences
INVERTEBRATES	
Land molluscs *(Asperites trochus)*	3
Marine clam (sp.?)	1
Beetles (sev. sp.)	15
Grasshoppers (sev. sp.)	56
Crabs (sev. sp.)	3
FISHES (sev. sp.)	5
REPTILES	
Ora *(Varanus komodoensis)*	66
Gecko *(Gekko gecko)*	24
Gecko *(Hemidactylus* sp.)	3
Skink *(Sphenomorphus* sp.)	3
Bamboo viper *(Trimeresurus albolabris)*	8
Rat snake *(Elaphe subradiata)*	29
Whip snake *(Dendrelaphis pictus)*	43
Cobra *(Naja naja)*	3
Russell's viper *(Vipera russelli)*	15
Hawksbill sea turtle *(Eretomchelys imbricata)* (+ eggs)	3
BIRDS	
Megapode *(Megapodius freycineti)* (+ eggs)	48
Jungle fowl *(Gallus varius)* (+ eggs)	4
Misc. small bird species	71
MAMMALS	
Bat (sp. ?)	2
Mouse *(Mus musculus)*	36
Rat *(Rattus rattus)*	196
Feral dog *(Canis familiaris)*	8
Feral goat *(Capra hircus)*	26
Palm civet *(Paradoxurus hermaphrodytes)*	20
Mongoose *(Herpestes javanicus* ?)	4
Wild boar *(Sus scrofa)*	808
Sunda deer *(Rusa timorensis)*	1979
Feral water buffalo *(Bos bubalis)*	15

Animals as large as horses and water buffalo are successfully attacked and some individuals, particularly on Flores, regularly attack village livestock. Humans are occasionally attacked and sometimes killed and eaten (see Auffenberg 1977, in press, for details).

PARASITES.—Ectoparasites include three species of ticks: *Amblyomma helvolum, A. robinsoni,* and *Aponomma komodense,* of which *A. robinsoni* is most common. No sporazoans were found in blood samples taken from four Flores specimens. Subcutaneous larval pseudophyllidean cestodes were very common in Flores specimens (estimated density 150/1.5 m adult *V. komodoensis*). They were not found on any Komodo specimens. The larger larvae formed lumps under the skin and were scattered over most of the dorsal part of the body. The monitors were probably infected by eating aquatic vertebrates (essentially absent on Komodo). All fecal specimens examined showed a low density of non-pathogenic amoeba *(Endolimax sp.)* and cestode ova. Mature intestinal cestodes included the

TABLE 4.—Parasites of *V. komodoensis* and western Flores populations of *V. salvator.*

Parasites	Place	*V. komodoensis*	*V. salvator*
AMOEBA			
Endolimax sp.	fecal	+	?
SPOROZOA			
Hemagregarine	blood	−	+
CESTODA			
Pseudophyllidae			
Larvae (Sphargana type)	subcutaneous	+	+
Duthiersia expansa	intestinal	+	+
Duthiersia venusta[1]	intestinal	+	+
Duthiersia crassa	intestinal	−	+
Duthiersia sp. indet.	intestinal	−	+
Spirometra sp. indet.	intestinal	+	−
Scyphocephalus bisulcatus	intestinal	−	+
Proteocephalidea			
Kapsulotaenia sandgroundi	intestinal	+	−
Acanthotaenia shipleyi	intestinal	−	+
NEMATODA			
Spiruroidea			
Tanqua sp.	gastric	−	+
ACARINA			
Amblyomma helvolum	skin	+	+
Amblyomma robinsoni	skin	+	−
Aponomma komodense	skin	+	−

[1]=*D. sarawakensis*

pseudophyllideans *Spirometra* sp., *Duthiersia* cf *D. expansa*, *D. venusta* (or *sarawakensis*), and the proteocephalidean *Kapsulotaenia sandgroundi*.

The endoparasitic data available (Table 4) suggest a rather extensive fauna, of which certain elements are shared between *V. komodoensis* and *V. salvator*, whereas others are not. In general, *V. komodoensis* is not heavily parasitized; *V. salvator* shows much higher density and diversity.

REMARKS.—Called mainly *ora* in the local dialect and *buaja darat* (= "land crocodile") in Malay by people not well acquainted with it. Additional data are provided by Dunn (1927a), Burden (1928), Mertens (1929c), Lederer (1933), Pfeffer (1959), and Darevsky and Kadarsan (1964).

Varanus salvator salvator (LAURENT)
Figures 34-35

Lacerta monitor Linné 1758 (part) (Type locality: "Indies").
Stellio salvator Laurent 1768:56 (Type locality: "America," in error).
Monitor nigricans Cuvier 1829:27 (Type locality: Java).
Hydrosaurus salvator Gray 1838:394.
Monitor bivittatus var. *javanica* Schlegel 1844:10 (Type locality: Java).
Monitor bivittatus var. *celebensis* Schlegel 1844:10 (Type locality: Celebes).
Varanus crocodilinus Owen 1845:265 (Type locality: restricted to Java).
Varanus salvator Cantor 1847:635.
Varanus togianus Weber 1890:169.
Varanus salvator salvator Mertens 1937:178.

SPECIMENS EXAMINED.—(12) UF 29002-3, 30171, 40432, Nggoer, Flores, 2-5 m; MZB 941, Udjung Kulon, Java; MZB 942, Kerto Malang, Java; MZB 943, Bogor, Java; MZB 947, Liroeng, Salibaboe; MZB 949, Atcheh, Sumatra; MZB 952, Madiun, Java; MZB 954, Liroeng, Salibaboe; and MZB 957, Udjung Kulon, Java.

DESCRIPTION.—Dorsal head scales large, flat, smooth, largest in supraocular region (Fig. 34); supraoculars well differentiated, 4-6 in Flores specimens (4-8 elsewhere; *fide* Mertens 1942); occipitals larger

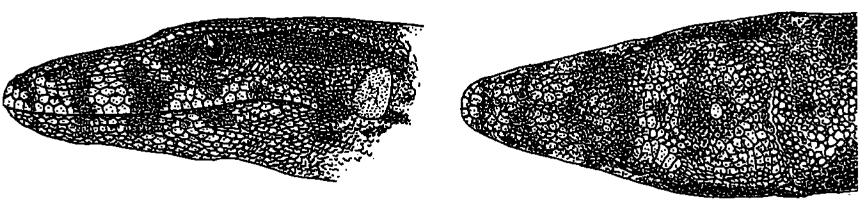


FIGURE 34.—Head of adult *Varanus salvator* (UF 29002), Nggoer, Flores.

than temporals; 45-48 scales across top of head from angle of mouth on one side to same place on other (48-60 elsewhere); neck scales smaller than occipitals, only slightly larger than the strongly keeled oval dorsal body scales; 148-153 scales at midbody; ventral scales rectangular, larger than dorsal scales, keeled, except near breast, 80-85 from gular fold to insertion of hindlimb; tail scales keeled dorsally and ventrally, not in obvious marked transverse rings, the two dorsovertebral rows enlarged, their keels providing a low double caudal ridge.

Ground color brownish-black with five faint (even in the young) crossbands produced by yellowish-white-edged scales, forming very ill-defined ocelli (rarely seen in live animals but evident when dried skins are held to the light), thus unlike the vividly marked Sumbawa specimens figured in Mertens (1942); feet black except (usually) for a yellow dot on dorsal surface of each toe just behind claw; tail almost uniformly grayish-black above, without obvious lighter colored bands; belly light yellow, with 8-10 faint black bars extending medially from sides, but not meeting at midline; throat with 3-4 black crossbands; a few black dots on anterior part of throat, chin provided with 2-3 narrow black cross bars that become faint in adults; sides of head yellow with 4 vertical brownish-black bars extending onto lower jaws, becoming faint from general darkening with age; dorsally head brownish-black with 3 darker lateral head bars extending over snout and down other side, but observable only in juveniles, head almost uniformly black in adults.

Although this species grows to nearly 3 m on the Asian mainland, Mertens (1942) pointed out the somewhat smaller size of specimens from the Lesser Sunda Islands, with which I agree ($\bar{X}$ SVL of 3 Flores adults = 42.5 cm, total length 90.0-134.5, $\bar{X}$ = 115.8 cm).

DISTRIBUTION AND HABITAT.—*V. salvator* has been reported from Sumba (Barbour 1912, Mertens 1930, 1942, Forcart 1949), Flores (Barbour 1912, Mertens 1942), and Sumbawa (Mertens 1942). The report by Hoogerwerf (1954) that it occurs on Padar based on footprints in the sand is ill-founded. I doubt that it exists there for this island lacks appropriate habitat. DeJong (1937) believed there were no differences in the spoor of *V. komodoensis* and *V. salvator.* The latter is clearly absent on Komodo; undoubtedly for the same reason, for on surrounding islands *V. salvator* is common near streams and permanent large ponds. On Flores, we rarely saw it farther than 100 m or so from the water's edge, even when we attempted to draw it into the surrounding savanna with carrion bait. However, *Varanus komodoensis,* the local savanna and deciduous forest species, is easily drawn into the streamside habitat of *V. salvator* with the same bait.

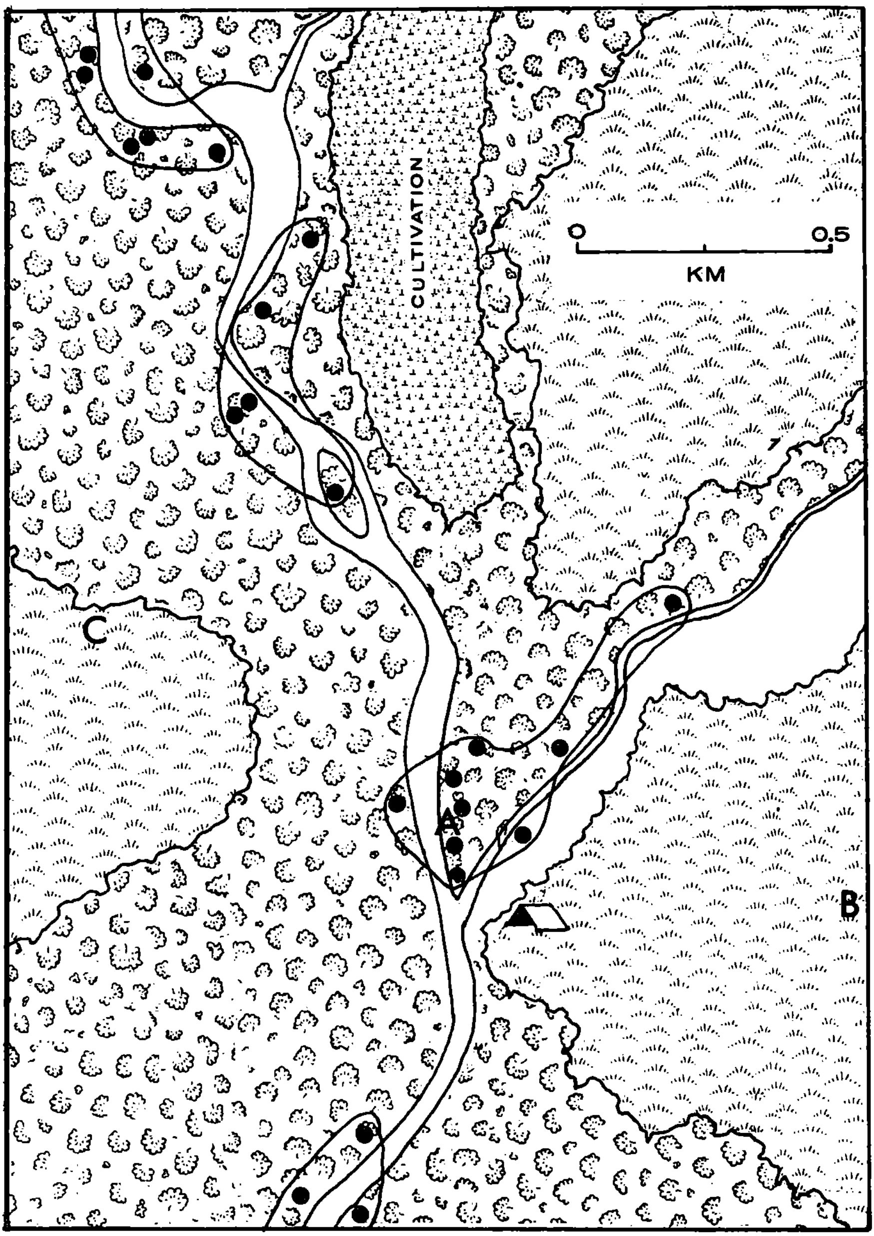


FIGURE 35.—Repeated sightings (dots) of four adult *Varanus salvator* along Nanga Loök in western Flores. Approximate boundaries of activity ranges are shown. A, B, and C show location of carrion baiting sites. *V. salvator* specimens came to site A, whereas *V. komodoensis* fed at all the stations.

At night they sleep on bushes overhanging the water or in burrows excavated in the stream banks.

On Flores, *V. salvator* occurs from brackish coastal mangrove swamps to elevations of at least 1000 m, dependent largely on the distribution of the surface water. In general, there is no correlation between its distribution and river bank ecology—all types of riverine habitats are exploited. In agricultural areas, they are often found near rice fields. Density along Nanga Loök was estimated at 15/km along the river above high tide effects, 8/km in coastal *Lumnitzera* and/or *Rhizophora* mangrove forests. The core area of the adult activity ranges are usually separated by about 500 m (Fig. 35).

FOOD.—Forcart (1949) described the protection of its young by a marsh hen *(Gallinula* sp.) against the attack of a large monitor and also a monitor's attack on a wild duck *(Anas giberifrons).* On Flores the water monitor is an opportunistic predator, feeding on a great variety of live prey, carrion, and even human feces. Living prey locally recorded are snakes *(Dendrelaphis pictus, Trimeresurus albolabris, Cerberus rynchops),* frogs *(Rana* cf *cancrivora),* lizards *(Sphenomorphus* sp., *Lamprolepis smaragdina),* mammals *(Rattus* sp., *Mus musculus),* wading birds *(Bucoroides* sp., *Nothophyx* sp.), and domestic ducklings and chicks. My data from Nanga Loök, a small river in extreme western Flores, suggest that they usually forage within 40 m of the water's edge, but during the monsoon season they move at least 500 m inland.

PARASITES.—The only ectoparasites found on Flores specimens were *Amblyomma helvolum*[1] (also commonly parasitized local *Varanus komodoensis*). A hemogregarine infection (sporozoan) was found in 25% of the Flores *V. salvator* examined[2]. Subcutaneous infection of larval cestodes (Order Pseudophyllidea; sphargana type) were exceedingly abundant in all *V. salvator* from the Nggoer, Flores, area, probably ultimately derived from frogs[2]. Intestinal parasites included a heavy infestation of the pseudophyllidian cestode *Duthiersia (D. expansa* in 50% of the Flores material, and an undescribed species[2]). One other pseudophyllidian of the genus *Scyphocephalus (bisulcatus*[3]*)* was found, as well as a protocephalidian of the genus *Acanthotaenia (shipleyi*[3]*).* Spiruroid nematodes *(Tanqua* sp.) were found in 66% of the specimens examined. Parasite data for *Varanus salvator* and *V. komodoensis* are summarized in Table 4.

[1]Identified by H. Hoogstral.
[2]Identified by S. R. Telford
[3]Identified by J. L. Pinnell

REMARKS.—Hoogerwerf (1954) and de Jong (1937) stated that eggs and young of *V. salvator* are eaten by *V. komodoensis*. On Flores, I found that when both species were attracted to carrion at the same time the larger *V. komodoensis* dominated the relationship usually with no or few overtly aggressive displays. Local villagers stated that when carrion is completely eaten large *V. komodoensis* occasionally attacked and ate the smaller *V. salvator* that were also attracted to the carrion.

Varanus salvator is called *biawak* in Indonesian, *weti* in the local Mangarrai dialect, and *alu* in Balinese.

SUBORDER SERPENTES

FAMILY TYPHLOPIDAE

Typhlina bramina bramina (DAUDIN)

Figure 36

Eryx braminus Daudin 1803:279 (Type locality: Vizagapatan, India).
Typhlops braminus Cuvier 1829:73.
Typhlops braminus braminus Mertens 1930:278.

SPECIMENS EXAMINED.—(40) UF 29406, 29410, 29424-38, 29441-48, 29450-51, 29454-56, 29458, all from Loho Lavi, Komodo, 20 m; UF 32600, Nggoer, Mangarrai District, Flores, 12 m; UF 33058, Bara, Flores, 200 m.

DESCRIPTION.—Snout rounded, no keel; nostril lateral; rostral extending to level of eyes or beyond (shorter in most other populations according to de Rooij 1915); nasal cleft completely divided; preocular present, nearly- to as large as the ocular, in contact with the second and third supralabials; 4 supralabials; eyes distinct. Body with 20 midbody scale rows. Greatest body diameter in total length (Komodo specimens): adults 34.7-56.9 midbody ($\overline{X}$ = 59.2). Tail as long as or a little longer than broad, ending in a spine.

Color brown, brownish-gray, or blackish-brown above, lighter below. Snout, chin, cloacal area, and tail tip often cream or whitish. Total length 79-165 mm ($\overline{X}$ = 135 mm) in Komodo area, to 173 mm in Sumbawa (Mertens 1930).

DISTRIBUTION AND HABITAT.—In the Indoaustralian area, *Typhlina bramina* has been reported from Australia, Sumba, Sumbawa, Komodo, and Flores (Mertens 1930, Forcart 1949).

Mertens (1930) stated that this blind snake is never found above 500 m in this area. On Komodo it is common in gallery forest areas near sea level. Many of our specimens were obtained by villagers while preparing garden plots. The snakes were found beneath the surface, usually within the upper 15 cm. Other specimens were collected from under stones along dry stream courses and in gallery forests. On Flores, one specimen was collected at night, crawling in the grass across the surface of a *Zizyphus* savanna.

REPRODUCTION.—Two to four elongate eggs (17.5 x 3.3 mm) are laid during the wet season (January dates recorded on Komodo) by females at least 130 mm SVL.

FOOD.—The guts of all specimens examined (12) contained only termites.

REMARKS.—Called *ular duwel* locally.

Typhlina polygrammica undecimlineata MERTENS

Typhlops florensis undecimlineatus Mertens 1927c:239 (Type locality: Semongkat, Sumbawa, 400 m).

Typhlops polygrammicus undecimlineatus Forcart 1949:377.

SPECIMENS EXAMINED.—(1) Uncatalogued juvenile in the private collection of the late Hilmi Oesman, from Komodo, "in mountains" (precise location of specimen unknown).

REMARKS.—Darevsky (1964a) recorded this subspecies from Komodo on the basis of a subadult collected beneath stones in moist forest at 400 m. Both his specimen and that in Oesman's collection had 11 dark brown dorsal, longitudinal stripes on a light yellow ground color. The specimen that I examined had a clear yellow venter, 22 scales rows at midbody, and a midbody diameter that went into the total length 39.6 times. The subspecies differs from its closest relative, *T. p. florensis*, in lacking stripes on the venter. *T. p. brongersmai* from Sumba is uniform dark blackish-gray above and yellow, white, or pink below (Mertens 1928a).

Typhlina polygrammica has been taken from 400 to 1000 m (Mertens 1927c); above the major part of the activity range of *Varanus komodoensis*, and thus infrequently visited by our party. Darevsky (1964a) reported a single Komodo specimen collected at 400 m.

Typhlops schmutzi new species
Figure 36

HOLOTYPE.—UF 29507, adult female, Loho Lavi, Komodo, 12 m, collected January 1970 by expedition members.

FIGURE 36.—Left, lateral head view of *Typhlops schmutzi* (new species, UF 294323) Loho Lavi, Komodo; right, *Typhlina bramina bramina* (UF 29424), Loho Lavi, Komodo.

PARATYPES.—(84) UF 29415-23, 29452, 29466-95, 29500-34, all from Loho Lavi, Komodo, 12 m; UF 29411-13, 29461-65, all from Loho Liang, Komodo, 0-30 m; UF 29414, Kampung Komodo, Komodo, 5 m; UF 37018, Poto, Flores, 52 m.

DIAGNOSIS.—Differing from all other described species of the genus in possessing, in combination, extreme slenderness, no subocular, nasal cleft arising from second supralabial, and a completely divided nasal.

DESCRIPTION OF HOLOTYPE.—Snout rounded, no horizontal keel, projecting; nostrils lateral. Rostral parallel-sided, dorsal portion about ⅓ width of head, just barely or not reaching level of eyes; nostril in a divided nasal, anterior one in contact with rostral and first two supralabials, posterior one with second supralabial, preocular, and rostral; preocular present, nearly as large as ocular, in contact with supralabials 2 and 3. Eyes distinct. Scales over eye larger than body scales, median head scales smaller than those on body. Four supralabials. Body with 20 middorsal scale rows. Greatest body diameter (1.8 mm) 70.6 times in total length (127 mm). Tail slightly longer than its base, ending in a small spine.

Color pinkish-brown, slightly lighter below; snout and underside of tail and its tip whitish.

VARIATION.—Scalation and coloration are remarkably constant in all the paratypes. Minor variations in scale proportions occur in the rostral, nasals, and preocular, but none is significant. Body proportions (greatest diameter into total length) 62.5-81.9 ($\bar{X}$ = 72.3). Tail length ⅓ to 2 times the width of the base, caudal scales 10-12. Range in total length 58-140 mm. Color of juveniles only slightly lighter than that of the adults.

DISTRIBUTION AND HABITAT.—Known only from localities near sea level on Komodo and the north coast of Flores. All the type material was collected from the soil, usually within 15 cm of the surface.

REMARKS.—Named for Rev. E. Schmutz, a talented naturalist of Nunung Mission, Mangarrai District, Flores.

FAMILY ANILIIDAE
Cylindrophis opisthorhodus BOULENGER)
Figure 37

Cylindrophis opisthorhodus Boulenger 1897:506 (Type locality: Lombok, 500 m).

SPECIMENS EXAMINED.—(1) UF 28763, Loho Lavi, Komodo, 10 m.

DESCRIPTION.—Eye diameter into distance from mouth 2 times, in distance to nostril 4 times; distance between eyes more than distance from eye to nostril; frontal as wide as the single supraocular, broader than the parietals; nasals in contact, prefrontals in contact; 6 supralabials, third and fourth in contact with the eye; scales in 23 rows middorsally, 21 anterior to the cloaca; ventrals only slightly enlarged, 216 (184-213 elsewhere), subcaudals 5 (5-7 elsewhere).

Color iridescent light brown above, with very narrow dark brown vertebral stripe, few very scattered dots laterally, tending to be arranged in a row on the third or fourth scale row on either side of vertebral stripe, often in groups of 2 or 3 anteriorly. Head pale brown above, with dark brown blotches, ground color darkening to rust brown from supraoculars to a point about one head length behind supraoculars, with cream vertical temporal bar outlined by a broken black edge, cream flecks in front of eye. Black to dark brown ventrolaterally, with large paramedian white markings, tending to form irregular bars across belly, or an irregular checkerboard in some places. Dorsal color pattern separated from that of venter by a black line on 1-2 scale rows. Anal region black with a white spot on either side of anal plate. Tail marked somewhat like head (local Malay name, *ular kepala dua*, the two-head snake), but red ventrally (faded to white in alcohol). Mertens (1930) stated that the pattern of the young is more contrasting than that of larger individuals. Total length of Komodo specimen 276 mm (maximum 283 mm, Sumbawa specimen, Mertens 1930).

Distribution and Habitat.—This is the first record from Komodo; previously reported localities are western Flores, Lombok, Sumbawa, and Flores. Mertens (1930) stated that all the known specimens have so far been near sea level. Ours was found about 10 cm below the surface in clay soils of a gallery forest (a second specimen, captured in the same place and under the same conditions, escaped before preservation).

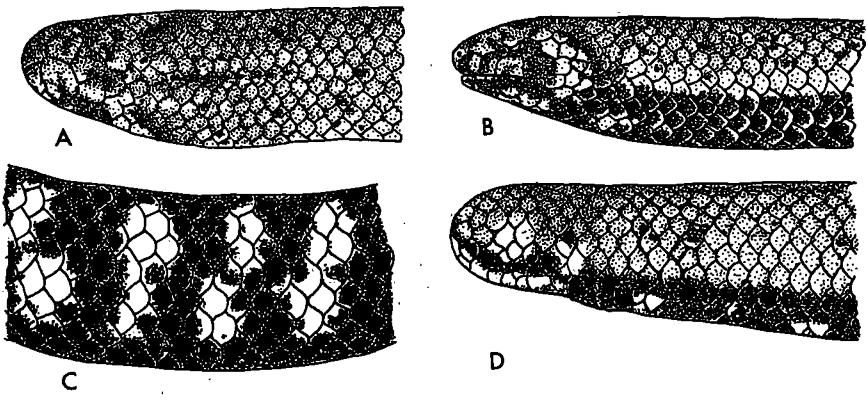


Figure 37.—*Cylindrophis opisthorhodus* (UF 28763), Loho Lavi, Komodo. (A and B) dorsal and lateral views of head; (C) mid-ventral pattern; and (D) lateral view of the tail (note resemblance to lateral head view).

FAMILY ACROCHORDIDAE

Chersydrus granulatus (SCHNEIDER)

Hydrus granulatus Schneider 1799:243 (Type locality not designated).
Anchrochordus granulatus Cantor 1847:59.
Chersydrus granulatus Gray 1849:61.
Achrochordus granulatus granulatus Loveridge 1948:380.

SPECIMENS EXAMINED.—(7) UF 39776-77, Suwong, Bali, at sea level; UF 28775-77, 28779, Loho Lavi, Komodo, at sea level; UF 28778, Kampung Komodo, Komodo, at sea level.

DESCRIPTION.—Head not distinct from neck; covered with small juxtaposed granular scales; nostrils on top of snout, close together, no rostral; a series of larger shields on lips, separated from mouth by a row of very small scales; no chin shields; about 100 scales around body, of which dorsals are longer, no widened ventral scales; tail short, laterally compressed, prehensile.

Gray to gray-brown with dark brownish-black to black transverse rings.

DISTRIBUTION AND HABITAT.—Widely distributed, found in large rivers and along sea coasts from northwestern India to Solomon Islands, not previously reported from Komodo; de Rooij (1917) listed it for Flores.

REMARKS.—Komodo specimens were obtained at night during low tide from mangrove forests dominated by *Rhizophora mucronata*, in the west end of the bay called Telok Slawi. Most were first seen when they were swimming actively, apparently having been frightened by our lights and movement. When at rest, only the tip of the nose is held above the water. The tail is coiled about twigs, stones, or roots, and most of the weight is carried by the widest part of the body (the posterior third), which rests on its side on the bottom. The anterior two-thirds of the body ascends to the surface, easily moved back and forth by the movements of the water.

One of the Bali specimens, collected in September, contained six embryos that would probably have been born in late October.

Mature Komodo males are at least 70 cm SVL; females are 76 cm and much heavier-bodied.

FAMILY COLUBRIDAE

Boiga cynodon (BOIE)

Figure 38

Dipsas cynodon Boie 1827:549 (Type locality: Sumatra).
Pareas waandersii Bleeker 1860:471 (Type locality: Bali)..
Dipsadomorphus cynodon Boulenger 1896:78.
Boiga cynodon Mertens 1930:315.

SPECIMENS EXAMINED.—(6) UF 28681, 28684-85, Loho Liang, Komodo, 0-30 m; UF 28682, Kampung Komodo, Komodo, 5 m; UF 28683, Kampung Sabita, Komodo, 12 m; UF 36203, Nangahele, Mangarrai District, Flores.

DESCRIPTION.—Snout longer than eye diameter; rostral broader than high, just visible from above; anterior palatine and mandibular teeth greatly enlarged; internasals broader than long, shorter than the prefrontals; frontal as broad as long, somewhat shorter than its distance from snout tip, shorter than parietals; loreal broader than high; one preocular, narrowly separated from frontal; two postoculars; temporals 2(3)+4; 9-10 supralabials, of which 4-7 enter eye; 4 infralabials in contact with anterior chin shields; dorsal scales in 19 rows, median row greatly enlarged; ventrals 247-261 ($\bar{X}$ = 257) (248-290 elsewhere), subcaudals 130-136 ($\bar{X}$ = 129.2) (114-159 elsewhere), anal entire.

Ground color grayish-brown to reddish-brown, with 35-37 irregular dark brown crossbands, often with black edges, sometimes a faint band or spot in ground color. Head nearly uniform light gray to light brown, without dorsal black ∩-shaped mark found in specimens farther west. Most have a narrow, partially black postocular stripe. Belly pinkish-brown, chin and supralabials white. Total lengths of five Komodo adults range from 102.1 cm to 171.7 cm.

DISTRIBUTION AND HABITAT.—This is the first record of *B. cynodon* from Komodo. Previous nearby localities are Flores (de Rooij 1917) and Sumbawa (Mertens 1930). From Flores its range extends westward through the entire archipelago north to India and the Philippines.

All specimens of this arboreal, nocturnal snake were found in lontar and coconut palm trees, where they remained as high as 15 m in the bushy tops during the daytime. Birds commonly roosted in the palms at night; the snakes apparently preyed on the sleeping birds, for we noted the snakes were often active at night. One of our specimens fell out of a lontar palm when the wind dislodged some of the dead fronds.

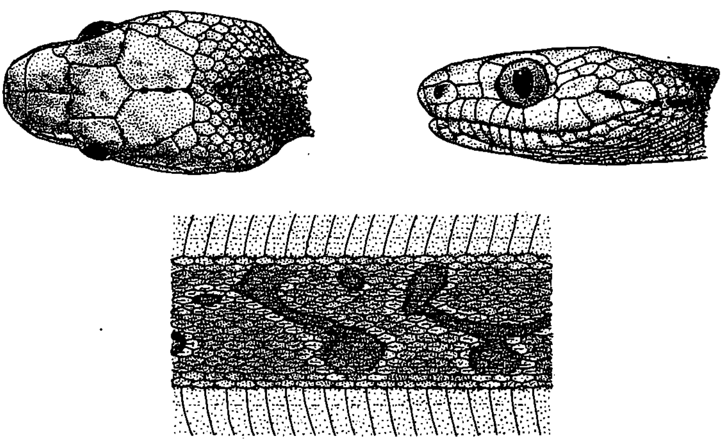


FIGURE 38.—*Boiga cynodon* (UF 36203), Nangahele, Flores.

REPRODUCTION.—The Komodo data are important, for reproductive behavior was previously unknown (Leviton 1968). On the basis of the following data, 1-23 eggs are laid during the monsoon season. One female specimen collected in October had a total of 26 follicles, of which 15 were small but with much evidence of yolk deposition; the remaining ones were small and translucent. The oviducts were smooth, flat. Two adult females were dissected in January; one showed 10 follicles, of which only one had advanced yolk deposition; the others were small, flat, and translucent. The ovaries in this specimen were small and flat. This female (SVL 78.9 cm) may have been in her first laying year. The second female (133.0 cm) had 55 follicles, of which five showed slight evidence of yolk deposition. That this female had recently laid her eggs was indicated by 23 still red oviductal scars. The oviducts were very thick-walled but not very convoluted.

FOOD.—Of six specimens examined for food, one contained a *Draco volans* and two had bird feathers in their digestive tract. Another was eating a *Gekko gecko* when captured.

Cerberus rynchops rynchops (SCHNEIDER)
Figure 39

Hydrus rhynchops Schneider 1799:246.
Homalopsis rhynchops Cantor 1847:94.
Cerberus rhynchops Günther 1864:279.
Hurria rhychops Stejneger 1907:304.
Hurria rhynchops Barbour 1912:123.
Cerberus rhynchops rhynchops Loveridge 1948:388.

SPECIMENS EXAMINED.—(61) UF 28601, 28604-5, 28608-12, 28614-15, Loho Lavi, Komodo; UF 28598, 28600, (with 8 embryos), 28606-7, 28613, Sabita, Komodo; UF 30161, Nangahele, Mangarrai District, Flores; UF 30152-60, Nggoer, Mangarrai District, Flores; UF 36171-79, 361867-95, Suwong, Bali; UF 36180-82, Benoa, Bali.

DESCRIPTION.—Frontal distinct or broken into small scales, nasal cleft in contact with supralabials 2-4; eye bordered by 5-6 scales, 1-2 postoculars, 1-2 suboculars; supralabials 10, rarely 9; infralabials 13-15, usually 14, 3-4 in contact with anterior chin shields; dorsal scales strongly keeled, in 23, 25, or 27 rows at midbody; ventrals on Komodo 148-153 ($\overline{X}$ = 150.5), 122-160 elsewhere; subcaudals divided, 54-66 ($\overline{X}$ = 58.2), 49-72 elsewhere.

Color olive to dark brown above, with black spots or transverse bands, sometimes indistinct; a light yellow to gray lateral band; black to brown postocular stripe passing through the eye onto the side of the neck; ventrally black, with a single row of yellowish to gray spots on each side; the darker chin stripes absent or very faint in all Komodo specimens. Newly hatched young are similar, though generally brighter patterned. The postocular stripe is sometimes represented by only a row of brown dots or a broken stripe.

SVL of mature individuals in the Komodo region is over 550 mm, maximum 750 mm. Hatchlings from this area (SVL 116-128 mm, $\bar{X}$ = 121) are much smaller than those from mainland Asia (130-160, *fide* Smith 1943).

TAXONOMIC REMARKS.—The Komodo material is clearly referable to *Cerberus rynchops rynchops* on the basis of the combination of scale and color characters. Other subspecies are known from the Philippine Islands (*C. r. microlepsis*), Papua (*C. r. novaeguineae*), and Australia (*C. r. australis*), and Loveridge (1948) gives a key and discussion.

DISTRIBUTION AND HABITAT.—On Komodo this species is found chiefly in shallow mangrove swamps dominated by *Rhizophorus mucronata* or *Sonnertia* sp. Hoogerwerf (1954) reported finding one in shallow water off the sand beach near Nangelele, Komodo. On both Komodo and Bali it was frequently seen at night during low tide, where it moved about within tidal pools and shallow creeks searching for fishes and crabs. At low tides during the day it usually spends most of the time in crab and fish burrows.

It is widely distributed in appropriate habitats from the west coast of India to northern Australia. In the Komodo area it has previously been reported from Flores (de Rooij 1917), Sumba (de Rooij 1917, Forcart 1949), and Komodo (Hoogerwerf 1954).

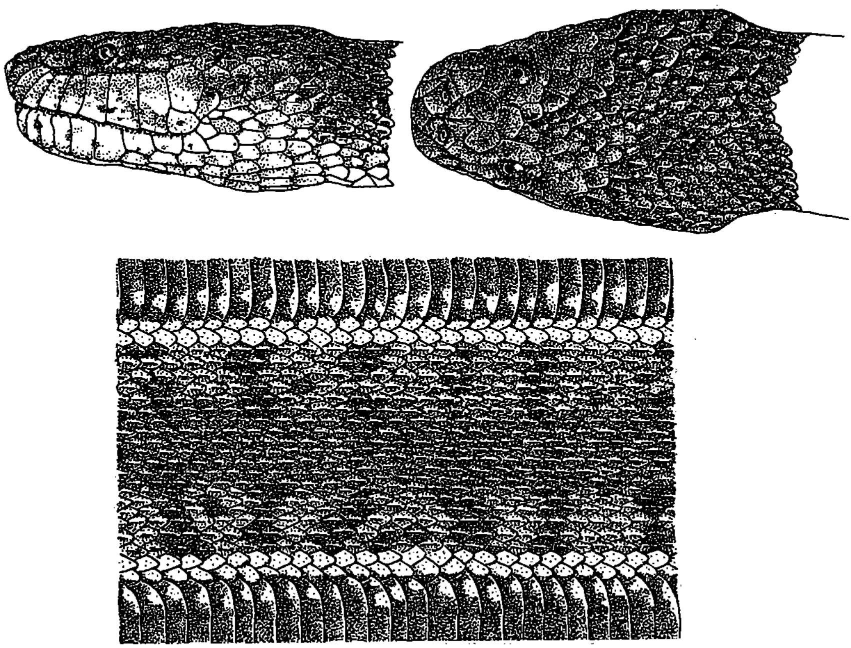


FIGURE 39.—*Cerberus rynchops rynchops* (UF 30159), Nggoer, Flores.

REPRODUCTION.—The sex ratio of 36 specimens examined is 1 to 12 in favor of females—a ratio that may reflect differing activity patterns more than actual ratio differences. Eight near-term embryos were found in females collected on Komodo in November. Total atretic follicles in 10 mature females taken November to January vary from 18-62 ($\bar{X}$ = 45.1), total corpora lutea 5-36, and enlarged follicles showing yolk deposition 6-38 ($\bar{X}$ = 20.5). All available evidence suggests that one litter a year is usual in the Komodo area. The young, which number from 5 to 38 per litter ($\bar{X}$ = 19.5), are brought forth from late November through February. The testes and vasa deferentia of the males examined showed developmental stages reflecting a similar seasonal reproductive cycle. The SVL of mature females varies from 550-750 mm ($\bar{X}$ = 590) and for males 570-600 mm ($\bar{X}$ = 590).

FOOD.—In all 18 specimens examined the guts of 50% contained food remains, and 66% of these contained the following identifiable parts: fishes of the families Gobiidae (*Amblygobius* sp.) 33% and Synodontidae (*Synodus ivermanni*) 33%, unidentifiable fishes 33%, unidentified Crustacea (genus unknown) 25%, and pistol shrimp (*Alphaeus* sp.) 12.5%.

PARASITES.—None noted.

Dendrelaphis pictus intermedius (MERTENS)
Figure 40

Dendrophis pictus Lidth de Jeude 1890:179 (part, *in* Weber).
Ahaetulla boiga intermedia Mertens 1927b:241 (Type locality: Sumbawa Besar, Sumbawa).
Dendrophis pictus intermedius Meise and Hennig 1932:288.
Dendrelaphis pictus intermedius Mertens 1934b:199.

SPECIMENS EXAMINED.—(25) UF 36198, Djarek, Flores, 80 m; UF 30092, 30164-66, 30170, Nggoer, Flores, 20 m; UF 30167, 2 km WNW Nuneng, Mangarrai District, Flores, 900 m; UF 30163, 4 km ENE Loök, Flores, 150 m; UF 28738-40, 28742, 28744-52, 30168-69, Loho Liang, Komodo, 1-30 m, UF 28741, 28743, Gunung Ara, Komodo, 500 m.

DESCRIPTION.—Rostral much broader than high; internasals about as long as prefrontals; frontal slightly shorter than its distance from rostral, shorter than parietals; loreal much longer than high; one preocular; supralabials 8-10, of which numbers 4-6 border eye; 5 in-

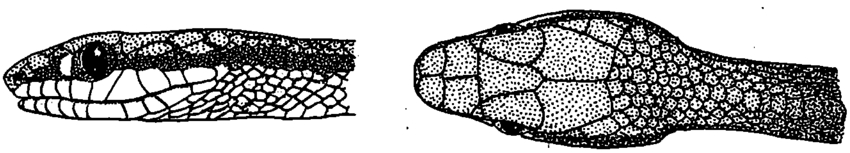


FIGURE 40.—*Dendrelaphis pictus intermedius* (UF 30170), Nggoer, Flores.

fralabials in contact with anterior chin shields; scales keeled, in 15 rows middorsally, the median vertebral row very enlarged; ventrals 185-208 ($\overline{X}$ = 196.9) on Komodo, 182-200 elsewhere; subcaudals 125-163 ($\overline{X}$ = 149.3) on Komodo, 143-160 elsewhere.

Ground color dark olive-green to brownish-green (sometimes with a faint metallic sheen); interstitial skin blue to black. A characteristic black longitudinal stripe beginning between eye and nostril and extending onto neck (Fig. 39), where it breaks up into flecks and disappears. A yellowish-green line on outer lateral scale rows. Ventrals olive-green; supralabials and chin yellowish-white. Juvenile color and pattern as in adults.

Distribution and Habitat.—This subspecies is restricted to Sumbawa, Flores, and Komodo (Mertens 1927b, 1934b, de Haas 1950, Meise and Hennig 1932); Darevsky (1964a) listed Padar and Rintja. *D. p. inornatus* is known from Sumba and Timor on the outer volcanic arc (Forcart 1949) and *D. p. pictus* from Lombok and Celebes westward to western India and north to southern China. The Komodo specimens were all collected from ecotonal situations, between monsoon forest and savanna, usually in low bushes or near them, through which they could move very quickly. On Komodo they are found from near sea level to 650 m (latter according to Dunn 1927b).

Reproduction.—The sex ratio of 15 specimens examined is 2:13 in favor of the females and, if correctly reflecting the local situation, is very skewed. It is much more likely that females are more often observed than males, and that the sex ratio is nearly equal. Two shelled ova (34.8-40.0 x 7.6-9.2 mm) were found in a female taken on Komodo in July. The total number of enlarged yolked follicles varies from 2-18 ($\overline{X}$ = 9.3). Follicles show gradual increase of size and yolking during the dry and early wet seasons (August through January). The vasa deferentia of the male collected in September showed recent activity, while those of an individual taken in January showed inactivity; both specimens were mature and nearly the same size. Mature females have an SVL of 530-700 mm ($\overline{X}$ = 626), males 510-580 ($\overline{X}$ = 560). Mertens (1930) reported four females with 5-12 eggs in April and June and suggested they may lay earlier on Sumbawa than on Komodo.

Food.—On Komodo they appear to subsist primarily on lizards. Darevsky (1964a) reported that a Padar specimen had eaten a *Lepidodactylus lugubris*. Mertens (1930) reported some specimens of this subspecies had eaten two species of the genus *Rana*. Of the 14 Komodo specimens examined 43% contained food remains in the gut, which included *Hemidactylus frenatus* (50% of those containing food), *Sphenomorphus* sp. (33%), and unidentified lizards (7%).

Parasites.—None obtained.

Elaphe subradiata subradiata (Schlegel)
Figures 41, 42

Coluber subradiatus Schlegel 1837:139 (Type locality: Timor)
Elaphe subradiatus Günther 1858:95 (part).
Elaphe subradiata Barbour 1912:31.
Elaphe subradiata subradiata Mertens 1930:298.

Specimens Examined.—(14) UF 39779-80 Nggoer, Flores, 12 m; UF 39778, Djarek, Flores, 80 m; UF 36202, 4.5 km E Maumere, Flores, ca 10 m; UF 28753, Loho Lavi, Komodo, 18 m; UF 28754, "Komodo"; UF 28756, 28759-62, Loho Liang, Komodo, 5-20 m; UF 28755, Gunung Ara, Komodo, 300 m; UF 28757, Kampung Komodo, Komodo, 5 m.

Description.—Head long, somewhat distinct from neck; eye large, pupil round; rostral broader than high; internasals shorter than prefrontals; frontal as long as its distance from tip of snout, shorter than the parietals; loreal deeper than long; preocular large; a subocular; two postoculars; temporals 2-2 or 2-3; supralabials 9, 5th and 6th entering eye, 4th very small; 5 infralabials in contact with the anterior chin shields, latter shorter than the posterior pair. Scale rows 23-25 at midbody, smooth dorsally, keeled laterally; ventrals 246-278 ($\overline{X}$ = 256.3), 226-248 elsewhere; anal entire; divided subcaudals, 102-121 ($\overline{X}$ = 111.1), 80-102 elsewhere.

Two color phases occur on Komodo. One is yellow-brown to olive above, with two black paravertebral stripes on each side of anterior part of body, often interrupted, sometimes uniform olive-brown, sometimes another stripe 3 scales below. This phase is found in specimens of all sizes, from hatchlings to the largest adults. The other phase is predominately barred (Fig. 41). Ground color is similar but alternate black λ-shaped bars extend from the ventral to near the vertebral line. The widest, darkest, and most evident parts of each bar are the two ventral termini and two places along the bar where the stripes would occur in the striped phase. Between these bars is a dark gray bar or rounded spot, with the darkest zones again in the stripe areas. Intermediates between the two phases are also represented in the material (Fig. 42). Of the 10 specimens available from Komodo, 4

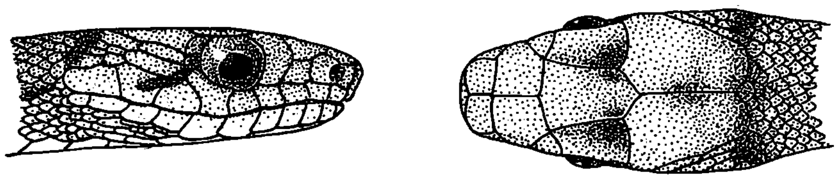


Figure 41.—*Elaphe subradiata subradiata* (UF 28762), Loho Liang, Komodo.

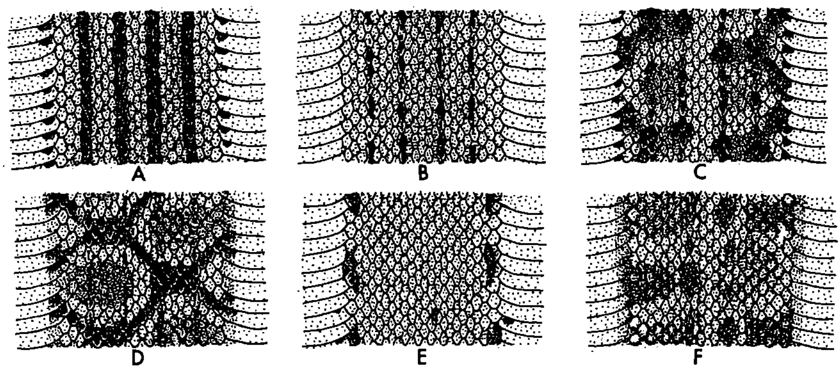
are barred, 4 are striped, and 2 are intermediate. Juveniles are similar to adults, but with a wide light brown band across the back of the head with a thin black band or band of spots at the nape. Head yellow to dark brown, usually with a dark postocular stripe. Lower surface yellow to white, with faint dusky edges on many of the ventral shields and black dots at the edge of ventrals about every six scales. Supralabials uniform yellowish-white. The largest in the series, which is also the largest reported to date, is a male from Flores (TL 2060 mm, SVL 502 mm); the largest Komodo specimen (N=10) has an SVL of 223 mm, but these all seem immature.

Distribution and Habitat.—Previously reported from Komodo by Dunn (1927a) and from Rintja by Darevsky (1964a), this species is also known from the neighboring islands of Sumba (Forcart 1949), Flores and Sumbawa (Mertens 1930, de Haas 1950), and eastward as far as Timor and Samao. Almost all the specimens the New York Zoological Society Expedition collected were taken in gallery forests extending downward from the higher heavily forested slopes. Mertens (1930) considered it eurytopic, reporting it from humid montane forests as well as dry coastal lowlands, including areas of *alang-alang* savanna.

Reproduction.—All the Komodo specimens are immature.

Food.—Large Flores specimens contained bird feathers, remains of *Rattus* sp., and *Gekko gecko*. The smaller Komodo specimens contained only remains of *Hemidactylus* sp.

Parasites.—None noted.



(B) UF 28759; (C) UF 28755; (D) UF 28757; (E) anterior body patterns of UF 28762; and (F) middorsal pattern of the same specimen. All individuals are from Komodo and of the approximate same size.

Lycodon aulicus capucinus Boie
Figure 43

Lycodon capucinus Boie 1827:551 (Type locality: Java).
Lycodon aulicus Boulenger 1893:352.
Lycodon aulicus capucinus Boettger 1898:37.
Ophites aulicus Griffin 1909:596.

SPECIMENS EXAMINED.—(18) UF 36201, Bara, Flores, 200 m; UF 28792, 28796-97, 28799, 28800-4, 28806, 36170, Loho Liang, Komodo, 2-30 m; UF 28793-95, 28798, 28805, Loho Lavi, Komodo, 5-10 m; UF 39894, Padar, 3 m.

DESCRIPTION.—Head slightly distinct from neck, eye rather small with vertical pupil; nostril large, maxillary curved medially, anterior teeth enlarged; internasals much shorter than prefrontals; frontal usually shorter than distance from tip of snout, shorter than parietals; loreal large, long, not entering eye, in contact with internasal; one preocular, in contact with frontal in 53% of Komodo specimens; 2 postoculars; 2+3 temporals; supralabials 8-9, with 3-4 entering eye; 4-5 infralabials in contact with anterior chin shields; 17 midbody scales, smooth, with apical pits; ventrals on Komodo specimens 181-214 (without strong sexual dimorphism as reported by Mertens [1930], because Komodo males vary from 181-214 [$\overline{X}$ = 198.0], females 196-213 [$\overline{X}$ = 204.9], 187-210 elsewhere); anal divided, 69-89 divided subcaudals ($\overline{X}$ = 76.8), 62-67 elsewhere.

Dorsal ground color gray-brown, with yellow to gray interstitial skin and adjacent scales forming a network that often delineates a series of irregular spots down back; head uniformly brown above, often with a darker edge posteriorly, an hourglass-shaped light gray to tan blotch on occiput; brown edges on otherwise gray to tan supralabials; chin dark on edges, especially anteriorly, otherwise white to cream; venter uniformly white to cream. Juveniles similar, but brighter patterned throughout.

The largest specimen previously reported (Mertens 1930) is 464 mm SVL, but UF 36201 (Bara, Flores) is 470 mm; average Komodo SVL 380 mm, tail 80 mm.

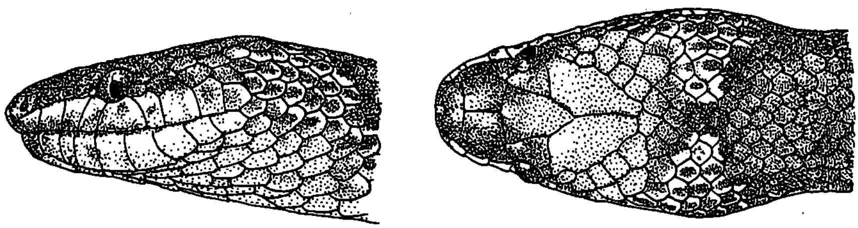


FIGURE 43.—*Lycodon aulicus capucinus* (UF 28806), Loho Liang, Komodo.

DISTRIBUTION AND HABITAT.—The species is widely distributed in Asia, being known from India and Ceylon east to the Philippines and Wetar, Lesser Sundas, in the southeast. The present subspecies occurs in the Lesser Sundas from Wetar and Serua westward to Sumatra. Darevsky (1964a) reported it from Komodo, Rintja, and Padar. De Rooij (1917) and Forcart (1949) listed it from the nearby islands of Flores, Sumbawa, and Sumba. On Komodo we found it in a variety of habitats, usually monsoon forests, where it was under stones and the loose bark of standing trees.

REPRODUCTION.—Mature males vary in SVL from 365-398 mm ($\bar{X}$ = 379.5); females are much larger, from 416-470 mm ($\bar{X}$ = 436.3). De Rooij (1917) reported that 3-7 eggs are laid in a single clutch. Though Komodo specimens were collected in both dry and wet seasons, it is not yet clear when eggs are laid there. Females taken in January have 9-28 follicles, up to 16 being enlarged, but yolked in only one specimen. Their size varies from 4.4-8.4 mm in diameter. The oviducts are smooth, flat, wider, but generally not convoluted or overly thickened. Females were collected only in the wet season. The dry season may be the breeding season, because mature males taken from August through November had turgid testes, with thick, convoluted, turgid vasa deferentia. Eggs are probably laid in November and December, just before the rainy season. Smith (1943) reported an incubation time of 33 days.

FOOD.—*Gehyra mutilata* has been reported by Mertens (1930) as eaten by a Flores specimen. Approximately half of the 18 Komodo specimens contained food, of which the contents of 8 could be identified. *Sphenomorphus florensis* and *Sphenomorphus* sp. were found in 50%, *Mus musculus* in 25%, *Emoia similis* in 12.5%, and a reptile egg *(Hemidactylus?)* and an adult *Hemidactylus frenatus* in 12.5%. Smith (1943) reported that geckos, skinks, and sometimes mice and frogs are eaten.

PARASITES.—None obtained.

REMARKS.—Dunn (1927b) reported that his Komodo specimen was taken at night climbing a tree. We, too, found this snake abroad at night. Smith (1943) remarked that they are good climbers and often nocturnal.

Psammodynastes pulverulentus (BOIE)
Figure 44

Psammadynastes pulverulenta Boie 1827:547 (Type locality: Java).
Psammadynastes pulverulentus Günther 1858:140.

SPECIMENS EXAMINED.—(27) UF 28790, Kampung Komodo, Komodo, 5 m; UF 28769-70, 28774 (plus 5 young), 28787 (plus 3 young), Loho Liang, Komodo, 1-30 m; UF 28670, 28772-73, Kali Inaloah, Komodo, 40 m; UF 28771, 28786, 28789, Gunung Ara, Komodo, 700 m; UF 28767, Ntodo Puljaran, above Kampung Komodo, Komodo, el 50 m; UF 28768, Gunung Longgo, Komodo, 150 m; UF 28781-85, 28788, 28791, Loho Lavi, Komodo, 12 m; UF 36167, Nggoer, Flores, 30 m; UF 36196, Poku, Flores, 500 m.

DESCRIPTION.—Head somewhat triangular from above, pupil vertically elliptic; anterior mandibular teeth greatly enlarged; snout slightly turned up at tip; canthus distinct; loreal present, single; one preocular (never 2 in Komodo material, though found elsewhere according to Boulenger [1896]); 1-3 postoculars; temporals 2-2; supralabials 8 (9), of which 3-5 enter eye; 8-9 infralabials of which 3 contact the anterior chin shields; 17 smooth scale rows at midbody, without pits; ventrals 150-176 ($\overline{X}$ = 165.3), 144-175 elsewhere (*fide* Mertens 1930, Boulenger 1896); anal entire; divided subcaudals 48-72 ($\overline{X}$ = 57.8), 44-70 elsewhere; greatest SVL 497 mm, tail 128 (de Rooij 1917), Komodo $\overline{X}$ = 357.6.

Brown, black, reddish-brown, or gray-brown dorsal ground color, females generally darker than the males, particularly on the chin; small, ill-defined darker blotches and light spots on the dorsum; head uniform above or with a faint V-shaped darker mark finely edged in

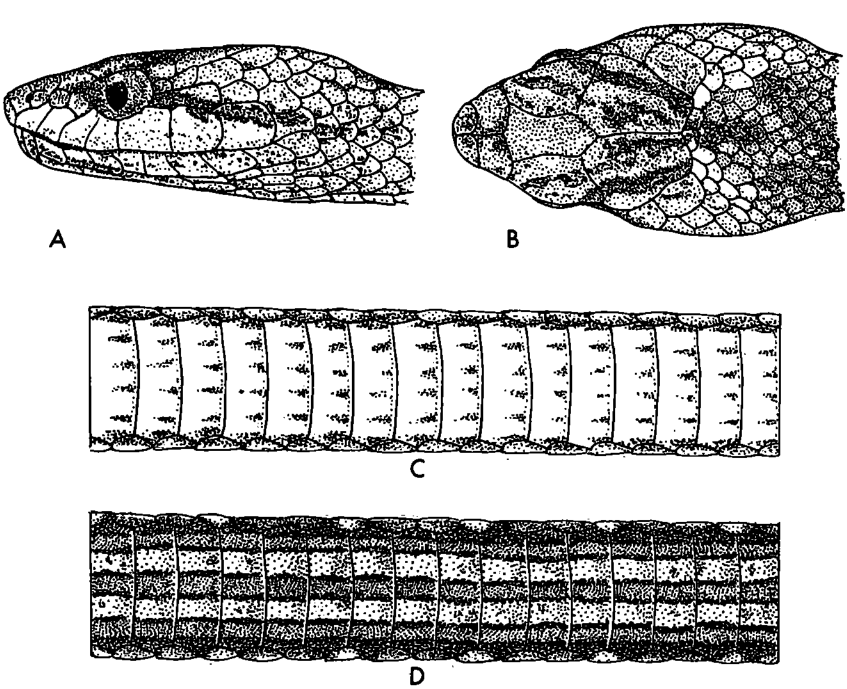


FIGURE 44.—*Psammodynastes pulverulentus.* Head, UF 28785 Loho Lavi, Komodo; mid-ventral body patterns, above, UF 28785, a male; below, UF 28790, Kampung Komodo, Komodo, a female.

dark brown or black, with supralabials yellow to cream with darker edges; ventrals with dark brown to black speckles or faint small dashes on a light ground color in males, females darker ventrally, sometimes with two lighter stripes (Fig. 44), chin darker, often with lighter median elongate spot or stripe. Juveniles similar, but more vividly patterned.

Distribution and Habitat.—Widely distributed from the eastern Himalaya Mountains southeastward through Indochina, Philippines, and Indonesia to Flores and Celebes. Previous records from the Komodo area are Flores, Sumba, and Sumbawa (Mertens 1930, Forcart 1949) and Komodo (Dunn 1927a). Barbour (1912) and Mertens (1930) reported that it is generally found in the mountains, usually between 400 and 1200 m elevation, though the latter stated that he found one on Flores below 200 m. Forcart (1949) reported specimens from the coast to as high as 350 m on Sumba. That they are found at such low elevations agrees with our observations on Komodo, for many of the specimens were taken near sea level in gallery forests along dry stream beds. Some were found in savanna environments, usually on rock-strewn grassy hillsides. A few were found under loose bark on fallen tree trunks and large branches, but most were under flat stones during the day. One was found in a rice field on Flores.

Reproduction.—Mature females were collected from August through February. Follicles varied from 7 to 32 ($\bar{X}$ = 18.1). Enlarged follicles 3-8 ($\bar{X}$ = 5.1); oviducts are thick walled and convoluted during this entire period. A November female (SVL 326 mm) contained 5 well-developed, scaled embryos (79-83 mm SVL) that would have undoubtedly been born in the earliest part of the wet season (December); another set of 3 embryos (94-88 SVL) very close to being born was found in a January female (SVL 497 mm). Females from the mainland have more young (5-10, *fide* Smith 1943). Mature females have an SVL of 320-410 mm ($\bar{X}$ = 376.3), males 288-370 ($\bar{X}$ = 336.9). Darevsky (1964a) stated that a Padar specimen contained a near term egg, but de Rooij (1917) and Smith (1943) stated they are ovoviviparous, fitting with my observations on Komodo.

Food.—Mertens (1930) reported *Rana microdisca* and *Sphenomorphus florensis* as being eaten. In 20 Komodo specimens dissected the following species were found: *Sphenomorphus florensis* in 10%, *Cyrtodactylus darmandvillei* in 5%, *Hemidactylus* sp. 5%, and *Sphenomorphus schegeli* 5%. One of the specimens contained the remains of an *Oreophryne jeffersoniana.*

Parasites.—Of the adults examined 25% were heavily parasitized with the nematodes *Hexametra quadricornis* and *Spinicauda komodoensis* (J. Pinnell, pers. comm.).

Remarks. Called *ular percha* locally.

FAMILY ELAPIDAE
Naja naja sputatrix BOIE
Figure 45

Naja sputatrix Boie 1827:557 (Type locality: Java).
Naia tripudians Lidth de Jeude, *in* Weber 1890:179.
Naia tripudians var. *sputatrix* Boulenger 1896:384.
Naja naja sputatrix Stejneger 1907:395.
Naia naia Barbour 1912:30.
Naja sputatrix malayae Deraniyagala 1960:223 (Type locality: Negri Sembilan, Malaysia).

SPECIMENS EXAMINED.—(16) UF 32572, Nggoer Flores, 15 m; UF 39833, 28674, 28679, Kali Besar, Loho Liang, Komodo, 30 m; UF 28673, 28677, 28680, 28678, Loho Liang, Komodo, 1-30 m; UF 28675-76, Kampung Komodo, Komodo, 8 m; UF 28672, Sabita, Komodo, 8 m; AMNH 31957-59, Komodo, "near sea level," AMNH 31974-75, Komodo, 650 m.

DESCRIPTION.—Rostral broader than high, very evident from above; internasals somewhat shorter than prefrontals, in contact with a single preocular; frontal about as long as its distance from rostral, as broad to slightly broader than supraocular; postoculars 3 (4 on one side of one specimen); temporals consistently 2+3; supralabials 7, of which numbers 3 and 4 enter eye; infralabials 9, first 4 in contact with first

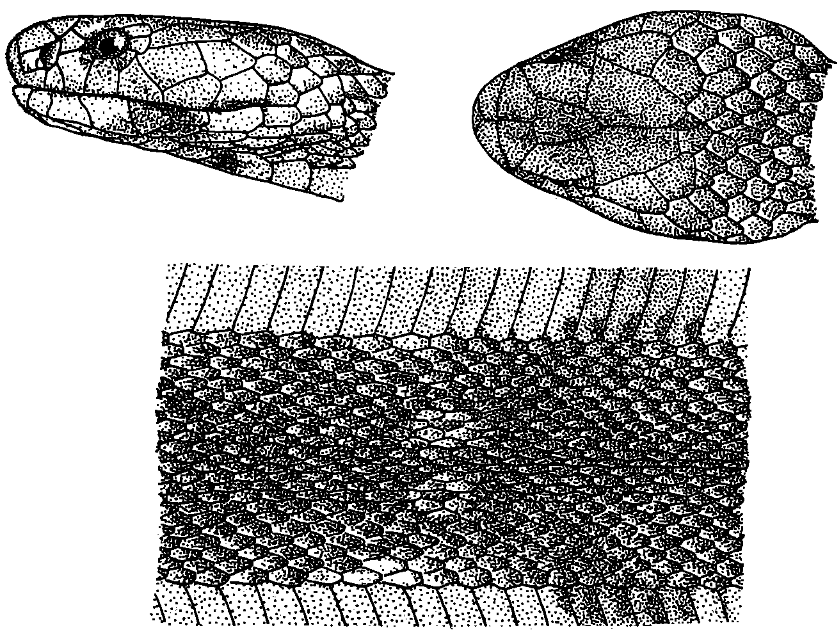


FIGURE 45.—*Naja naja sputatrix* (UF 28677), Loho Liang, Komodo, head and neck.

pair of chin shields, which is longer than posterior pair; scale rows: neck (through marking) 21 (23 in two specimens, 19 in the Flores specimen); midbody consistently 19 (17 in Flores specimen); ventrals and subcaudals remarkably consistent: males 160-173/47-55, females 175-182/51-56. Sex ratio in preserved material 1 male: 3 females.

Color light to dark brown dorsally, each scale with a yellow to whitish anterior edge; head above uniform, usually same color as body, sometimes darker; neck only slightly expandable, markings from nothing to a barely discernible small light mark on either side of the vertebral line (most common) to a faint V-shaped mark, the apex directed posteriorly (Fig. 45); ventrally yellowish-white, sometimes a few faint scattered spots; faint brownish-gray throat band in most specimens, which is often interrupted. On the basis of Dunn's (1927b) description of Komodo material, Mertens (1930) presumed the Komodo material to be a slightly different color than specimens from more western islands, a conclusion not justified by the present material. Juveniles uniform brown, darker anteriorly, no lighter marks on scales; head dark brown above, snout and sides of head yellowish-brown; ventrally uniform yellowish-white.

In his study of the Sunda herpetofauna, Mertens (1931) stated that if it were not for the very wide zone of intermediates, the Sumatra and Javanese specimens *(N. n. sputatrix),* the Lesser Sunda material could easily be considered a separate race.

DISTRIBUTION AND HABITAT.—Previously reported from Komodo (Dunn 1927b) and the nearby islands of Sumbawa and Flores (Klemmer 1963). Dunn (1927b) reported specimens taken on Komodo from sea level to 650 m. We found none higher than this. We found *Naja naja sputatrix* abroad both day and night. Though Mertens (1931) found them only on the ground, some of ours were shot from heights up to 11 m in trees overhanging dry creek beds. Specimens were also seen in *Imperata* and *Zizyphus* savannas, as well as in gallery and deciduous monsoon forests, particularly around rock piles and outcrops with many fissures and holes.

REPRODUCTION.—Mature females have an SVL of 84.8 cm, males 88.3 cm. At sea level hatchlings (SVL 235-240 mm) were found in January and February. The ovarian scars in one female suggest that as many as 16 eggs may be laid in a clutch; yolked follicles 2.2 to 5.2 mm (range = 1-16) were found in January-February specimens. Eggs are probably laid at the end of the dry season (November). Males have turgid testes and turgid, convoluted vasa deferentia in October and flat testes and non-convoluted vasa deferentia in January-February.

FOOD.— *Lycodon aulicus* and *Elaphe subradiata* were reported as food by Dunn (1927b), and Mertens (1931) reported mice, *Rana can-*

crivora, and *Mabuya multifasciata.* None of my Komodo specimens contained any identifiable food.

PARASITES.—The nematode *Ophidascaris wui* is common in the digestive tract of Komodo specimens.

REMARKS.—Komodo villagers show relatively little fear of this snake. It apparently rarely bites or spits, and then only with considerable provocation or when restrained. Only one death attributed to this species was reported to me—an old, feeble woman who had stepped on one in the savanna and was bitten on the heel. Komodans call this *ular sendok,* the "spoon snake," because of its shape when in a reared position. Shed skins were noted from August through October.

FAMILY VIPERIDAE

Vipera russelli limitis MERTENS

Figures 46, 47

Vipera russelli limitis Mertens 1927b:183 (Type locality: Pulau Ende, off SE coast of Flores).

SPECIMENS EXAMINED.—(59) UF 28616, 28619, 28621-23, 28625-26, 28629, 28631-32, 28634-35, 28637, 28639-39, 28661-64, 28666-71, Loho Liang, Komodo, 1-30 m; UF 28617-18, 28624, 28627, 28636, 28665, Kampung Komodo, Komodo, 20 m; UF 28620, 28630, 28633, 28638, 28641-42, 28660, Loho Lavi, Komodo, 12 m; UF 28628, Gunung Puaki, above Loho Lavi, Komodo, 120 m; UF 28665, Kampung Kechil, Komodo.

DESCRIPTION.—Head small and long, moderately distinct from neck, but habitus generally more slender in appearance than nominal form (Fig. 46); canthus distinct; rostral broader than high, in contact with 6 scales; head scales small and strongly keeled; supraoculars very small, with 7 scales between them; 2 scale rows between eye and supralabials; nostril in large nasal, in contact with nasorostral, but not the supranasal; a very large postnasal found in 3 specimens; first supralabial always touching lowest postnasal (usually not the case in the nominate form); supralabials 9-11, usually 10; infralabials 11-14, usually 12, numbers 4 and 5 in contact with anterior chin shields; dorsal scales keeled, except outer row, in 27 rows at midbody; ventrals 139-167 ($\overline{X} = 155.8$) (no statistically significant sexual difference); subcaudals divided (rarely 1-2 single members in series), 46-65 ($\overline{X} = 50.3$) in males, 40-56 ($\overline{X} = 44.5$) in females, the difference in means being significant ($P = > 0.05$).

Ground color brownish-gray to dark gray; dorsally with a longitudinal row of blackish-gray or dark brown blotches with white and black edges, often round to oval on anterior third of body, and often variously connected vertebrally to form zig-zags and other anomalous patterns on posterior two-thirds (Fig. 47); those on tail often fused to produce solid (in 20%) or broken (56%) stripes. Lateral body surface with similar smaller blotches having white and black borders, often forming a longitudinal solid (in 45%) or broken (53%) stripe on side of tail (newborn and 1st-year individuals with a sulfur yellow tail line); above this series and below vertebral row a single (10%) or double (90%) row of less evident spots; also a series of small spots on edges of ventral scales (Fig. 47). Thus Komodo specimens have from 5 to 9 (usually 7) rows of body spots. Head markings reduced when compared to nominate form. A pair of small ground-colored oval to subtriangular spots on dorsoposterior part of head, separated by apex of a light-colored V (which is characteristic of nominate form) in 58% of Komodo material, tending to disappear at end of first year of life; dorsoposterior spots in all Komodo specimens separated from dark temporal zone by an area of ground color in all but 2 specimens; interorbital dark spot or stripe always present, heavily pigmented and obvious in 55%, faint in 33%, and nearly absent in 12%; dark subocular spot present in all but 2 specimens; supralabials white with black to brown flecks. Chin white, vividly marked with numerous black to very dark brown triangles; venter white to cream with fine gray punctations and somewhat hemispheric-shaped black, dark brown to dark grayish-brown markings linearly arranged (in 55%), or with fewer dark markings nearly lacking gray punctations (in 40%) or without any punctations (5%).

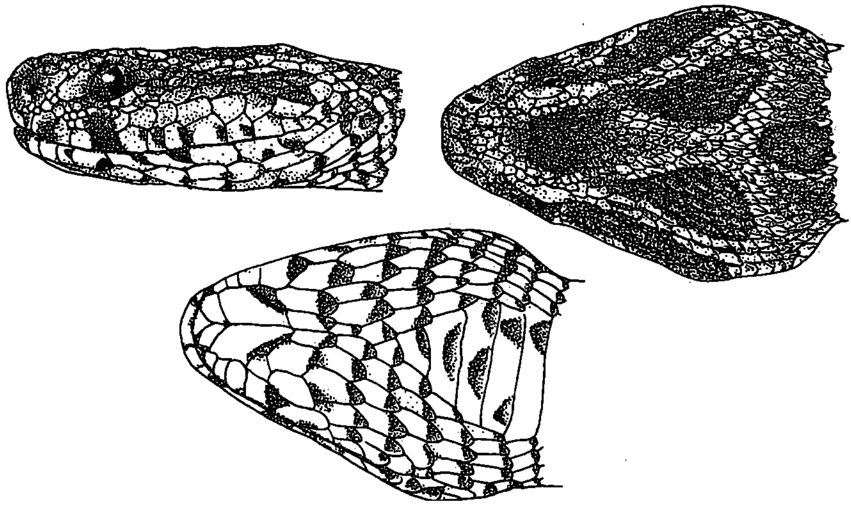


FIGURE 46.—*Vipera russelli limitis* (UF 28617), Loho Liang, Komodo.

DISTRIBUTION AND HABITAT.—This geographic race is restricted to the Lesser Sundas and known only from Flores and Komodo. Dunn (1927b) reported it previously from Komodo. All the Komodo specimens were collected near the coast (1-120 m) in *Zizyphus* savanna and the beachside *Pandanus* community. Most were found in or near the wooded borders of more open situations, often near stone piles in which they commonly took refuge. Many were found on the rocky banks of dry stream beds.

REPRODUCTION.—Newborn with umbilical scars (170-275 mm SVL, $\bar{X}$ = 189.4) were obtained on Komodo only during January. Mature females were collected from the last third of the dry season in October into the middle of the wet season in January. Follicles vary from 20 to 42 ($\bar{X}$ = 31.2); from October 5 to 15 they show beginnings of yolk deposition (15-27 mm in diameter); the oviducts are smooth, thin walled. In December the embryos (up to 13) are well formed. Males are available from July through February. From July through September the testes and vasa deferentia are turgid, the latter highly convoluted. From late November through February the testes are more flaccid and the vasa deferentia less convoluted. Thus it appears that breeding takes place in the middle to late dry season, and the young are born in

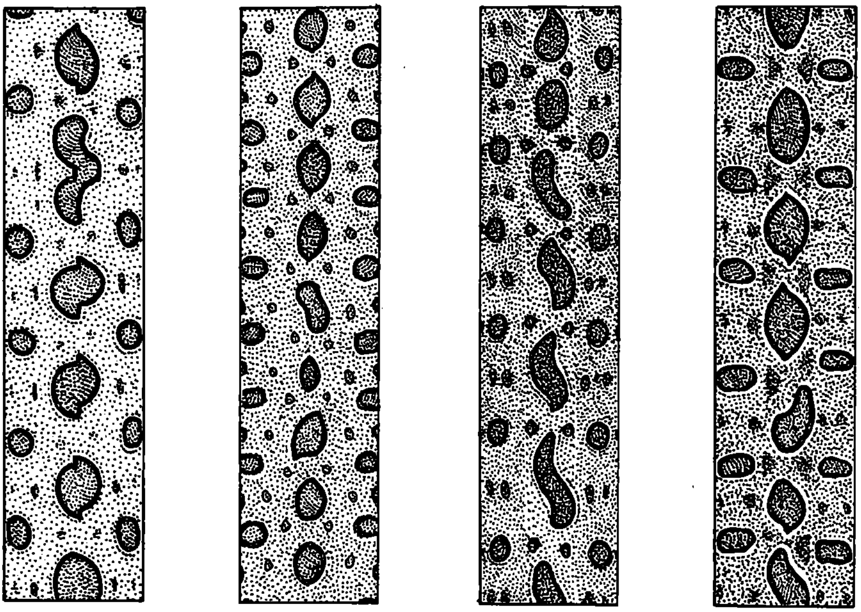


FIGURE 47.—Variation in mid-dorsal patterns of juvenile *Vipera russelli limitis* from Komodo. From left to right, UF 28669, 28639, 28644, and 28665.

the early part of the wet season. Mature females are 550-700 SVL ($\bar{X}$ = 610), males 530-630 ($\bar{X}$ = 570).

FOOD.—Of the 56 specimens examined, 51% contained food or food remains, of which only those in 24% could be identified. Of these, newborn and juvenile specimens contained elytra and other parts of adult coleopterous insects (21.8%), of their larvae (8.3%), and of moths (1.8%). *Hemidactylus frenatus* (7.2%) were found in juveniles and adults, *Cosymbotes platurus, Mus musculus* (both 2.2%), skinks (genus ?) (5.5%) in adults, *Emoia similis* in newborns (1%), and *Kaloula baleata* (1%) in adults. Vegetable matter occurred in 7.4% and sand and stones in 3.6%.

PARASITES.—Nematodes of the species *Kalicephalis willeyi* were found in 4% of the 56 specimens examined.

REMARKS.—Indonesian populations of *Vipera russelli* have been extensively discussed by Dunn (1927a), Kopstein (1936), Mertens (1927c 1930, 1957), Hoesel (1953, 1958), and Brongersma (1958), all based on relatively few specimens. The new, extensive material from the Lesser Sunda Islands supports the validity of the trinomial, though it is not a markedly distinct race. This is based mainly on the presence of a subocular spot in all but 2 specimens. The light-colored V on the head is only found in about half the specimens now available, in spite of the importance placed on the character by Mertens (1930). The 7 rows of dorsal spots in *V. r. limitis* also serve to distinguish it from *V. r. siamensis* (with 5) and *V. r. russelli* (with 3). Furthermore, the maximum size reported in the Lesser Sundas is 835 mm, whereas mainland snakes become twice that length (Mertens 1930).

In general most specimens were easily angered and inflated their bodies, hissed, and struck when annoyed, but on several occasions expedition members accidentally stepped over their well camouflaged bodies, and the snakes made no attempt to bite. A small pet 5 kg wild boar was struck in the forehead by a specimen 400 mm SVL, and after much swelling and obvious discomfort recovered within a week. Komodo villagers greatly fear this snake (which they call *misa*), for it has caused more snakebite deaths on this island than any other species. Most were seen during the late afternoon to twilight.

Trimeresurus albolabris GRAY
Figure 48

Trimeresurus albolabris Gray 1842:48 (Type locality: "China").
Lachesis gramineus Boulenger 1896:554 (part).
Lachesis fasciatus Boulenger 1896:63 (Type locality: Djampea Island, near Celebes).
Lachesis gramineus albolbris Mell 1922:126.
Trimeresurus fasciatus Dunn 1927b:5.
Trimeresurus gramineus gramineus Mertens 1930:27.

SPECIMENS EXAMINED.—(95) UF 30127-50, Nggoer, Flores, 10-20 m; UF 30151, 4.5 km ENE Loök, Flores, 200 m; UF 28719-23, 28725-26, 28728-33, 28735, 28737, 28716, 28714, 28708, 28705-5, 28702, 28699, 28691, Loho Liang, Komodo, 2-30 m; UF 28734, Nggolo Vai, Loho Liang, Komodo, 10 m; UF 28695-96, 28736, Kali Besar, Loho Liang, Komodo, 60 m; UF 28687-88, 28706-7, 28700, 28692, 28690, 28709, 28713, 28717, Loho Lavi, Komodo, 1-15 m; UF 28689, 28697-98, 28715, Gunung Ara, Komodo, 300 m; UF 28703, near Sabita, Komodo, 8 m; UF 28701, Kali Inaloah, near Gunung Amasobang, Komodo, 24 m; UF 28693-94, Galong Sambe, near Poreng, Komodo, 150 m; UF 28710-12 (plus 17 young), 28718, 28724, "Komodo"; UF 36446, near Deussi, Timor, 150 m.

DESCRIPTION.—Distinct canthus, head scales small, smooth, supraocular narrow, sometimes divided; 1-2 scales between internasals or latter in contact; 8-13 scales between supraoculars; 2-3 postoculars; 1 subocular, sometimes in contact with supralabial 3, usually separated from labials by 1-3 scale rows; 8-12 supralabials, second bordering loreal pit anteriorly, third largest; temporal scales with short keel (a few individuals with weak or no keels); dorsal scales strongly keeled above, smooth on two lateral rows, in 19-21 rows (usually 21); ventrals 153-168 ($\bar{X}$ = 161.2); subcaudals divided, 53-81 ($\bar{X}$ = 63.8), males 60-81, females 51-65; tail prehensile; greatest reported SVL to 805 mm, tail 125 (Mertens 1930), largest SVL of Komodo specimens 760 mm.

Usually bright green dorsally, often olive or even blue (in approximately 1 out of 8 Komodo and western Flores specimens), often with distinct darker transverse bands; supralabials yellow to greenish-white (sometimes light blue) in all but largest specimens, which are sometimes suffused with gray or olive; tail usually with rusty-colored streak dorsally; venter greenish-yellow, greenish-white, or sometimes light blue; iris brown to red (latter apparently more common in blue phase individuals).

DISTRIBUTION AND HABITAT.—From Sumatra and Borneo eastward through the Sunda Islands to Timor, except for the Celebes-Halmahera Island groups (Pope and Pope 1933). Forcart (1949), de Haas (1950), and Mertens (1930) reported the species from the nearby

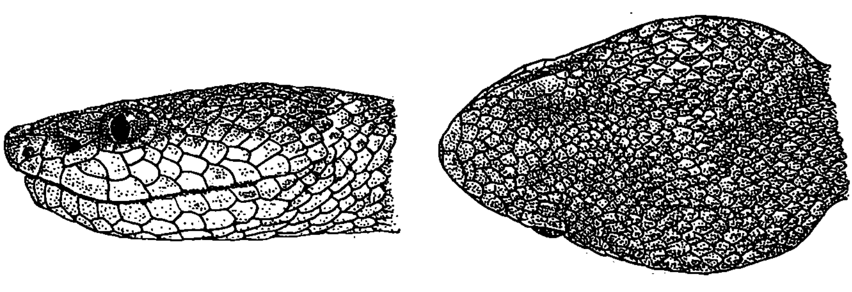


FIGURE 48.—*Trimeresurus albolabris* (UF 28691), Loho Liang, Komodo.

islands of Sumbawa, Sumba, and Flores; Darevsky (1964a) reported it from Rintja and Padar.

Certainly one of the most commonly encountered snakes on Flores and Komodo, this species is found in a variety of habitats, though it is most common in monsoon forest. It occurs from sea level to 700 m on Komodo and reaches maximum abundance along stream courses, where it is often seen abroad at night, prowling in the bordering shrubs and small trees near the bank. Specimens were found as high as 15 m in tamarind trees in the daytime, when they were usually asleep, coiled in the common crotch of several branches. A few were found on the edges of savannas, usually crawling about in the dense stands of the tufted grasses of the genus *Andropogon.*

REPRODUCTION.—On Komodo up to 17 young are born alive in the early monsoon season. Supporting data are: 3 July-August females had small, translucent unyolked follicles, the oviducts smooth, flat and translucent. A September female contained 11 large yolked follicles 6.2-13.2 mm in diameter, and the oviducts were large, thick-walled, and highly convoluted. The testes of males caught at the same time were enlarged and turgid and the vasa deferentia convoluted but flattened. By October and November, the latter are nearly smooth and not convoluted. This condition continues at least through February. Up to 17 near-term embryos (all with scalation and color pattern discernble) are found in females collected in November. Newly born specimens are found in January, and 12 females caught in December-January had no embryos, but small follicles and flat, smooth oviducts. These data suggest that breeding probably takes place in September, and the young are born in late November and December. Juveniles caught in January all show an umbilical scar and are 140-195 mm SVL ($\overline{X}$ = 175). By the following January, they are 290-310 mm SVL. Sexual maturity is probably attained in the third year.

FOOD.—Of 56 specimens examined, 16 contained remains of food that could be identified to the following species in 9: *Hemidactylus frenatus* in 4 specimens, *Lepidodactylus lugubris* in 2, *Sphenomorphus florensis* in 1, *Mus musculus* in 1 (also reported by Dunn 1927b), and *Kaloula baleata* in 1 (also reported by Dunn 1927b). In addition, 7 others contained remains of unidentified lizards. Mertens (1930) reported *Rattus rattus*, miscellaneous frogs (usually *Rana cancrivora*), and lizards (usually *Mabuya multifasciata*) from specimens collected on other islands.

PARASITES.—Pentastomideans *(Raillietiella* sp.), ascaridoidians, oxyuroideans *(Polydelphis* sp.), and the nematode *Hexametra quadricornis* are common in the intestines (approximately 28% are parasitized).

ZOOGEOGRAPHY

Geology and History

The Lesser Sunda Islands lie between two large continental masses—the Sunda and Sahul shelves, parts of which are covered by relatively shallow seas. The Sunda Shelf is a large, continental extension of Southeast Asia, uniting Sumatra, Borneo, and Java with Malaysia. The Sahul Shelf lies to the east, uniting New Guinea and the Aru Islands with Australia. The Sahul Shelf was very stable throughout the Tertiary, but the Sunda Shelf had a complex geological history.

Between the Sunda and Sahul shelves are two whirl-shaped, more or less parallel, island arcs; Komodo is located on the inner arc. The islands of the outer arc are composed largely of raised marine sediments (some of deep water origin), and those of the inner arc are mainly volcanic. Associated with both arcs are several shallow basins and troughs, of which the sediments are relatively unknown.

Komodo is largely comprised of igneous rock, usually hydrothermally altered; the remaining strata are predominantly limestone. Until recently, although no absolute ages had been determined for any of these rocks, Komodo was thought to be no older than late Tertiary (Ehrat 1928a). New data obtained during the present study show that its history extends into the late Mesozoic. This conclusion is based on potassium-argon isotope dates obtained from igneous rock samples taken immediately below and above a fossil wood zone (described by Ehrat 1928a; Piazzini 1960; and others). Samples from below the fossil zone were taken from: (1) the top of the basaltic lacolithic dome of Gunung Insilung, near Nggoer Village, Mangarrai Province, Flores (130 ± 10 mil yrs, Geochron Labs, Inc.), (2) Banu Mate, 400 m, the highest extruded sheet of basaltic rock on the flanks of Komodo (134 ± 19 mil yrs, same lab), and (3) a basalt porphry from the larger of the two volcanic necks comprising Ntodo Klea, Komodo (49.0 ± 4.3 mil yrs, same lab). The latter is believed to represent the latest volcanic eruption on the island and obviously is much younger than the fossil wood zone. Invertebrate fossils from the raised coral reefs on the flanks of the Ntodo Klea complex range in age from early to middle Tertiary (F. G. Thompson, pers. comm.). Thus the igneous activity responsible for the formation of the western half of Komodo occurred during the Jurassic. This land surface was later covered with a forest of large trees. Volcanism was again prevalent during the Eocene and created the Ntodo Klea complex on the eastern part of the island. At

[1]There is presently no evidence for more than one fossil wood zone, though future work may disclose several strata.

this time the eastern half of Komodo was significantly enlarged through the uplift of coralline strata, which continued throughout much of the Tertiary and was undoubtedly responsible for the formation of Padar. Thus the land surface of Komodo was not formed in the Plio-Pleistocene, as is often assumed in zoogeographic studies (Burden 1928; Darevsky 1964a; and others), but in the late Mesozoic.

Rintja and extreme western Flores share a similar geologic history. In fact, Komodo, Rintja, and Flores may have been connected during the Eocene and Oligocene and again separated in the Mio-Pliocene by submergence resulting from volcanism on Flores (Brouwer 1916, 1917; Erhat 1928a).

Regional Structural History.—The structural history of the East Indies began in the upper Paleozoic. It is currently represented by a few deposits scattered from Borneo to New Guinea. Although a few deposits suggest deep water sedimentation, the vast majority indicate neritic to littoral sedimentation. Thus, it is highly probable that during the Carboniferous large islands were already scattered throughout the shallow East Indian sea. This is further indicated by the presence of both fossil plants and clastic material in the sediments (Umbgrove 1949). By at least the late Jurassic, portions of Komodo and western Flores (perhaps connected) were above the sea. These and other ancient Sunda Islands developed along a geosynclinal arc extending in a loop from the edge of the Mesozoic Sundaland (Fig. 49). Another chain of islands is believed to have formed along the western edge of the Pacific Plate, extending from near what is now Japan to Fiji and probably beyond.

By the early part of the Cenozoic the Southeast Asian geosynclinal arc had moved much farther southeast (Fig. 49). Subsidence was characteristic in the area, for Paleocene and Eocene limestones are common, but at least part of Komodo was still an island. Large land surfaces also existed in the outer arc east of Timor in what is now northern Celebes, almost all of Sumatra, Malaya, southwestern Borneo, and the regions between (Umbgrove 1949; Fig. 49). The early Tertiary fluviatile sediments on Celebes indicate that at least some of these islands were quite elevated.

One of the most widespread geological phenomena of the Miocene East Indies was the extensive volcanism. Although there is no evidence of Miocene volcanic activity on Komodo or western Flores, diastrophism, caused by powerful compressive forces (probably brought about by the collision of the Australian plate with the southeastern fringe of the Asian Plate), was common in all surrounding areas and resulted in widespread folding and thrust faulting (Umbgrove 1949). The Pliocene rocks show that surface leveling was extensive and that the sea again invaded some areas. Though there is disagreement on the extent of Pliocene submergence on Borneo and Celebes (cf. Umbgrove 1949 and van Bemmelen 1949), all agree that, with the exception of extreme southwestern Sumatra and much of Java, the present Greater Sunda area was above the sea. In addition, land surfaces are known to have existed during the Pliocene in many parts of the Lesser Sunda chain (Sibinga 1927).

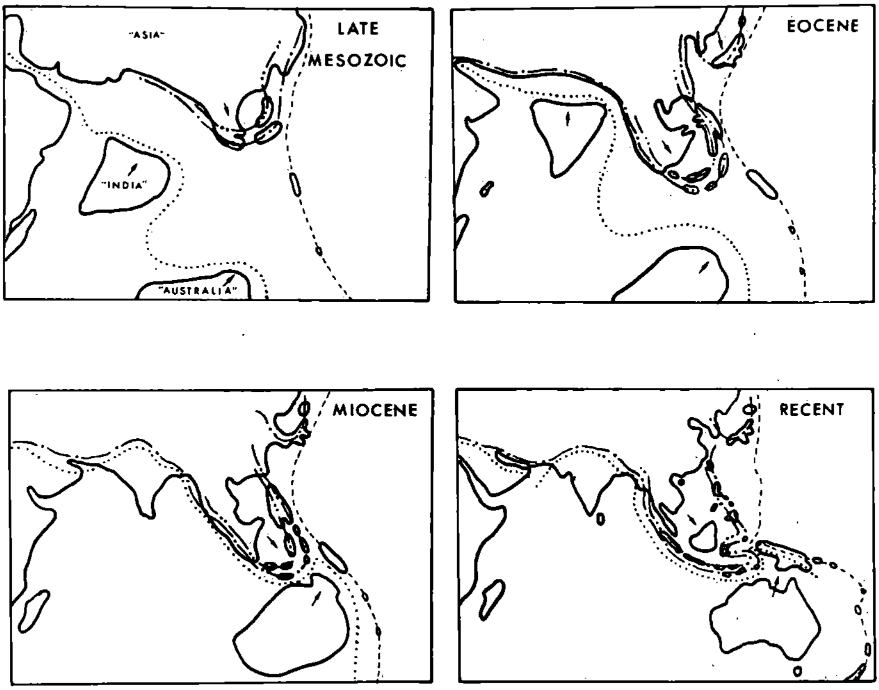


FIGURE 49.—Major phases in the geological development of Southeast Asia. In the last half of the Mesozoic the Australian and Indian blocks were drifting northeastward. Two volcanic arcs, each provided with island festoons, formed a lobe extending southeastward from the Asian mainland. Another volcanic arc. also probably with islands along its length extended along the western edge of the Pacific plate from near what is now Japan to near the present position of Australia. Arrows indicate the major directions of plate movements. By the Eocene the double volcanic arc was much larger and the single arc along the western edge of the Pacific plate was probably starting to be deflected by the Australian plate. In the Mid-Pliocene the Asian and Australian plates collided. Continuing compression caused great distortion of the double arc in the Pleistocene to Recent.

PLATE TECTONICS.—The outline above shows that the extent and shape of land surfaces in the entire Sunda area were continuously modified during the Tertiary. The most important displacements from a biogeographic standpoint took place in the last half of the Tertiary and are related to major tectonic movement of continental plates. According to Carey (1970) and others, the inner and outer Sunda volcanic arcs were greatly distorted in Mio-Pliocene times, when the Australian continental plate (including what is now the Sahul Shelf and New Guinea) collided with the expanding southeast lobe of the Asian continent. That Cenozoic plate tectonics are important in zoogeographic studies is clear (Colbert 1969, and others), although theorists are not always in agreement regarding continental positions. In this part of the world we are rather fortunate, because Runcorn (1962) has shown that the northeastern movement of Australia has been relatively steady and unidirectional from the early Triassic to the Recent. During the same period, the Lesser Sunda volcanic arcs and their associated oceanic basins were moving southeastward (Fig. 49). The collision of Australia with the arcs occurred during the Mio-Pliocene, which explains the extensive vertical and horizontal movements in the archipelago during this time. Such contact explains why Timor in the outer volcanic arc appears to have been pressed up against the inner arc at the projection of the Sahul Shelf (Fig. 50); why the Miocene volcanics of eastern Flores are overthrust onto younger ones; why Halmahera and Celebes look as though they had been pushed northwestward, and so on (for details see Brouwer 1916; Sibinga 1927; Molengraaff and Brouwer 1929). Given an understanding of the late Tertiary tectonic history of the region, interpreted in the light of plate tectonics, it is obvious that at least the Cenozoic movements involving the Australian continental block and the Sunda volcanic island festoon are extremely significant in the dispersal of the land biota of that region.

EUSTATIC CHANGES IN SEA LEVEL.—During the Pleistocene glaciation sea levels are believed to have been lowered by approximately 90 m in the East Indies (Kuenen 1950). It is certain that during these times Borneo, Sumatra, Java, and the Malay Peninsula were all connected by dry land (Molengraaff 1921). To show the extent of such connections and the increase of land surfaces, it should be pointed out that Timor was separated from the Australian mainland by only 99 km (Hooijer 1969). At the same time, Komodo, Padar, Rintja, and western Flores were probably broadly connected to one another (see Fig. 2). Whether the entire Sunda Shelf was inundated during high Plio-Pleistocene sea levels is still uncertain, but it is reasonably clear that Komodo, Rintja, and western Flores were above sea level during these

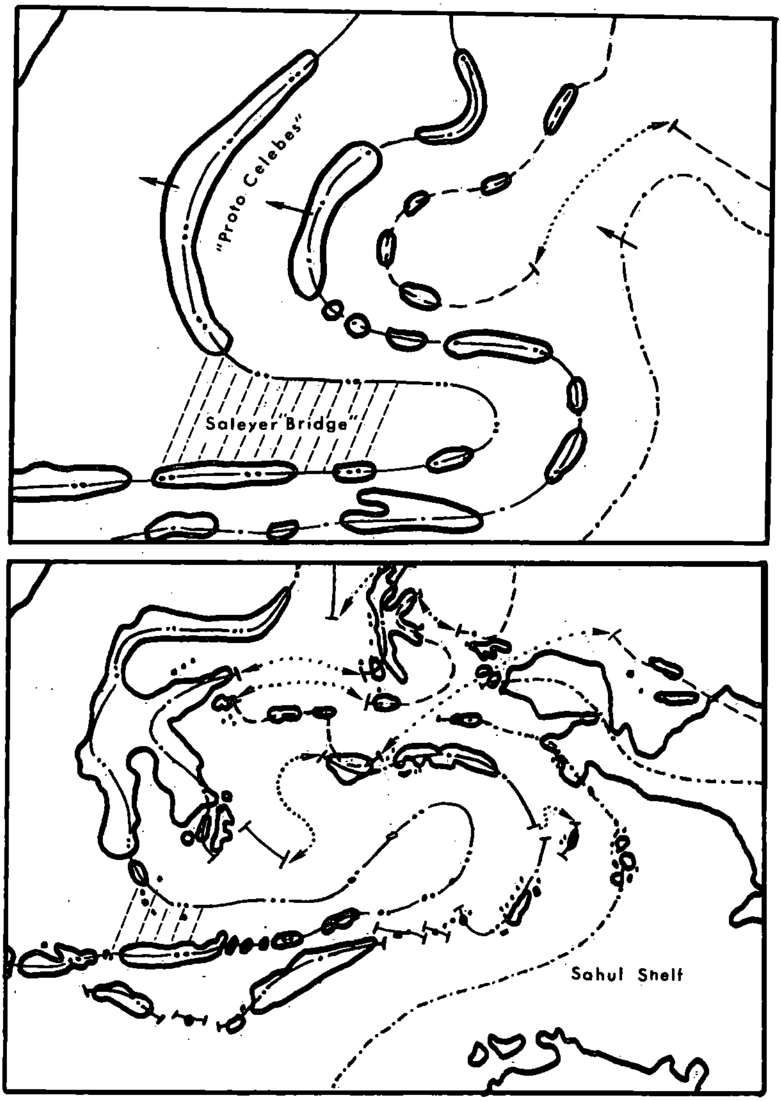


FIGURE 50.—The upper drawing shows the probable extent of the double Asian and single Pacific volcanic arcs during the Pliocene. Note the position of the hypothetical "protocelebes," formed of two islands at that time. The "Saleyer Bridge" is here interpreted not as a land connection between the Celebes and the Sunda Islands, but as a region in which exchange between these two areas was likely. The lower drawing shows the present configuration of the three volcanic belts (after Molengraaff and Brouwer [1929] and others, see text). Note the composite nature of the present islands of Celebes, Halmahera, and New Guinea. Each composite island allows interchange of faunas between previously isolated chains or island continents.

periods; though much or all of Padar may have been submerged. Ample evidence shows considerable tectonic movements during the entire post-Tertiary in this area, so that the present and past separation of these islands may have resulted either from eustatic rise in sea level following glacial melting or from actual lowering of the sea bottom by tectonic activity—probably both. Subsidence of the basins of the Java and China seas almost certainly occurred in the Pleistocene (Umbgrove 1949), for distinctly marked drowned river valleys trail across the bottom—in some places deeper than 100 m. In any event, no evidence exists of past connection of Komodo to Sumbawa in the west or to Sumba southward, regardless of sea level or bottom depth changes.

Zoogeography of the Lesser Sunda Reptiles

The most commonly adopted zoogeographic scheme recognizes two major regions in this part of the world—the Oriental (Tropical Asia and nearby islands, such as Ceylon, Sumatra, Java, Borneo, Formosa, and the Philippines) and Australian (Australia, New Guinea, and the small islands nearby). The faunas of each are extraordinarily different. What happens where these faunas meet in the Indo-Australian Archipelago has long fascinated zoogeographers. In fact, the exact boundary between the Oriental and Australian Regions has been the focus of several generations of zoogeographers (for complete discussion see Mayr 1944). Each argued the validity of their own boundary lines, the location varying from Bali to Fiji. On the basis of plants Burkill (1941) suggested still others, in some cases running more east-west than the generally north-south lines contrived from animal distributions.

Not only are the phytogeographic regions of this area quite different from those based on animals, but the dispersal routes into the Lesser Sundas are interpreted as having been much more complex (Steenis 1935). Thus, botanists and zoologists are far from agreement in respect to the boundary line separating the Oriental and Australian Faunal Regions.

Of all the lines based on animals, those derived from mammal and bird distributions are the least similar to those derived from plants. This is probably because mammals and birds radiated late in geological time. Many organisms probably utilized land bridges or island chains absent or unsuitable during the dispersal of recent mammal groups. These earlier dispersing groups include the fishes, reptiles, amphibians, plants, and most invertebrates. It is, thus, unfortunate that much of the geographic analysis upon which boundaries were established is based on the distribution of mammals and birds, for the boundaries and suggested immigration routes may emphasize rather recent geologic history.

Another major problem is that zoogeographic conclusions have been based on recent distributions, because fossil land faunas were unknown from the Lesser Sundas (see Darlington 1957). It is now known that a few large vertebrates, including proboscidians, were found throughout the Lesser Sundas during the past. Middle and late Pleistocene deposits on Timor contain two pigmy stegodont species closely related to Siwalik species of India and Pakistan (Hooijer 1969, 1970, 1972a). A giant land tortoise found in the same deposits is also known from Java, Celebes, and the Siwaliks (Hooijer 1971). The close relationship of the extant insect faunas of the East Indies and those of the Himalayan area was first pointed out by Wallace (1876). The closest relatives of the Celebes land tortoise, *Geochelone forsteni*, are found in humid mountain forests of India and Southeast Asia (Auffenberg 1976) and the dwarf "buffalo," or anoas, of the Philippines and Celebes are morphologically closest to certain Pliocene Siwalik fossils.

It is now clear on these and other bases that at least a part of the late Tertiary Himalayan fauna extended as far eastward as the Lesser Sundas and that in the late Pleistocene this fauna, or at least certain elements of it, were found as extant insular relicts in the East Indies (Hooijer 1969, 1970, 1972). That several large mammal species found it possible to move eastward over a series of theoretically important water gaps suggests that the zoogeographic boundary lines should not be taken too seriously. In any event, the Lesser Sundas represent a transition zone separating Australia and Asia. This was recognized as early as 1926 by Merril. Dickerson *et al.* (1928) named the region "Wallacea," an appropriate and useful term (Smith 1941, Darlington 1957, 1965, MacArthur and Wilson (1967).

ALTITUDINAL FACTORS.—The present distributions of at least the lower vertebrates, many invertebrates, and plants in the Lesser Sundas suggest a more complex distributional pattern than a simple two-directional east-west movement. Only the latter has been emphasized in zoogeographic studies in the area. Steenis (1935) and Shaw (1941) both elaborated the important point that the lowland and mountain floras of this region are often unrelated. Of these two altitudinally distinct floral "layers," one may have its main affinities to the west and the other to the east. These conclusions are important, for it is evident that any biogeographic explanation for the lowlands may be invalid for the uplands.

In general, botanists have more commonly analyzed their distributional data from the standpoint of the complexity of past geographic and ecologic differences than have zoologists. Thus Merril (1926) concluded that the flora of the Lesser Sundas area is composed of at least (1) an ancient, more or less original, perhaps Cretaceous (or even earlier) element, now consisting mostly of relict forms; and (2) an extensive mesophilic, lowland flora, consisting of many superimposed layers of "infiltrations" from many directions, dependent on past land connections, winds and currents, and vicissitudes of dispersal over water barriers. It is now clear that it is advantageous to consider the validity of several superimposed biogeographic divisions within the Lesser Sunda Island reptiles and amphibians as well.

REPTILES AND AMPHIBIANS.—Other than a few remarks by Kampen (1923) and Dammerman (1928), no major zoogeographic analysis of the Lesser Sundas herpetofauna was attempted until Dunn (1927a, 1927b), who concluded that all the endemics were ultimately derived from Sundaland, although their origin was remote. Regarding nonendemics, he showed that the total herpetofauna is more Asiatic than Australian. Furthermore, there are more Oriental than Australian snakes but more Australian than Oriental lizards. The latter is doubtful in my opinion. His conclusion that the herpetofauna is comprised of an overwhelmingly modern, unmodified Asiatic element and a small and rather modified Australian element is consistent with most phytogeographic studies; but I propose to show that the Australian contribution is possibly nonexistent as far west as Komodo.

The most extensive analysis of the herpetofauna is by Mertens (1930). Because it is so important, the details are discussed below. Darlington (1957) emphasized the gradual transition of Australian to Oriental reptiles and amphibians. However the distributional patterns are extremely complex, and he cited samples of families, genera, and even species that are continuously distributed from one end of the chain to the other; of genera that occur in both regions but are absent on some of the intervening islands; of genera confined to the middle islands; and of many others extending for varying distances toward Australia, with progressive subtractions increasing with distance from the Orient. Most important, he agreed with Dunn (1927a, 1927b) and Mertens (1930) that comparatively few Australian reptile groups have dispersed toward the Orient. Darevsky (1964b) followed Mertens but stressed a higher level of endemism on Komodo than previously believed (partly because of his description of several new species, some of which are shown in this paper to be invalid).

Sea barriers are obviously important in the dispersal of reptiles and amphibians through the Sunda Islands (Mertens 1928b, 1950). As shown by Inger (1966), the most widely distributed amphibians in the Philippine Archipelago are species prone to transport by man. Lesser

Sunda species he listed are *Gekko gecko, Hemidactylus garnoti, H. frenatus,* and *Kaloula baleata.* To this can be added the Komodan *Typhlina bramina, Lycodon aulicus* (Leviton 1965), and possibly *Cryptoblepharus boutonii.* These species have in all probability crossed most present sea barriers with the help of man. In addition, two turtles, the crocodile, and both *Cerberus* and *Chersydrus* are found in the marine environment, so that salt water presents no barrier to them. This leaves 27 species that successfully passed either east or west over sea barriers to reach Komodo. Of these, 14% are endemic to the Komodo area, 39% are found throughout much of the Lesser Sundas, and the remaining 47% range much beyond these islands. All of the latter are Oriental in origin (Table 5). They include several distributional patterns, with both ubiquitous and relictual elements. Wide-ranging eurytopic forms with a continuous distribution from India to within the Lesser Sundas are represented by *Boiga cynodon, Naja naja, Varanus salvator, Rana limnocharis,* etc. (Fig. 51A). Relictual species in this wide-ranging group are xeric-adapted and show a discontinuous distribution from India to the Lesser Sundas; the range of *Vipera russelli* (Fig. 51B) is typical of this pattern.[1] *Varanus komodoensis* may represent the near-terminal part of the same relictual pattern, for Hooijer (1927b) believed the range of this species to have been much broader in the past.[2] In any event, that the ancestor of this species may have ranged as far as India is very likely; apparently other Pleistocene savanna reptiles of the Lesser Sundas, such as the extinct giant tortoise *Geochelone atlas,* had somewhat similar histories (Hooijer 1971) but were extirpated by man in the last remnants of their range during the Pleistocene.

The Komodo endemics require additional comment. As Mertens (1930) pointed out, they are all related to Celebes species, or to species from areas in which the Celebes may have been an important stepping stone to the Lesser Sundas, presumably across the Saleyer "Bridge" (see Fig. 50 for approximate location), first proposed by Sarasin and Sarasin (1901) as an actual land connection and thus largely disregarded since. Of all the Lesser Sunda species also found in the Celebes, only four show no differentiation on either side of the "bridge"; all are generalized Asiatic frogs living at low elevations. Speciation is common in the remaining genera: *Crytodactylus (laevigatus* and *darmandvillei), Cylindrophis (opisthorhodus), Lycodon (florensis),* and *Oreophryne.* Most students (Dunn 1928, Darevsky 1964a) are of the opinion that *Oreophyrne* moved into this area from the east (New

[1]The presumed previously continuous strip of savanna from India to the Lesser Sundas is presently broken by the extensive tropical evergreen masif of Malaysia-Sumatra (see Steenis 1935, 1938, Champion 1936, Wood 1950, and Gentilli 1961 for further discussion of phytogeography of the pertinent areas).

[2]My current studies tend to refute this partially (MS Fossil Sunda Varanids, with R. Franz).

TABLE 5.—General distribution of probably non-human influenced Komodo area herpetofauna.

Endemic	Lesser Sundas	Wide Range
Varanus komodoensis	*Cryptoblepharus darmandevillei*	*Lepidodactylus lugubris*
Sphenomorphus schlegeli	*C. laevigatus*	*Gekko gecko*
Cryptoblepharus burdeni	*Sphenomorphus florensis*	*Hemiphyllodactylus typus*
Typhlops schmutzi	*S. striolatus*	*Draco volans*
Oreophyrne jeffersoniana	*S. emigrans*	*Mabuya multifasciata*
	Emoia similis	*Dibamus novaeguinea*
	Typhlina polygrammica	*Dendrelaphis pictus*
	Elaphe subradiata	*Psammodynastes pulverulentus*
	Cylindrophis opisthorhodus	*Boiga cynodon*
		Lycodon aulicus
		Trimeresurus albolabris
		Vipera russelli
		Naja naja

Guinea?). However, perhaps like *Rana papua* (Mertens 1930), a more centrally located area, such as the Celebes or Molucca, is most likely the distributional center (Fig. 51C). Brown and Parker (1977) showed that the most primitive species in the genus *Lepidodactylus* are found in the Lesser Sundas and New Guinea, and thus have a range similar to that of *Oreophryne.*

The presence in the Lesser Sundas of reptiles and amphibians with close relations to primitive Celebes species is probably best explained by an interchange having come about over the Saleyer "bridge" area during the juxtaposition of the Celebes and the middle part of the

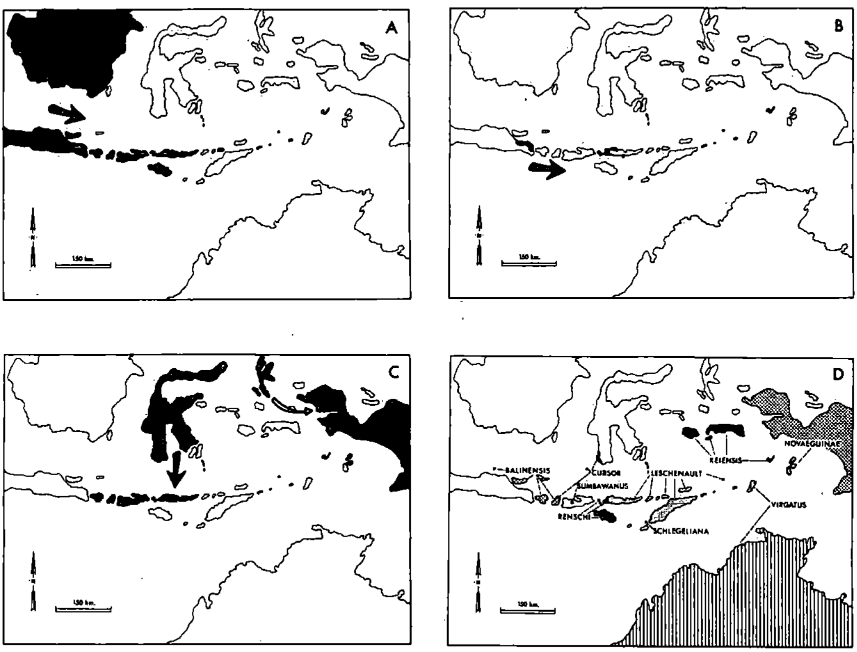


FIGURE 51.—Major distributional patterns of reptiles and amphibians in the Sunda area. (A) Eurytopic Asian organisms with wide ranges extending from India eastward through most of the Sunda area. The example shown is for *Naja naja.* (B) organisms with remote Asian origins, showing discontinuous distribution in xeric habitats at the present time. The example shown is *Vipera russelli.* (C) Distribution of the genus *Oreophryne,* an example of distribution affected by the "Saleyer Bridge" (solid arrow) into the middle of the Lesser Sundas. The hollow arrow indicates the probable immigration route into the Papuan area. (D) The distribution of the *Cryptoblepharus boutonii* complex, and example of a widely distributed littoral group with possible Australian origin.

Lesser Sunda chain in the Pliocene during compression of the arc after collision of the Sunda and Sahul shelves (Fig. 50). Thus this fauna probably evolved on the originally festooned island arc itself before diastrophism brought two originally more distant parts of the arc together, and part of the fauna was exchanged.

Another major distributional pattern is represented by those species with supposed Australian centers of origin: the scincids *Sphenomorphus florensis, S. striolatus, S. emigrans,* and *S. schlegeli;* the widely distributed littoral *Cryptoblepharus boutonii,*[1] and *Python timorensis* (Fig. 51D). If Australian, they could only have moved onto the island arc after the Miocene near contact between the two shelf areas. That the ancestral home of *Sphenomorphus* is Australian is doubtful in view of its distribution and speciation pattern coupled with the known geologic history of the area. I suspect it spread eastward in the island Archipelago to Australia and beyond. *Python timorensis* falls into the same general pattern, its presumed Australian relatives reaching that area in the Mio-Pliocene as well.

In general, the fossorial species present zoogeographic puzzles, particularly if land surfaces are required for dispersal, but the distribution of similar ecotypes in other parts of the world shows that waif dispersal is actualy fairly common, perhaps in logs or other substantial debris. *Typhlina polygrammica* is said to originate in Australia (Mertens 1930) but the evidence is meager, and it is more likely that it is an ancient Lesser Sunda endemic that was accidentally transported east into Australia by man. The remaining fossorial species (some endemic to the Lesser Sundas) also have their closest relatives in Asia.

Based on the discussion above and data in publications mentioned previously, I conclude that the herpetofauna of Komodo represents two or perhaps three means of entry: (1) a moderately ancient to fairly recent island hopping route from mainland Asia involving the Greater Sundas; (2) a fauna that moved far onto the island arc very long ago, differentiated along it, and was later partly redistributed with massive land changes in the Mio-Pliocene; and possibly (3) a very minor post-Miocene movement of Australian faunal elements as a result of Sunda-Sahul shelves contact. Although the basic features of this proposal have been previously outlined by Mertens (1930) and Dunn (1927 b), the consideration of plate tectonics affords temporal and geographic adjustments to the acknowledged dispersal patterns.

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[1]The rather unusual distribution of this largely littoral species (East Africa, Madagascar, Mauritius, and Reunion, but missing from the remaining Indian Ocean islands, and then found on the Lesser Sundas and Australia eastward) has been emphasized by Mertens (1931), who is of the opinion that some of the distributional anomally may be due to the activities of man. In fact, the distribution of the outrigger canoe is nearly congruent (Doran 1971). The range of the land snail *Rachis punctata* (Africa, Ceylon, western India, Madagascar, and Komodo and Padar) is similar (Djajasasmita 1972) and perhaps similarly explained.

A HYPOTHESIS OF THE ZOOGEOGRAPHIC DEVELOPMENT OF THE LESSER SUNDANESE HERPETOFAUNA

1) UPPER MESOZOIC.—Even though it is extremely unlikely that any modern taxa extend this far back into geologic time, it is significant that forested land surfaces were present in the Lesser Sundas at this time, irrespective of the statements of earlier zoogeographers that Komodo and environs are geologically young. In fact no evidence suggests that Komodo was ever completely submerged since this time.

2) EARLY TERTIARY.—By this time two parallel volcanic arcs moving southeastward from Asia provided land surfaces of varying sizes in the protosundanese area, some or all of which were undoubtedly colonized by primitive Southeast Asian taxa (tropical). Both the arc and the adjacent lobe of the mainland moved southeastward toward the equator on a collision course with the northeastward-moving Australian continental block (with its own unique primitive biota). In addition, one or more volcanic islands existed along the western edge of the Pacific Plate, probably with unique, primitive biota of their own, although also ultimately derived from the Asian mainland (temperate).

3) MIDDLE TO LATE TERTIARY.—By this time the Asian and Australian continental plates came into contact, with the result that the volcanic arc began to show distortion, particularly along its most eastward and southern edges. This was the first opportunity for significant faunal interchange between Australia and the Sundas, but the greatest movement (perhaps all?) was eastward, and the most significant groups involved were probably scincids, varanids, and agamids. Less important groups in terms of the number of immigrants probably included some pythons (*timorensis* group) and frogs (*Oreophryne*).

4) PLIO-PLEISTOCENE.—This very important period saw continued compression and disruption of the volcanic arc allowing important interchange of the herpetofauna of both the inner and outer arcs. Most important, the previously most eastward, most isolated portion ("protocelebes") was folded westward in such a way that it was pushed close to Flores and Komodo, allowing movement of the ancient outer Lesser Sunda herpetofauna onto the base of the arc. The juxtaposition brought about by the crustal movement is undoubtedly the basis for the "Saleyer Bridge" concept of Sarasin and Sarasin (1901), rather than the small Tukangbesi Islands between Celebes and Flores. Furthermore, the westward movement of the Celebes portion of the loop brought it close to Borneo, allowing for movement of a more modern herpetofauna onto the Celebes. Thus the westward movement of the loop allowed two very different faunas to move into the Komodo area

(an ancient ultimately Asian-derived "protocelebes" plus a more modern one from Sundaland across Borneo to Celebes and/or along the arc itself). The compression of islands of the outer and inner arcs to form the strange K-shaped islands of Celebes and Halmahera allowed further interchange of inner and outer arc populations.

It was apparently also during this period that the islands along the western edge of the Pacific Plate with their biota fused with the leading northwestern edge of the Australian Plate and formed most of New Guinea (Figs. 44-45), and when the Arafura Sea, now separating the latter and Australia, was probably formed.

The geomorphic development outlined above is applied to the peculiar distribution of the varanid lizards *V. indicus* and *V. salvator* in Figure 52 as an example of the probable development of some of the complex species distributional patterns found in this area at the present time.

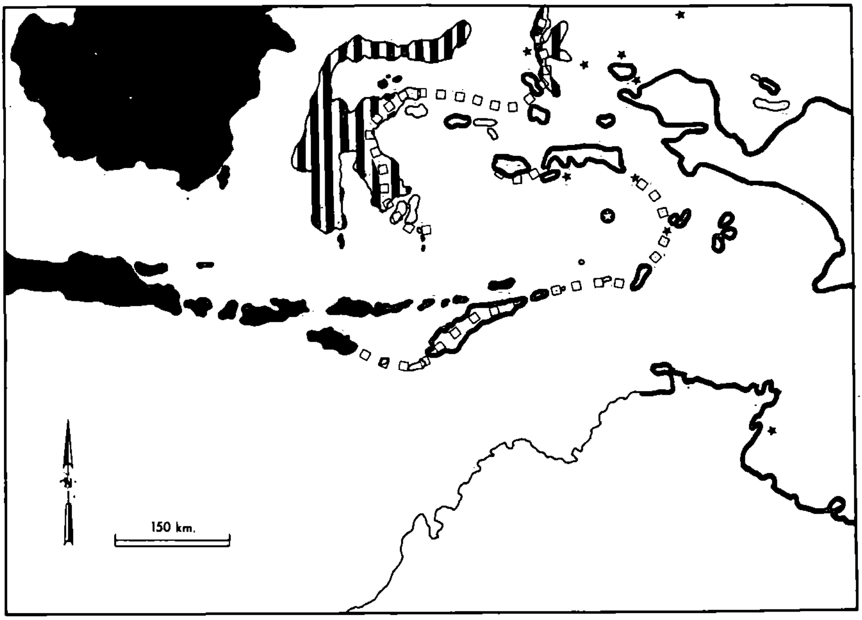

FIGURE 52.—Distribution of *Varanus* species in the Australian area. *V. salvator* has been reported from the solid islands. The range of *V. indicus* in this area is shown by a heavy border line. Those islands from which both have been reported are indicated by vertical bars (distributions based on Martens 1942). Note how *V. salvator* is only found west of the outer band of the double volcanic arc (hollow squares, see Fig. 50 for details), whereas *V. indicus* is found from this band eastward. The only exception (star) is in the Banda Islands on the inner band. Both species are found on the same islands only when the islands are comprised of both inner and outer bands of the volcanic arc (see Fig. 50).

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MSS must be submitted in duplicate (please no onionskin) and satisfy the following minimal requirements: They should be typewritten, double-spaced (*especially* tables, figure captions, and "Literature Cited"), on one side of numbered sheets of standard (8-1/2 x 11 in.) bond paper, with at least one-inch margins all around. Figure legends and tables should be typed on separate sheets. All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All illustrations should have a cover sheet. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lower case letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for illustrations is 8-5/8 x 14 in (twice typepage size); illustrations should not be less than typepage width (4-5/16 in.). Designate the top of each illustration and identify on the back with soft pencil by author's name, MS title, and figure number.

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