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New Flying Lizards and Predictive Biogeography of Two Asian Archipelagos

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NEW FLYING LIZARDS AND PREDICTIVE BIOGEOGRAPHY OF TWO ASIAN ARCHIPELAGOS

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ABSTRACT. Two new flying lizards, genus *Draco*, are described from Sangihe Bank, Far Moluccas, Indonesia, and Batanes Bank, Typhoon Islands, Philippines. General species-group level characters of *Draco* are described and depicted. The two Banks and archipelagos are compared to the Lesser Antilles, strikingly similar in physiography. *Draco* is compared to *Anolis* and similarities in patterns of distribution and evolution are predicted.

INTRODUCTION

> *We should look for knowledge where we may expect to find it . . . .*
>
> *Then came all legendary monsters. . . , noisome brutes with horny scales. . . , uncouth primeval things, and winged serpents.*
>
> W. Somerset Maugham (1908)

Three remarkably similar tropical archipelagos connect very large oceanic islands to each other or to continental shelves. All support remarkably similar lizards.

In the New World, the Lesser Antilles extend from close to the continental shelf of South America, and the large coastal island of Trinidad, nearly to the Greater Antillean Puerto Rico Bank. The Far Moluccas extend from close to the huge island Bank of Sulawesi (Celebes) nearly to the Greater Philippine Bank and the large island of Mindanao. The Typhoon Islands extend from close to the continental shelf of Eurasia, and the large coastal island of Taiwan, nearly to the Greater Philippine Bank (Fig. 1). All three archipelagos are roughly Y-shaped, or doubled for part of their length. All are of volcanic origin. All have at least some islands on some banks with oceanic limestone at elevations too high to be accounted for merely by Pleistocene interglacials. Thus, in each case, some of their islands and banks probably date from at least the Miocene. The three archipelagos are diagrammed in Figure 2.

Darlington (1957:516–517) first suggested the biogeographic analogy of the Philippines to the Antilles. He had clearly in mind the resemblance of the larger, main Philippine islands to the Greater Antilles. In my analogies to the Lesser Antilles, Mindanao on one hand, Luzon on the other, become the counterparts of Greater Puerto Rico.

The name "Far Moluccas" is herein coined because no name for the group collectively currently exists. Indonesia possesses Miangas and the Kawio, Sangihe, Nenusa, and Talaud island groups, but these names do not conform to banks. The Sarangani Bank is within the Philippines.

There is no prevailing wind in the Far Moluccas. Trades often hold sway, but equatorial westerlies often generate south winds at two to five degrees north latitude. Still air—the doldrums—often overrides any surface wind. The humidity is maximal. As in the Lesser Antilles, clouds tend to lie at about 650 m. These create montane rain forest and moss forest or "elfin woodland" zones. There are no arid areas comparable to the rain

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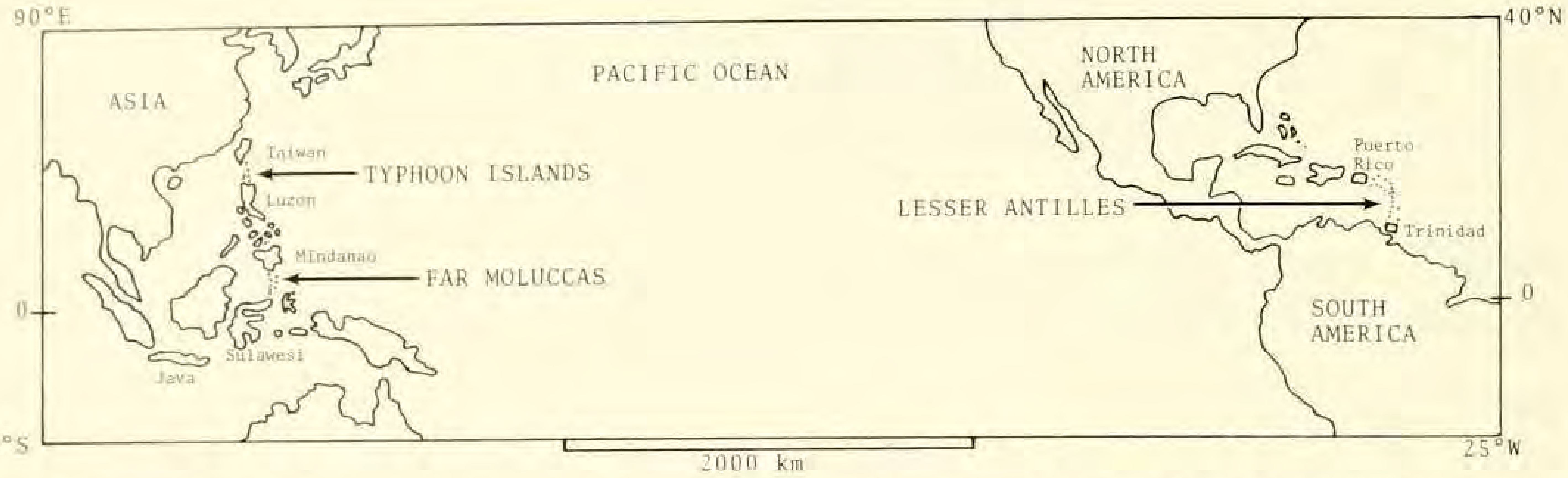


Figure 1. A portion of the world indicating positions of the three compared archipelagos and some other place names mentioned in the text.

shadow zones of the high, montane, cloud-barrier islands in the Lesser Antilles: the near-constant rain and inconstant winds preclude them.

The name "Typhoon Islands" is herein coined as well because no prior name for the whole group exists. Ten of 12 banks are within the Philippines. Five, centrally located, make up the Province of the Batanes. Five, in the South, are collectively called the Babuyans and assigned to Cagayan Province, Luzon. Two banks belong to China. The larger of these, Hungtou Hsu Bank, harbors the large island of Lanyu, or Botel Tobago, or Orchid Island (Ota, 1987); the other is tiny Lu Tao.

The Typhoon Islands lie closely congruent with the principal pathway of the greatest of Earth's cyclonic storms – Pacific typhoons – and span Luzon Strait from the oceanic Philippines to just east of the continental shelf island of Taiwan, China. Much of the warm surface water of the tropical Pacific passes through the Far Moluccas, the Celebes, and Sulu Seas, and forms a huge clockwise gyre in the South China Sea. This water exits again into the Pacific through Luzon Strait. Most of the tropical Pacific's surface water is deflected northward off New Guinea and the Philippines. The present island chain lies where the confluence of these two streams forms *Kuro Siwo*, the Japan (or Black) Current. The Pacific Ocean and South China Sea have different tidal regimes that dramatically affect water movement in Luzon Strait.

To the east of the Typhoon Islands the open Pacific extends some 9,500 km: the greatest fetch of the northeast Trades on Earth. Immediately to the northwest begins the huge Eurasian landmass that generates the seasonal wind patterns called monsoons. These often disrupt or cancel out the strongest Trades. In conflict and concert, these vast forces of wind and water make this island realm the most tempestuous in the tropical world. A concise description of these forces in humanized terms is provided by Gonzales (1966).

All three archipelagos have depauperate highly endemic herpetofaunas in keeping with their oceanic island histories. All have surely garnered their herpetofaunas by overwater "waif" dispersal. The two Asian archipelagos are little-known, but the Lesser Antilles may fairly be said to have provided a disproportionately large share of the data from which biogeographic and ecological theories have been forged.

If the Lesser Antilles today are well-known and well-studied, can we use this knowledge to predict anything of the herpetofaunas of the Far Moluccas and Typhoon Islands? Has biogeography, with its descendent ecological and evolutionary theory, become a predictive science, or is it to remain strictly descriptive, requiring novel sets of postulates

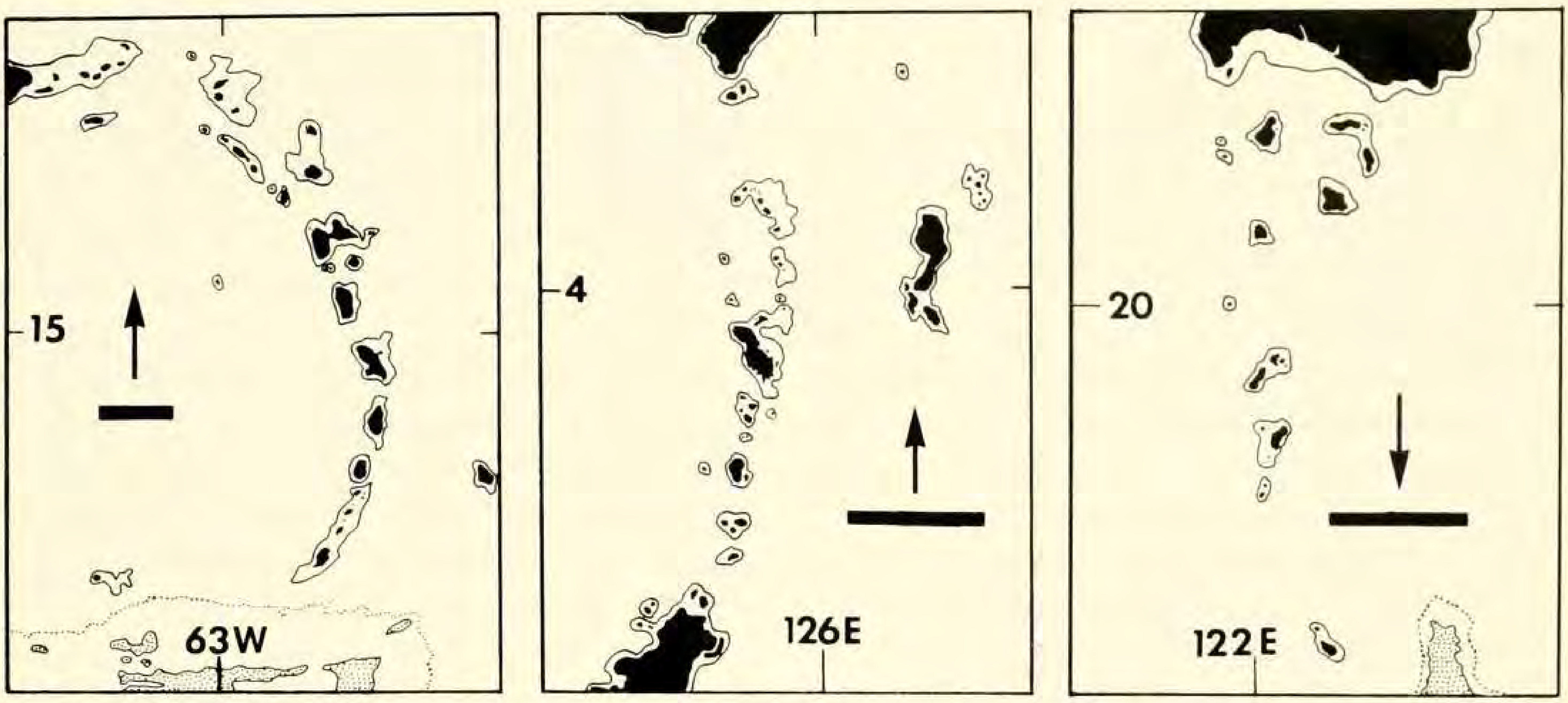


Figure 2. Three archipelagos, left to right: The Lesser Antilles, the Far Moluccas, and the Typhoon Islands. Lines indicate oceanic island banks; the islands are black. Dots indicate continental shelves and lands on them. Bar, in each case, equals 100 km. Longitude east or west of Greenwich is indicated at bottom; a latitude north of the equator is indicated on left. All are shown in mercator projection. Arrows point north. Note the Typhoon Islands are depicted upside-down to enhance comparison.

case by case?

Critical to understanding Lesser Antillean biogeography is the "bank" concept discussed below. Separate banks have at least partially endemic herpetofaunas. Present-day islands on the same bank have weakly differentiated or essentially identical herpetofaunas (Williams, 1969; Lazell, 1972). I shall herein transfer the bank concept, and my notions of its biogeographic relevance, to the Far Moluccas and Typhoon Islands.

My comments on *Anolis* and Lesser Antillean biogeography and physiography are distilled from Lazell (1972). *Anolis* are the most conspicuous and abundant members of the Lesser Antillean herpetofauna. Diurnal, scansorial lizards, they are ornamented with extensible fans and (often) bold patterns and bright colors.

I have made three forays into the Asian archipelagos and found new species of *Draco* each time exactly where predicted. The first new species, *Draco biaro*, has been described (Lazell, 1987a). Two more require description now, and it is time to codify my predictions. Some of the Asian banks and their islands are very difficult of access and a few are dangerous. However, I believe the opportunities for discovery they present are nothing short of wonderful.

Like trunk and big tree *Anolis*, *Draco* are conspicuous, diurnal, scansorial lizards. They are often brightly colored and boldly patterned. Like *Anolis*, they have an extensible, median throat fan or dewlap. In addition, *Draco* have four other fans: a pair of lateral neck lappets and the huge patagia, or wings, supported on thoracic ribs. The patagia are important in courtship and combat displays, as is the throat fan. *Draco* tend to perch high on tree trunks, often head up. They escape by climbing up in a rather graceless, saurian gait. They seem reluctant to enter crowns of trees. They may be selected against doing so by crown-dwelling, lizard-eating snakes.

Draco usually launch and glide when pursued toward tree crowns. I have the impression that they never go down by any method other than gliding, but there are likely exceptions I have not witnessed. It is said by local people that severe storms kill off large numbers of *Draco*. This may limit them on, or exclude them from, small islands.

METHODS

Because I explicitly adopt the view that *Draco* are *Anolis* analogs, I expect the same approaches to study and the same sorts of characters to prove successful in resolving species problems in *Draco*. The first and most fundamental method derives from the exhortation of Williams (1959): these lizards ". . .must be known intimately – anatomically, ecologically, ethologically – . . . if the many puzzles the genus poses are to be solved." This means simply that the animals must be known in life, preferably in the field, under natural conditions. Historically, this view derives from the industry of Samuel Garman in the Lesser Antilles. Barbour (1914) noted: "At first, certain of the so-called conservative zoologists objected at the making of such a large number of new species. Time, however, has justified Garman's work. . ." This view finds an even earlier root in the efforts of Philip Gosse in 1844–46 in Jamaica, as reported by Underwood and Williams (1959).

The clear picture of *Draco* systematics developed by Inger (1983) at Nanga Telakit on Borneo depended on knowledge of the animals in life. Inger could not have derived it from examination of preserved museum specimens alone, but considered coloration, patterns, behavior, and ecology.

The difficulty for systematists is codifying field knowledge of animals as characters that lead the field biologist to recognize and rank taxa and that other systematists can utilize. *Draco* represent a novel challenge because no one has previously considered a number of taxa from distant portions of the generic range in life. I have now come to know *Draco* on Hainan Dao, China, in Indonesia, and in the Philippines. I have examined hundreds of museum specimens in the light of the generic revisions provided by Hennig (1936), Musters (1983), and Inger (1983). It is apparent that some characters thought trenchant and diagnostic at high levels, like number of patagial ribs and presence of a tympanum, vary within some very small demes and are never diagnostic at any level higher than local species. Color characters, virtually unknown to the previous revisors except as patterns retained in alcohol or in life at local sites, are the most useful for distinguishing forms. Extrapolating from *Anolis*, we might expect morphologically similar species, difficult or impossible to distinguish on mensurable or meristic characters, to be quite distinct in colors. That is exactly what Inger (1983) found at Nanga Telakit, Sarawak, Borneo. That is also what Taylor (1922) reported on Mindanao, but recent revisors (including Inger) did not credit his observations (but see Ross and Lazell, 1991).

The coloration and pattern of the patagia are especially critical. I have diagrammed frequently observed patterns and components so as to codify an applicable vocabulary (Fig. 3). Some require further comment.

Costate patterns typically involve enlarged, distinctively colored scales in zones centered along the patagial ribs. Intercostate patterns, just the opposite, involve pigmented skin in the membrane expanses between the ribs.

Reticulated patterns may extend over the entire patagium or be confined to smaller areas on it. For example, one sees reticulated intercostate patterns.

Radials are notable features of most *Draco* patagia. They do not truly radiate from any point, but arise more or less antero-medially and extend, often bifurcating one or more times, postero-distally. It is frequently difficult to determine if the scales in the radials are actually enlarged or merely appear so because they are distinctively colored. Frequently pattern components, sometimes extending from trunk figures onto the proximal patagia, seem to be becoming concentric elements, but fragment into spots or short bars centered along the radials.

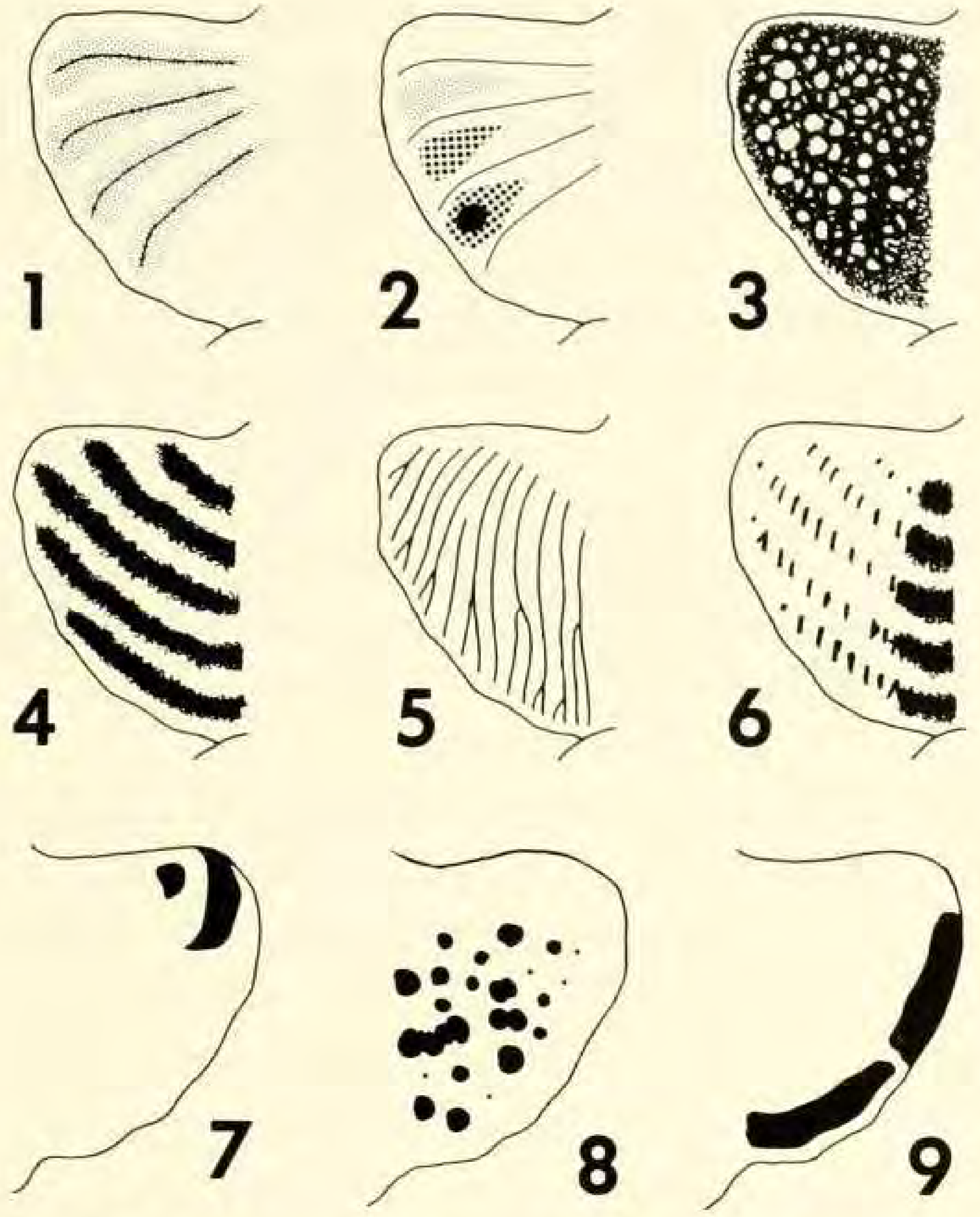


Figure 3. Diagrammatic patagia of *Draco*. Top is anterior. Patterns, in dorsal view, include: 1, costate; 2, intercostate (ocellate posteriorly); and 3, reticulate. Pattern components, in dorsal view, include: 4, concentrics; 5, radials; and 6, concentrics picked up on radials. Pattern components, in ventral view, include: 7, bracket; 8, spots; and 9, marginal (anterior) and submarginal (posterior) zones.

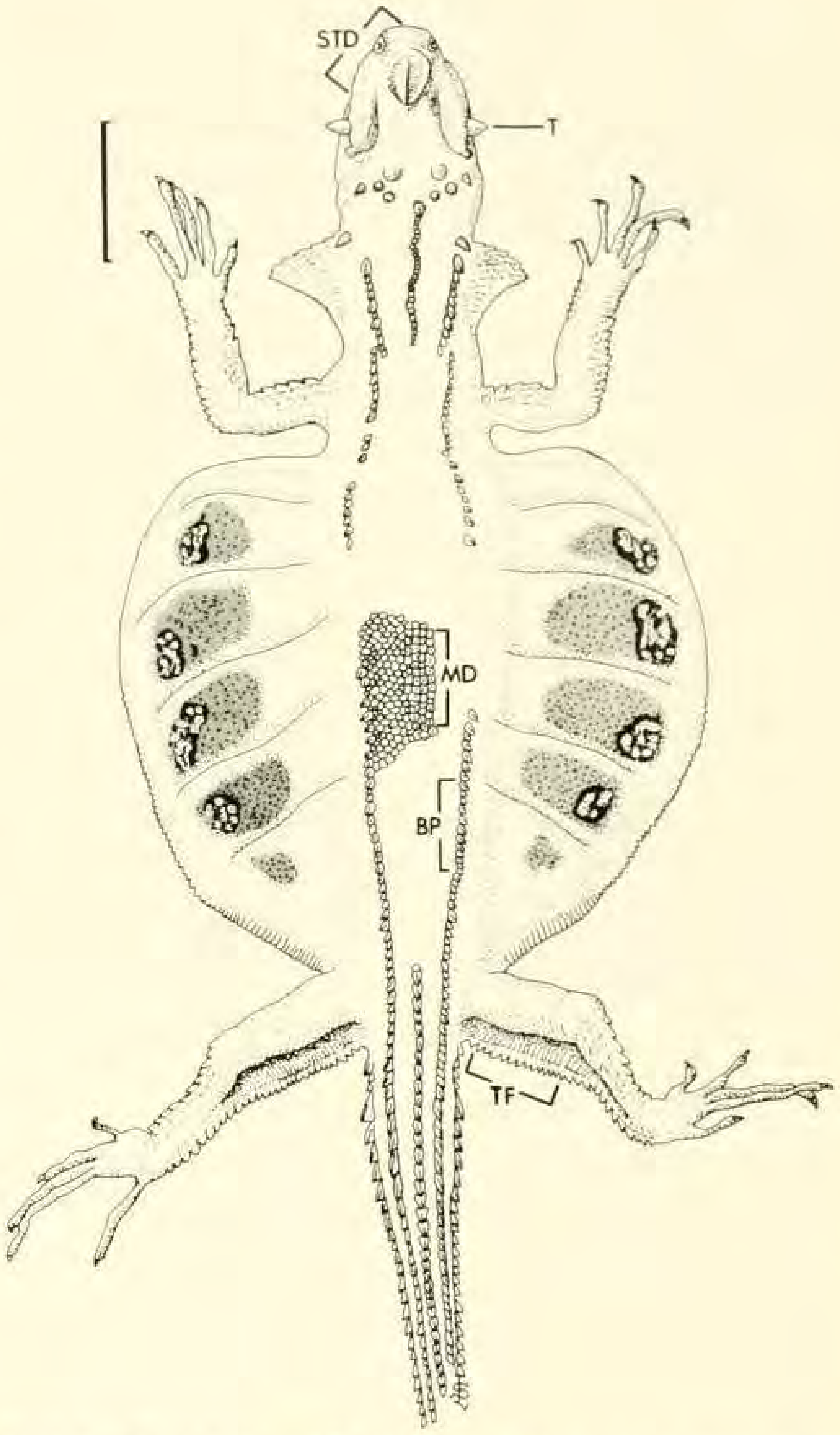


Figure 4. Dorsal view of *Draco everetti* showing measurements, scales, and counts of systematic value. STD, standard distance: tip of snout to center of eye. T, supraciliary thorn. MD, middorsal scales counted in STD. BP, basipatagial scales counted in STD beginning at level of last rib. TF, thigh fringe scales in STD. Bar, upper left, is one cm. (From Ross and Lazell, 1991.)

The ventral patagia are usually quite differently colored and patterned from their own dorsal surfaces. Of course, in front of strong light, the dorsal components may show through the membranes. The reverse is also true, though usually less noticeable. The pattern components I have depicted ventrally in Figure 2 may also occur dorsally. Sometimes ventral elements may underlie and correspond to dorsal elements, and vice versa.

The bracket pattern often encloses other markings or distinctive colors. Brackets may begin at the patagial margin and become submarginal posteriorly. There are often marginal or submarginal spots, bars, or zones along the patagial borders.

I discuss my use of standard distance counts in Ross and Lazell (1991, and references therein). Briefly, these enable scale count and size comparisons from various different areas of the body and therefore seem more useful than longer counts which may confound real differences. Places where I usually make standard distance (STD) counts are shown in Figures 4 and 5. Juveniles are not used in STD counts because of their disproportionately short snouts.

The tails of *Draco* may bear several sorts of scales of disparate sizes, even on the same lizard. These are easily quantified by counting the number of scales on different aspects of the tail contained in the length of the extended lower leg (Fig. 6). Statistical significance of diagnostic scale counts has been

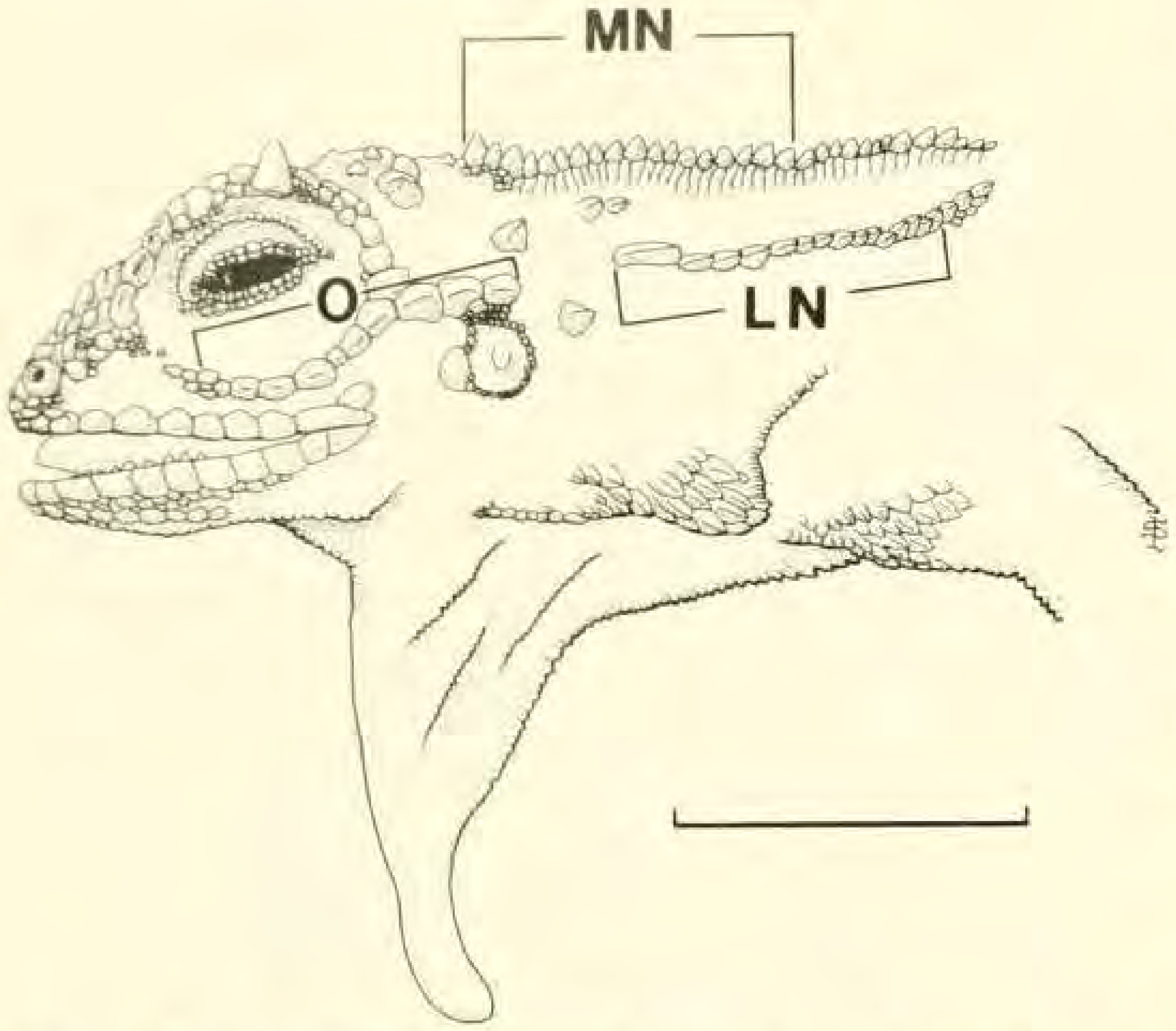


Figure 5. Head of *Draco everetti* showing scale counts made in STD. O, oculotemporals. MN, middorsal nuchal crest scales beginning at first enlarged scale. LN, lateral nuchal crest scales beginning at first enlarged scale and extending for the minimum count of contiguous scales. Bar, lower right, is one cm. (From Ross and Lazell, 1991.)

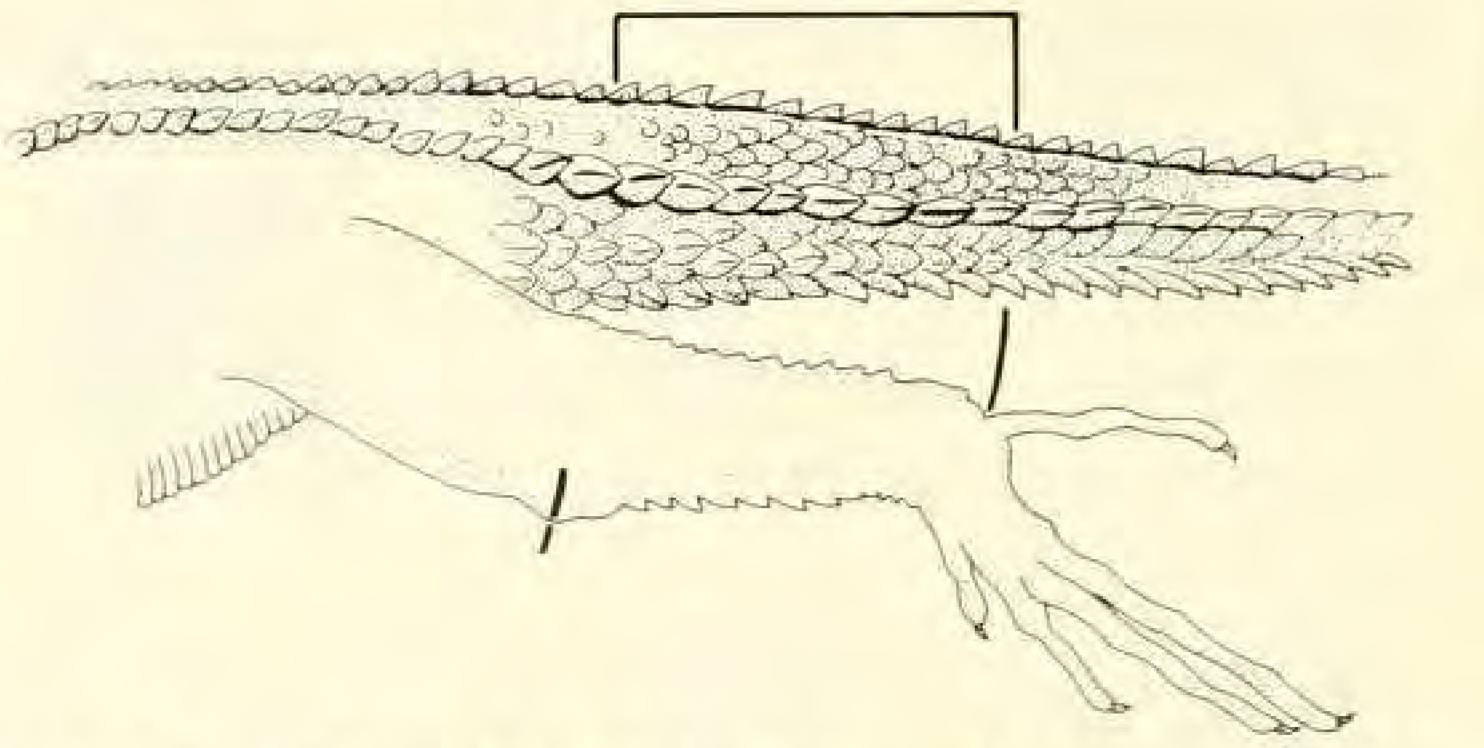


Figure 6. Side view of tail of *Draco everetti* showing method of counting various sorts of caudals and crest scales in the length of the extended lower leg. In this specimen the length of the lower leg is one cm. (From Ross and Lazell, 1991.)

evaluated with student's T test.

Draco, like *Anolis*, often change colors and even patterns. This ability to make physiologically controlled color changes is direct evidence of the great adaptive importance of color to the living lizards (Lazell, 1967). In describing colors I try to use familiar terms and eschew various rigorous standards simply because changes in shade, darkness, or pallor may occur both frequently and rapidly.

My views of evolutionary systematics are derived directly from Simpson (1961) and codified in Lazell (1972, and works cited therein). They would seem to bear some repetition here in light of the chaotic, mutually exclusive, and contradictory systematic views promulgated by various warring factions of biologists today. I seek to classify organisms on the basis of relationship.

Relationship, however, is not a property of organisms. Relationship cannot be measured, weighed, or quantified. Relationship is imponderable and can only be subjectively assessed. I use mensurable and meristic characteristics of organisms in attempting to assess relationship. I use colors too, and often prefer them, giving them great weight. I use indirect evidence about organismal lineages. I use inferences about behavior, ecology, and lineage histories.

I embrace the notion of Darwin (1873): "The periods during which species have undergone modification . . . have probably been short in comparison with the periods during which they retained the same form." Evolutionary rates vary. They vary between lineages at the same time, between lineages at different times, and within lineages at different times. Gould (1982, and works cited therein) has virtually built a career around the celebration of spectacularly different evolutionary rates, quite without acknowledging his debt to Darwin (but see Dawkins, 1987:229–230, 236, and 240–252). My study of island populations and patterns of differentiation beautifully demonstrates to me – albeit indirectly – the reality of different evolutionary rates.

Because I know relationship is imponderable and evolutionary rates are variable, I reject the cladistic notion that relationship is precisely the inverse of lineage age. I know new species have evolved in isolation while older species have retained older parapatric interbreeding subspecies. I am not the least bit troubled by the existence of a relatively young taxon at a higher rank than a relatively old one. Insular patterns of dispersal and evolution necessitate that many species will become "paraphyletic" while spawning other, new species. Some of the latter might evolve into novel genera without notification to the folks back home, so to speak. Evolution in an isolated lineage descended from one member of a pair of closely related lineages need in no way alter the relationship of members of that pair to each other.

Simply put, two parapatric, intergrading subspecies may remain exactly that, while the isolated descendent of one of them proceeds to evolve into a new species somewhere else. I see this phenomenon frequently, for example in the members of the *Anolis cristatellus cristatellus, A. c. wileyae*, and *A. ernestwilliamsi* complex in the Antilles (Lazell, 1983).

Believing that evolutionary relationship is precisely equal to the inverse of lineage age makes no sense to me.

Hennig (1936) was appalled at the proliferation of *Draco* species being described from small islands. His references are obscurely cited but fortunately available in Jacobs (1983). Hennig (1936, fig. 7, p. 163) used some color characters, notably deriving concentric patagial groups from attendant trunk markings. I do not find this method particularly useful because patagial markings may be quite independent of trunk pattern. Although he acknowledged the importance of color in species recognition, Hennig proceeded to synonymize many quite distinctively patterned, widely isolated forms.

My view of insular forms is in essence diametrically opposed to Hennig's. I am wholly convinced, by the arguments of Mayr (1940, and numerous since), that geographic isolation results in speciation. The second law of thermodynamics precludes isolated populations from remaining genetically similar. Even in the absence of strong selection pressures, the complex processes of molecular replication guarantee entropic, divergent drift. As long ago elucidated by C. C. Li (1955) and others, genetic differences are simply never neutral in the face of selection. At the very least, numerical advantage results in ultimate populational sweep. In fact, selection pressures on the colonists of oceanic islands are normally great and disparate.

The processes of overwater waif dispersal and irregular colonization – some of those biological and historical factors celebrated by Lack (1976) – necessitate different islands operating as very distinct evolutionary theaters. When a group of forms presents a pattern of regular, progressive change in an archipelago, it may be appropriate to regard those forms as expressing geographic variation in one species (Wright, 1941, 1943; Lazell, 1964a, 1964b; Gould and Paull, 1977).

Quite opposite situations may obtain. For example, geographically proximate forms may be more different from each other than one or the other is from a more distant population (Gould and Paull, 1977:20–21). This may be interpreted as classic character divergence resulting from failed invasions and, therefore, as clear proof of full species level (Williams, 1969; Lazell, 1972:103–104; Goodyear and Lazell, 1986).

I will classify absolutely distinct, geographically isolated (dichopatric) forms as full species unless I see indicative evidence that they fit into a larger pattern of geographic variation in a more widespread species (Lazell, 1972:15–16).

THE FAR MOLUCCAS

Figure 7

There are 16 banks between Sulawesi and Mindanao. In addition, the Nain Bank lies just off the northwest side of the tip of the Minahasa Peninsula. I visited Nain and Mantehage, the largest islands on this Bank, in 1986. People there knew flying lizards, *chichak terbang*, but I could secure no specimens. In light of what I now know about the

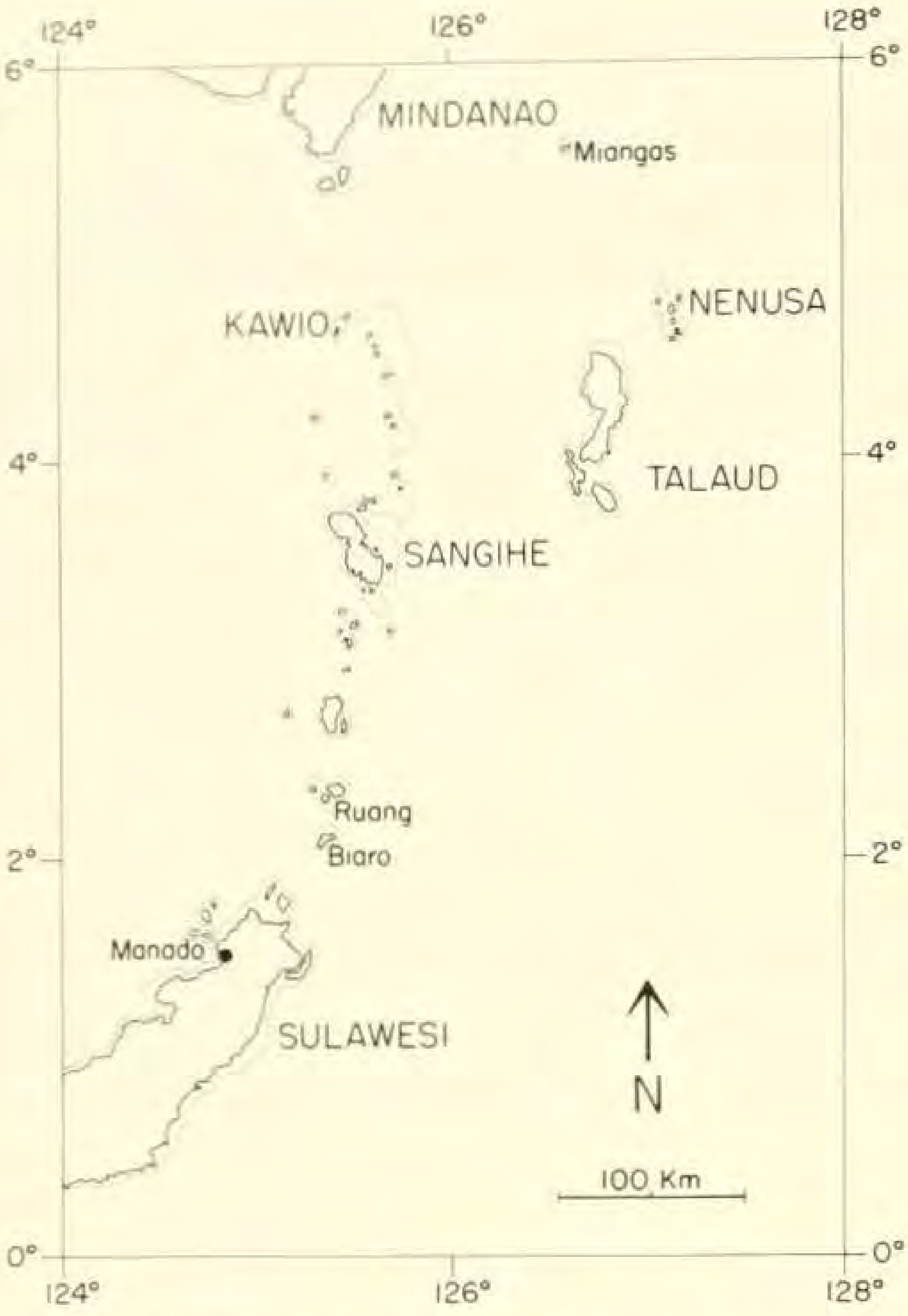


Figure 7. The Far Moluccas, between Mindanao, Philippines, and Sulawesi, Indonesia. Bank edges, at the approximate sea level during a glacial maximum, ca. 100 m below present, are dotted. (Modified from Lazell, 1987b.)

local apparent absence of *Draco* in some areas, I believe Nain Bank should be revisited.

At the present time it is reportedly unsafe for Americans (or other foreigners) to attempt going to the Sarangani Bank, Philippines. Some of the Indonesian islands, like Miangas and the remote Kawios, are hard to locate from the open sea in a small boat. Some of these small islets may lack *Draco* (as Aves and Saba lack comparable *Anolis* species in the Lesser Antilles). I note that Miangas, however, looks analogous to Sombrero, and that remote cay supports a generalized trunk perching *Anolis* (with no trunks to perch on). Miangas certainly supports palm trees, for Magellan called it "Palmas" (Morrison, 1974).

After a two-year absence, I returned to the Far Moluccas in March, 1988. Despite inclement weather, 37 specimens of a strikingly distinctive new *Draco* were collected on Sangihe.

Draco caerulhians sp. nov.

Type. MCZ 173321, Fentje Kodong coll., 20 March 1988 (Fig. 8).

Type-locality. Manganitu, Sangihe, Indonesia. See Figure 9.

Diagnosis. A small *Draco* (males to 74 mm, females to 82 mm, SVL) with five ribs in the patagium and a well-developed tympanum. Scales small: 14–18 (av. 16 ± 1.2) middorsals and 12–18 (av. 15 ± 1.5) midventrals in STD; 20–25 (av. 22 ± 1.6) paired dorsal caudals in length of extended lower leg; 8–12 (av. 10 ± 1.1) postrostrals. No lateral nuchal, basipatagial, or caudal crests; no spike-like or thorn scales. Patagia concentrically patterned; male dorsal patagia of somber brown and dark gray-brown marbling; female dorsal patagia of rich ochre-yellow to orange-brown and contrasting dark gray-brown marbling. Male throat fan and ventral lappets yellow.

Description of the Type. MCZ 173321 is an adult male 72 mm SVL, with a 129 mm tail (179% of SVL). STD is 7.9 mm, 11% of SVL. Twelve scales border the rostral posteriorly. There are 16 smooth middorsals, 15 keeled midventrals, and 18 oculotemporals in STD. The midnuchal crest consists of six blade-like scales anteriorly declining to tectiform scales rapidly; it is not especially prominent. There is no lateral nuchal crest, but a few scales in a small patch about one STD posterior to the orbit are enlarged; the biggest is blunt and not higher than long. There are no enlarged basipatagials.

There is no caudal crest. The middorsal caudals are the largest, paired, and keeled. There are 23 in the length of the extended lower leg.

The throat fan is bluntly hooked, about 17% of SVL, and about 90% of head length.

The adpressed hindlimb just reaches the

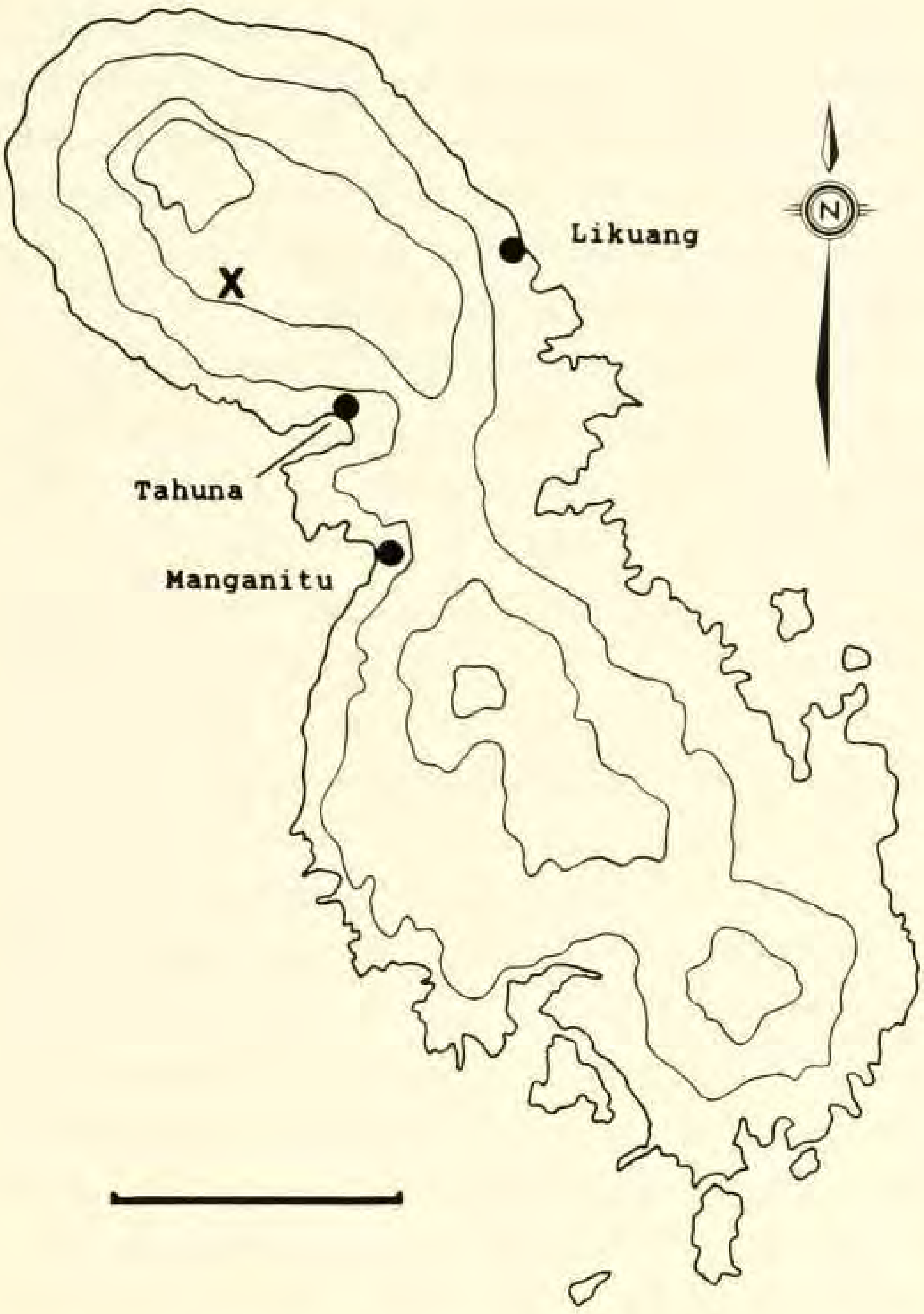


Figure 9. Sangihe, Far Moluccas. Contours approximate 200, 500, and 1,000 m but are drawn from a Bartholomew map of scale 1:5,000,000, and thus are not accurate. Localities where *Draco caerulhians* was collected are named and dotted. X marks the spot for RMNH 24252. Bar, lower left, is 10 km.

axilla. The nasal turrets are oriented dorsolaterally. There are five ribs in the patagium.

Coloration in life was gray-brown with a boldly contrasting head and neck pattern but somber patagia. Dorsal nape and midnuchal crest were marked with sooty black set off by tan-white. The light color shaded to ochre-yellow lateral nape spots, facial spots, and marbling. The chin was blue-gray with yellow spots. The blue-gray extended onto the base of the throat fan where it blended with yellow to produce green tones and dissipated distally into gray streaks. The throat fan was predominantly bright lemon yellow.

The lappets were dark gray-brown spotted with ochre dorsally, and rich, deep yellow ventrally, edged with dark blue-gray.

The chest was bright yellow shading to cream-gray on the abdomen. The underside of the tail was ash-gray and contrasted with the abdominal color.

The dorsal patagia were chocolate brown with about 15 ashgray radials broken by five concentric bands of sooty marbling. The ventral patagia were pale blue-gray with soot-black margins and two irregular sooty blotches roughly corresponding to dark dorsal concentrics.

Color change was dramatic but affected the head and trunk, not the fan or patagia. In the lightest, at-rest condition, described above, the dorsal pattern consisted of forward-pointing gray V shapes set off by lighter gray-brown. In the dark, disturbed condition, the pale tan-white of the nape became rich fawn-brown and the dorsal pattern emerged as sooty diamonds.

When caught, this individual gaped, displaying spectacular, brilliant blue gums and inside lower lip. Blue extended over the roof of the mouth. The upper lip was bright, opaque white. The tongue was rather translucent flesh-pink with a smoky-gray tip.

Male Paratypes. A total of 21 collected at Manganitu by F. Kodong, J. Rimbing, R. Tahulending, and J. Lazell on 20 March 1988: MCZ 173319, 173323, 173325, 173327, 173329, 173331, 173334–50. One of these, MCZ 173342, 73 mm SVL, has been donated to the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH, #25764) after examination.

Adult males measured 55 to 74 mm, average 64 mm, SVL. Seemingly complete tails are 177–185% (av. 181%) of SVL. STD is 11–12% of SVL in all adults. Two juveniles, MCZ 173339–40, both 48 mm SVL, have disproportionately short snouts.

Squamation is similar to that of the type. There are 8–12 (av. 10) scales bordering the rostral posteriorly. There are 14–18 (av. 16) smooth middorsals and 14–18 (av. 16) keeled midventrals in STD. In all, the oculotemporals are weakly differentiated from the other head scales; there are 15–20 (av. 18) in STD. In all, the midnuchal crest begins as a few blade-like scales and diminishes rapidly to low, tectiform scales.

In all, there are from one to a few enlarged scales on the lateral nape about one STD posterior to the orbit. The largest of these is rarely higher than long and never forms a prominent spike or thorn.

A few individuals (e.g., MCZ 173327, 173339–40) have one to three slightly enlarged basipatagials, but these do not form a crest.

The caudals are always low and keeled. The middorsal pair are the largest. There are 20–25 (av. 23) in the length of the extended lower leg.

The throat fan is always bluntly hooked and short, 82–91% (av. 88%) of SVL.

The nasal turrets always orient dorsolaterally and there are invariably five ribs in the patagium. The adpressed hindlimb usually reaches the forearm insertion, but may fall a little short of it.

The tympanum is always differentiated, much larger than the surrounding scales, and its diameter is more than 10% of STD.

Coloration in life was basically similar in all males, including the juveniles, MCZ 173339–40. MCZ 173327 had the dullest facial coloring, approaching simple gray and white. MCZ 173331 had the brightest green throat fan tones, green tones where his yellow facial spots blended with the blue-gray ground color, and the brightest yellows. MCZ 173325 was the darkest specimen seen. Even in his lightest extreme he had an ochre chest, bold, dark gray streaks in the bright yellow throat fan, and the chin and head very dark gray spotted with orange-yellow.

The balance of warm brown and darker, sooty-color on the dorsal patagia shifts. Some agreed with the type in having the lighter color predominant and the darker appearing as concentrics upon it. Others, like MCZ 173329, had largely sooty patagia upon which brown appeared as concentrics. The lighter color (brown) corresponds to the dorsal trunk ground color and the darker (sooty) emanates from the V-shaped or diamond dorsal trunk markings.

The ventral patagia vary in amount and intensity of dark marking. Most had the bold, near-black margin described for the type and two to four irregular sooty blotches in a roughly concentric pattern on the pale gray-blue ground color. In several, the dark markings were slate-gray and one, MCZ 173344, had very reduced, slate-gray ventral concentrics.

In all, the throat fans were largely lemon yellow, brightest distally. Some showed little proximal gray streaking (e.g., MCZ 173329). The lappets varied from lemon yellow to deep sulfur-yellow ventrally with blue-gray to sooty borders.

All gaped when caught, showing brilliant blue and white.

Female Paratypes. Eight females were also collected at Manganitu by F. Kodong, J. Rimbing, and J. Lazell, 20 March 1989: MCZ 173320, 173322, 173324, 173326, 173328, 173330, and 173332–3. One of these, MCZ 173328, 70 mm SVL, is now RMNH 25763.

Females average larger than males: 59–82 (av. 73) mm SVL. The difference is statistically significant at the 95% level of confidence. Their tails are 171–181% (av. 178%) of SVL. I could detect little difference in squamation between the sexes. The females had 14–17 (av. 16) middorsals in STD and 12–16 (av. 14) midventrals in STD. The count for midventrals is lower than in males but not significantly different. The oculotemporals are similar, 15–19 (av. 18) in STD. There is a slightly enlarged lateral nape scale, usually smaller than that seen in males. The midnuchal crest is less developed in females; it consists merely of enlarged dorsal granules.

The caudals of females are like those of males, 20–25 (av. 22) in the length of the lower leg. There is no extensible throat fan in females. The loose skin of the throat is gray, usually with lighter and darker tones in longitudinal streaks. The tympanum is always differentiated and its diameter is at least 10% of STD. In two, MCZ 173324 and 173333, the tympanic border is encroached by incomplete sutures from adjacent scales, as in Musters (1983, figure 2b, p. 5).

The nasal turrets and five patagial ribs are as in males.

The adpressed hindlimb usually falls a little short of the forelimb insertion, but may reach it in MCZ 173328 and 173332.

This species is strikingly dichromatic. The females are much more brightly colored and boldly patterned than the males. In life, females averaged lighter, warmer brown than males; their dorsal trunk markings were more elaborate. In the boldest condition, six sets of transverse markings are apparent. The anteriormost is similar to the male's nape pattern but colored in soot-gray and brown. The remainder were roughly diamond-shaped, sooty markings with brown interiors middorsally. The third, on the back of the chest, elaborated to wavy, scalloped bands extending laterally to correspond with a bold upper arm band. The fourth, at midbody, extended onto the patagia (see below), as does the fifth. The sixth is on the tail base. Between the bands, from third to sixth, were bold ash-gray spots. Anterior to the third the spots are irregular and indistinct. Posterior to the sixth the tail was simply banded in shades of brown.

The head and chin were patterned in beige to golden brown and chocolate to gray-brown. The chest was cream-color, usually marked with irregular gray spots or marbling. The belly was near-white and the underside of the tail was a slightly contrasting shade of gray.

Dorsally the patagia were rich ochre-yellow to orange-brown with four to six irregularly concentric zones of sooty to chocolate brown. Or, one may interpret the pattern as dark with light, yellow to orange, concentric zones. The light color was an intensified extension of the dorsal ground color; the dark was elaboration and branching from the dark trunk figures.

Ventrally the patagia appeared largely yellow: usually bright, deep yellow to ochraceous orange. Concentric zones of gray-brown marbling terminated distally in sooty blotches which often amalgamated to form a sooty margin.

Among females, MCZ 173320 had the most brilliant ventral patagia: rich orange-yellow. MCZ 173324 had the dullest, with dark dorsal patagial color showing through to subdue and gray the yellow tones.

The blue and white gape is constant and striking.

A female paratype, MCZ 173322, is depicted in Figure 8.

Additional Specimens. Specimens from two other lowland localities were collected by Kodong and Lazell and one was secured on the flank of the highest peak, Gunung Awu, by Dr. Frank Rozendaal.

Two males and a female from Tahuna, MCZ 173314–6, captured 18 and 19 March 1988, were indistinguishable from most topotypic Manganitu specimens.

A pair, MCZ 173317–8, from Likuang on the opposite, eastern coast, are very similar too, but had the most ovate middorsal figures, less diamond-shaped than is typical. Also, this male, MCZ 173317, was the only one seen without any blue-gray or gray streaking proximally in his lemon-yellow throat fan.

The specimen from Gunung Awu, RMNH 24252, is an adult male 65 mm SVL. Rozendaal (in litt.) reports it was taken on the SSW slope of the mountain at about 500 m. It has the best-developed oculotemporal series seen in this species, only 14 scales contained in

STD. Color photos made of the fresh-dead specimen in May 1985 (dorsal and ventral of whole animal, and side view of head) depict a dark specimen with an olive cast dorsally, the venter and fan pale yellow muted with gray. There were very dark gray streaks – the boldest seen on any specimen – invading the throat fan. The specimen was shot and it is difficult to evaluate how much color change was affected by trauma. The possibility of a distinctive montane population on Sangihe is considerable.

Because geographic variation in this species cannot be evaluated with the limited material before me, I elect to designate only specimens from Manganitu as formal paratypes. While these additional specimens have aided me in forming my view of the species *D. caerulhians*, they might represent one or more different subspecific taxa.

Etymology. The name *caerulhians* is Latin, a noun in apposition, meaning the blue gaper.

Comparisons. Draco caerulhians requires close comparison only to the other small-scaled, crestless, and spikeless forms in the *lineatus-spilonotus* assemblage. This assemblage, however, is vastly more complex than imagined by Hennig (1936), Inger (1983), Musters (1983), or Lazell (1987a). I have been able to examine the types of *spilonotus* (BMNH 1946.8.27.27) and *bimaculatus* (BMNH XXII.1.g.). *D. lineatus* Daudin (1802), from Java, has no type. Hennig (1936:195–196) saw only three Javan specimens. Musters (1983:35) examined these and a fourth. Inger (1983:2) saw no Javan material and based his view of the species on the type of *spilonotus*, 18 more Sulawesi ("Celebes") specimens, and 21 from Amboina. I have never seen *lineatus* and my earlier view of *spilonotus* (Lazell, 1987a:6–7) cannot now be reconciled with fresh material I obtained alive much closer to the type-locality of Manado, Minahasa, Sulawesi: MCZ 173351–5, discussed below and depicted in Figure 8.

Trinomials are, at present, inappropriate: they presuppose relationships unknown and unverified by any biological observations. I have already reverted to the position of Taylor (1922) and Inger (1983) that Philippine *D. bimaculatus* is distinct from *lineatus* or *spilonotus* (Ross and Lazell, 1991). I see none of these as conspecific with *Draco biaro* Lazell (1987a). I must now give *spilonotus* its due because two apparently quite distinct, yet rather similar, forms occur within short distances of Manado, Sulawesi. Only one can be real *spilonotus* and I view the chance of either being conspecific with a Javan, continental shelf form as remote. In any case, *Draco lineatus* is a virtually unknown taxon. Even the Javan specimens seen by Musters (1983:36–37) are "faded" and in "bad condition." In my opinion, redescription of *D. lineatus*, complete with a neotypic designation based on material known and documented in life, should proceed from a study of geographic variation on and around Java, and precede any attempt to ally oceanic island taxa with *lineatus* at species level.

From 24 to 30 March 1988 colleagues and I attempted to locate *Draco* in and around Manado. The closest population we could find was at the foot of Gunung Kalabat, around the village of Airmadidi, ca. 18 km east of Manado.

The four males, MCZ 173351–4, and one female, MCZ 173355, from Airmadidi are immediately distinct from the Batu Putih specimens I collected in 1986 (Lazell, 1987a:6–7) in lacking green. The males have small, blunt throat fans 69–79% (av. 74%) of head length, which is 18–22% (av. 21%) of SVL. Throat fans for the Batu Putih specimens are 96–102% (av. 99%) of head length (Lazell, 1987a). It is about 20 km, straight-line, from Airmadidi to Batu Putih. Both localities are near sea level, but separated by mountains approaching 2,000 m. My experience at Airmadidi on 25 March 1988 provided a sort of déjà vu, recalling 18 June 1958 on Dominica, Lesser Antilles (Lazell, 1962). All previous authors have agreed that the size and shape of the male throat fan is a trenchant character in *Draco* and I am not inclined to disagree.

The types of *Draco spilonotus* Günther (1872) are both males: BMNH 1946.8.27.26 and 27, the latter designated lectotype by Musters (1983:50). I have examined both. In throat fan size and shape they agree with the Airmadidi series, not those from Batu Putih (fan is figured by Hennig, 1936:168). Apart from the lack of green coloration, so striking at Batu Putih, the Airmadidi specimens closely resemble the Batu Putih series described (Lazell, 1987a) in pattern and patagial coloration. Like the Batu Putih males, Airmadidi males may have bright salmon-red (MCZ 173354), orange (MCZ 173352), or brilliant yellow (MCZ 173351, 173353) patagia.

The pattern of the lectotype of *spilonotus*, BMNH 1946.8.27.27, is beautifully preserved; the patagia are now pale yellow. This specimen was a nearly precise match in coloration and pattern for MCZ 173353 on 6 November 1989, at which time the Airmadidi MCZ specimen had been in fluid more than 18 months. Structurally, the lectotype differs from the Airmadidi series in many characters. I give the measurements and counts of BMNH 1946.8.27.27 followed by those of Airmadidi males, MCZ 173351-4.

The SVL is 60.5 (49-64, av. 59). The STD is 11% of SVL (12-13, av. 12). The throat fan is 71% of head length (69-79, av. 74) and 15% of SVL (18-22, av. 21). The tympanum is well developed and 17% of STD (present only in two, where only seven and nine percent). There are 11 postrostrals (8-10, av. 9). There are 13 middorsals in STD (14-15, av. 14) and 13 midventrals (14-15, av 14). There are 26 lamellae under the fourth toe (25-27, av. 26).

There are 18 pairs of midcaudals in extended lower leg (16-18, av. 17 ± 0.7). These relatively large midcaudals provide the quickest quantitative distinction between Sangihe *caerulhians* and Sulawesi *spilonotus*.

Perhaps notably, the oculotemporals of the lectotype of *spilonotus* are large; there are only 12 in STD (14-20, av. 16).

The paralectotype, BMNH 1946.8.27.26, is a male 58 mm SVL. The throat fan, 11 mm, is 91% of head length and 19% of SVL. There are 18 midcaudals in the length of the lower leg. There is an enlarged tympanic scale 14% of STD. In all other respects except middorsals in STD this specimen agrees with the Airmadidi series. With only 13 middorsals in STD, however, it agrees with BMNH 1946.8.27.27, the lectotype. The color pattern is well preserved and agrees with the other Minahasa males. The patagia are pale yellow with a little dark spotting proximally in concentric bands.

The most proximate geographic relative of *Draco caerulhians* is *D. biaro*, from the isle of Biaro ca. 150 km and six banks to the south. The two are immediately distinct in coloration and pattern but very similar in squamation. A well-developed tympanum is always present in *D. caerulhians*, and always has a maximum diameter greater than 10% of STD. More than 90% of *D. biaro* have the tympanic area clothed in small, granular scales. In one *D. biaro*, a juvenile MCZ 170919, sutures enter the tympanic region partially partitioning the thin skin there; perhaps with age these would have developed into an arrangement of small scales as the tympanic skin thickened. In any case, the condition is not like that seen in *D. caerulhians*.

Only one available *D. biaro*, MCZ 170899, has an enlarged tympanic scale approximating that of *D. caerulhians*. In this individual the enlarged scale is only 8.8% of STD.

In all adult *D. biaro* there is an enlarged, thorn or blade-like lateral nuchal scale within

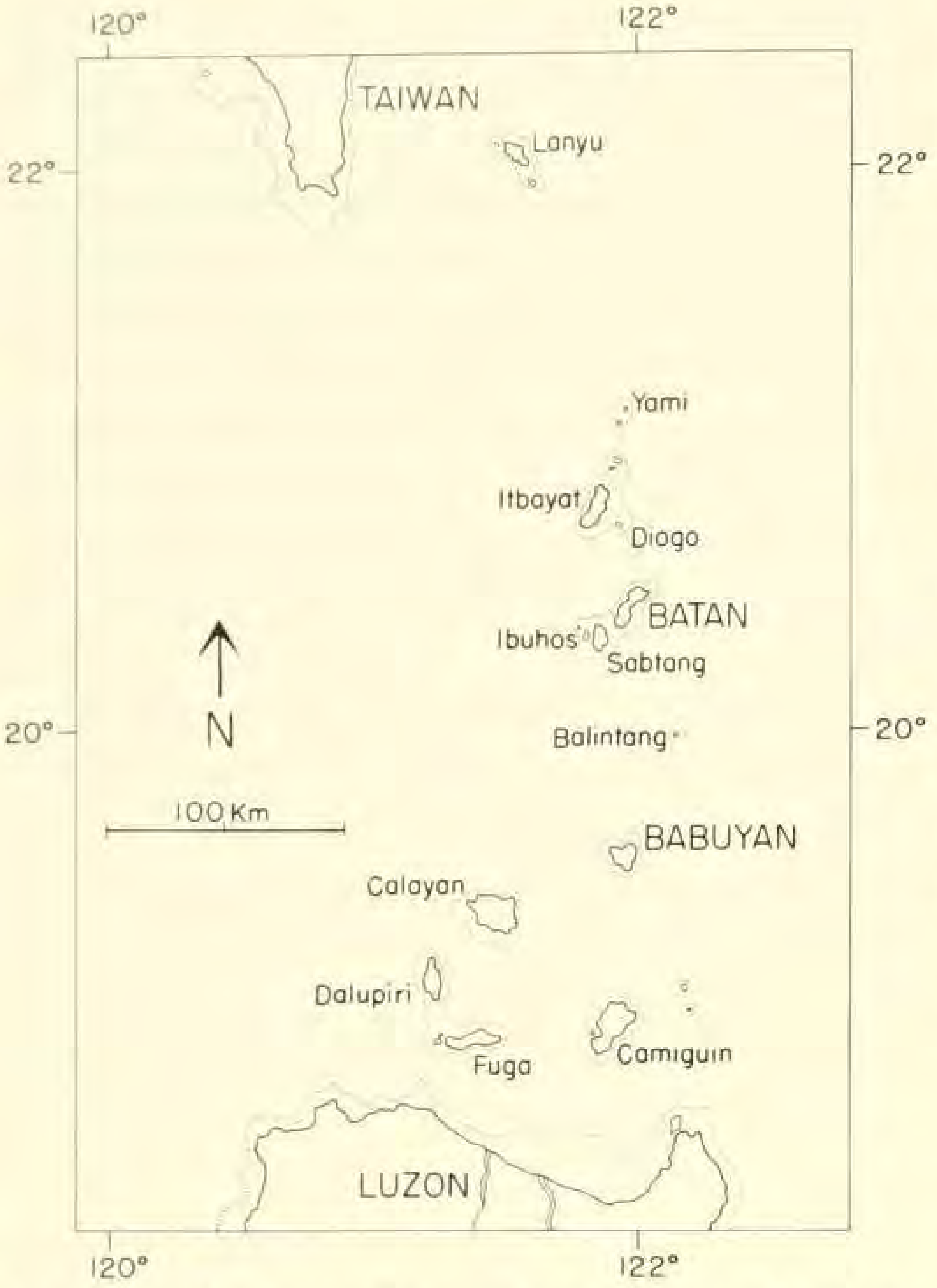


Figure 10. The Typhoon Islands, between Taiwan, China, and Luzon, Philippines. Continental shelf and Bank edges, at the approximate sea level during a glacial maximum, ca. 100 m below present, are dotted.

a patch of somewhat enlarged scales a little more than one STD posterior to the orbit. This scale is always at least as high as its greatest basal diameter. In *D. caerulhians* the patch is present and one scale is usually notably enlarged, but it does not form a blade or thorn, and is never as high as its greatest diameter.

Sexual dimorphism is strong in *Draco caerulhians* but very weak in *D. biaro*. For example, the enlarged lateral nuchal is most prominent in males of *caerulhians*, very weak in females. It is equally well developed in both sexes of *D. biaro*. More significantly, I believe, the difference in size between the sexes of *D. caerulhians* is significant at the 95% level of confidence: 16 males are 60–74 (av. 69) mm SVL, while 8 females are 68–82 (av. 74) mm SVL.

Males of *D. caerulhians* are drab and somber, like all of those of *D. biaro*, except for their bright yellow fans and ventral lappets. Female *D. caerulhians* are spectacularly distinct with their bold patagial patterns of bright ochre to orange-yellow.

Ecology and Behavior. Inclement weather prevented the sorts of prolonged observations one is often able to make of *Draco*. Nevertheless, those seen alive by me occupied the generalized *Draco* niche: conspicuous, diurnal trunk dwellers seen at rest at 2 to 10 m above the ground. Coconut palms and fruit trees are favorites. Whitten *et al.* (1987) discussed deforestation of Sangihe. While I do not doubt that human omnipresence has vastly modified Sangihe's vegetation, the island today is covered with large trees. Most of it seems good *Draco* habitat.

A male, MCZ 173316, from Tahuna was observed giving an apparently full display involving throat fan, lappets, and patagia while perched on a coconut palm at ca. 5 m above ground.

THE TYPHOON ISLANDS
Figure 10

In February and March, 1988, I joined Charles A. Ross, U.S. National Museum of Natural History (USNM), in the Philippines. He reported collecting specimens of an apparently novel *Draco* in the Batanes, central in the Typhoon Island chain. I approached Dr. Henry Jarecki who not only arranged financial support for our expedition, but who enthusiastically participated in the field work on Luzon, Negros, Mindoro, and the Batanes, which resulted in garnering the fresh specimens and comparative material enabling the description of *Draco jareckii*.

Draco jareckii sp. nov.

Type. National Museum of the Philippines (NMP) 1797, originally MCZ 173411, collected at Basco, Batan Island, Batanes Prov-

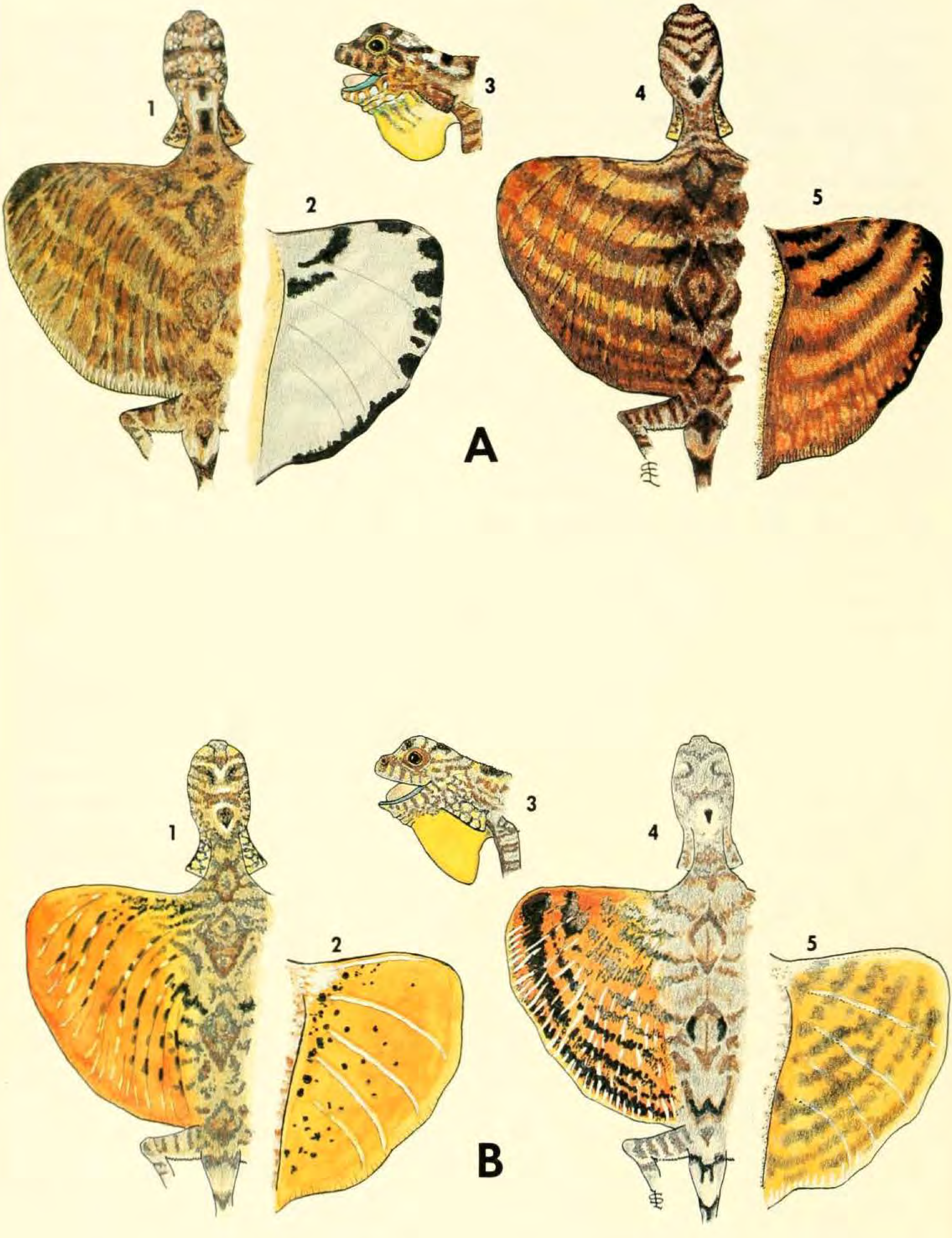
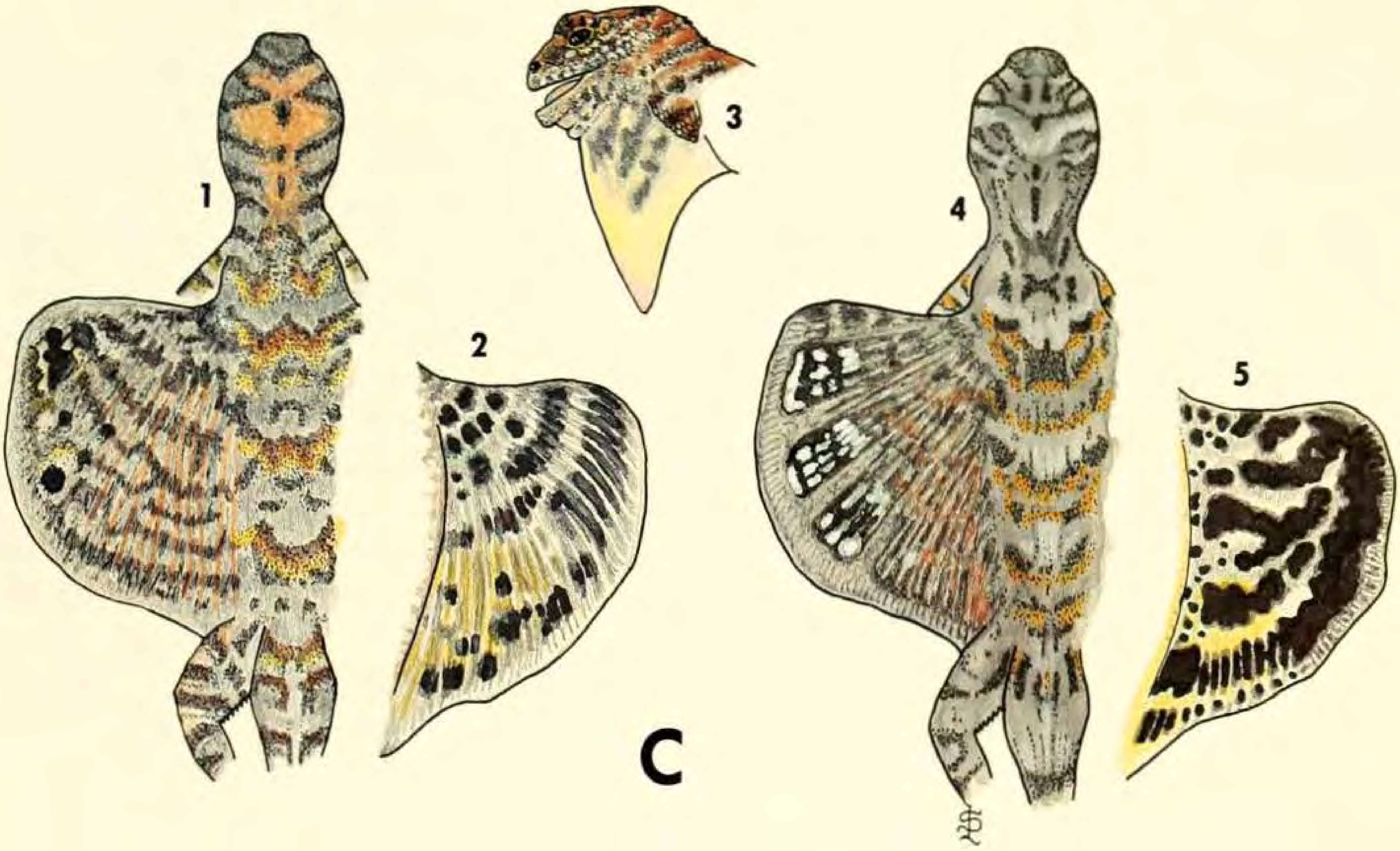
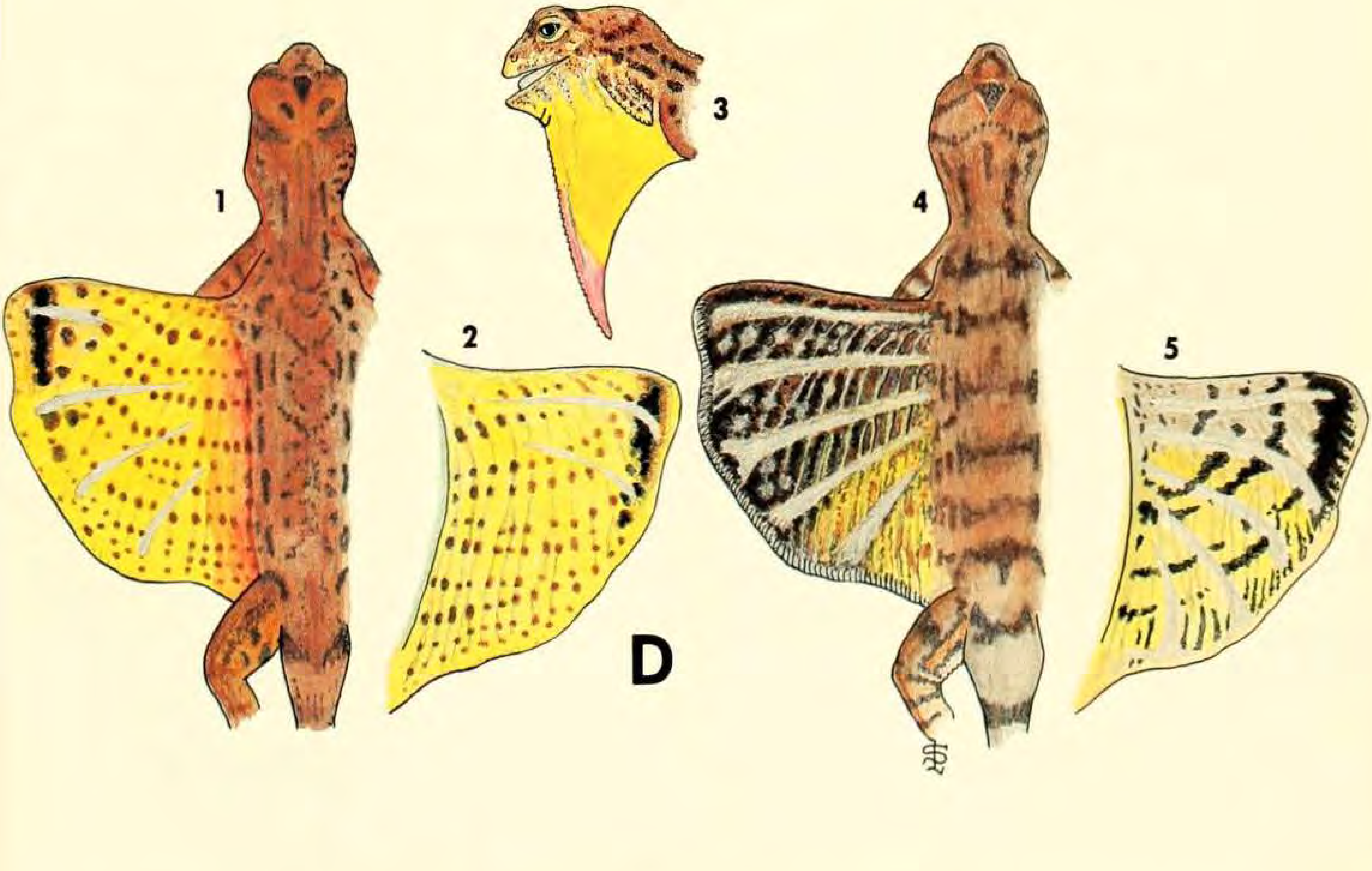


Figure 8. Four species of *Draco*. A, *D. caerulhians*, Manganitu, Sangihe, Far Moluccas; male MCZ 173321, type; female, MCZ 173322, paratype. B, *D. spilonotus*, Airmadidi, Sulawesi; male MCZ 173352; female, MCZ 173355. C, *D. jareckii*, Basco, Batan, Typhoon Islands, male, NMP 1797 (formerly MCZ 173411), type; female, MCZ 173416, paratype. D, *D. spilopterus*,





Alaminos, Laguna, Luzon; male, MCZ 173352; female, MCZ 173355. In each case 1 is male, dorsal view; 2 is male patagium, ventral view; 3 is male head; 4 is female, dorsal view; and 5 is female patagium, ventral view.

ince, Philippines, 11 March, 1988, by J. Lazell. Figure 8.

Type-Locality. Figures 10 and 11.

Paratypes. A total of 28 from Batan Island: MCZ 44142-4, 173412-6, and U.S. National Museum (USNM) 266500-13, Basco and north and east of Basco, up to 3 km. MCZ 173405-6, 173410, Ivana. MCZ 173408, Sitio Diptan. MCZ 173409, Imnajbu. MCZ 173404, Sitio Nacamaya.

Diagnosis. A *Draco* of moderate size, 67–90 mm SVL in both sexes. Patagia reduced, the greatest lateral width of a patagium 25–30% (av. 28 ± 1.6%) SVL. Five patagial ribs. No tympanum. In STD, 9–12 (av. 11 ± 0.9) keeled middorsals, 13–16 (av. 15 ± 0.8) keeled midventrals, 14–20 (av. 17 ± 1.7) oculotemporals, and 13–19 (av. 16 ± 1.7) midnuchal crest scales. There are 13–18 (av. 15 ± 1.2) paired, cristate midcaudals. There are 6–8 (av. 7 ± 1.0) postrostrals. The patagia in both sexes are largely dark, patterned in shades of gray.

Description of the Type. An adult male 76 mm SVL, tail 127 mm, and STD 8.9 mm (12% of SVL). The greatest width of the patagium, measured from the lateral chest, is 23 mm, 30% of SVL. The rostral is tiny, scarcely larger than the seven scales which border it.

There are 11 sharply keeled to mucronate middorsals, 14 strongly keeled to tectiform midventrals, and 15 oculotemporals in STD. Enlarged, mucronate basipatagials, interrupted by undifferentiated scales, form a cristate line; the minimum STD count made of contiguous scales in this series (including some undifferentiated small ones) is 13.

The midnuchal crest is prominent, consisting of spike- or blade-like tectiform scales anteriorly; there are 16 in STD.

Enlarged spike-like scales, interrupted by undifferentiated granules, form a cristate lateral nuchal line; the minimum STD count of contiguous scales is 21. There are scattered tubercular or spike-like scales on the sides of the head and neck, but no supraciliary thorn.

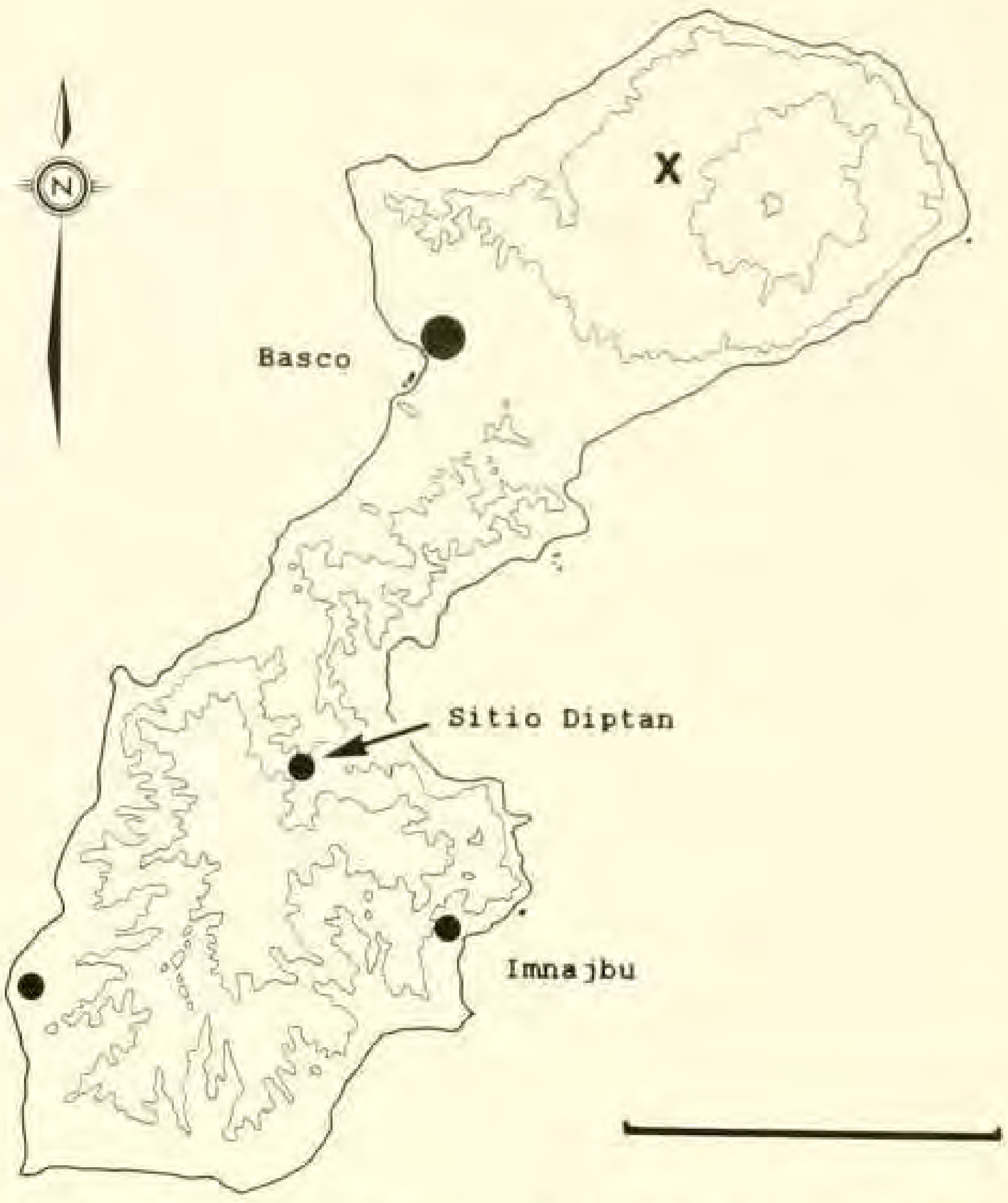


Figure 11. Batan, Batanes, Typhoon Islands. Contours are at 100, 500, and 1,000 m. Localities for *Draco jareckii* are dotted. X marks Sitio Nacamaya. Bar, lower right, is 5 km.

There are notably enlarged longitudinal scale rows on the tail. The most prominently cristate are the paired middorsal caudals (midcaudals); 15 pairs of these are contained in the length of the extended lower leg.

There are 28 subdigital lamellae under the fourth toe, counting from its plantar separation.

In life the type was patterned largely in shades of gray-brown dorsally. Dull fawn brown on the head and anterior trunk was broken by sooty to slate-gray brown tones, especially posteriorly. On mid-trunk and tail, brown gives way to shades of lead to ashy gray with a greenish tint posteriorly. Laterally the head was patterned in ash-gray and warm brown, shading to yellowish on the upper eyelid.

The throat fan is moderately long, blade-like, and was lemon yellow with a beige-pink tip and gray marbling basally. The 22 mm fan is 29% of SVL and 138% of head length.

The lappets are clothed in large tectiform scales dorsally and were not distinctively colored. Ventrally, however, they bear smaller scales and were pale yellowish-gray with dark gray mottling.

The belly was near-white with a faint yellow cast laterally.

The dorsal patagium was mottled in shades of ash to slate-gray, with brown tones postero-basally, in irregularly concentric zones. The shades of gray contrast especially antero-distally. The radials are inconspicuous.

The ventral patagium is rather similar, but of a more contrasting ash and soot, roughly concentric pattern. A suffusion of yellow was discernable between the ribs posteriorly.

Color change seems very limited and involves lightening or darkening of the dorsal trunk. Gape color was not noted in *Draco jareckii*.

Male Paratypes. Because I collected living specimens all over Batan Island (Fig. 11) and detected no hint of geographic variation, I designate all specimens from that island I have examined as paratypes. These are MCZ 173405–9, 173413–4, 44142, 44144, USNM 266501–6, 266508–9, 266511, and 266513.

The smallest apparently adult male is MCZ 44144: 68 mm SVL, tail 124 mm, STD 8.3 mm (12% of SVL). A smaller male, MCZ 173407 from Ivana, 49 mm SVL, has a typically juvenile short snout.

The largest male, MCZ 173405, also from Ivana, is 90 mm SVL, tail 164 mm, STD 10.0 mm (11% of SVL).

Males have 10–12 (av. 11) middorsals, 13–16 (av. 15) midventrals, 15–20 (av. 18) oculotemporals, 12–14 (av. 14) basipatagials, and 17–21 (av. 19) lateral nuchals in STD.

There are 13–19 (av. 16) prominent middorsal nuchals anteriorly in STD.

The patagia are strikingly narrow. Their greatest widths, measured from the lateral chest, are 25–30% (av. 28%) from SVL. Two of nine adult males have broken and healed patagial ribs. MCZ 173405, the biggest male at 90 mm SVL, has two broken and healed ribs in the left patagium; MCZ 173409, 87 mm SVL, has one in the left also. One male, USNM 266505, has two holes with healed edges in the right patagium, between the second and the third ribs.

The throat fans are of moderate size for the genus: 27–31% (av. 29%) of SVL; 130–143% (av. 137%) of head length. All are blade-like, tapering to acute points.

Coloration in life is not especially variable. Topotypic Basco males MCZ 173413–4 had light yellow fans with bright pink tips. The gray on the basal portions of their throat fans was in spots not amalgamating to marbling, and paler than in the type. A male from Ivana, MCZ 173405, achieved the darkest coloration seen: chocolate brown and soot-black with golden tints reduced and present only as lateral highlights on transverse trunk markings. Another from the same locality, MCZ 173406, had a lot of golden tinting on the trunk but none on the legs. This specimen had the most pink on the throat fan.

The male from Sitio Diptan, MCZ 173408, had the palest throat fan noted, but still pale yellow with a pink tip. This specimen had mustard-color smudges on the ventral patagia.

A juvenile male from Ivana, MCZ 173407, gives evidence of the ontogeny of coloration in this species. It is 49 mm SVL. The dorsal coloration was ash and slate gray without brown tones. There was no ventral yellow. The ventral patagia, however, showed the richest yellow seen in a male. The throat fan was grayish and showed mottling of yellow and pink in the areas where these colors dominate in adults.

Female Paratypes. I regard all specimens from Batan as paratypic: I have examined MCZ 44143, 173404, 173410, 173412, 173415–6, USNM 266500, 266507, 266510, and 266512. In size and squamation the sexes are similar. Females vary: 67–90 (av. 81) mm SVL. The smallest, MCZ

173412, from Basco, has a 121 mm tail and 8.6 mm STD (13% of SVL). The largest, MCZ 173416, also from Basco, has a 175 mm tail and 12.1 STD (13% of SVL).

There are 9–12 (av. 11) middorsals, 14 or 15 (av. 15) midventrals, 14–18 (av. 16) oculotemporals, 10–14 (av. 13) basipatagials, and 17–23 (av. 20) lateral nuchals in STD.

The midnuchal crest is well developed. There are 15–18 (av. 17) spike-like, testiform midnuchals anteriorly in STD.

There are 13–16 (av. 15) pairs of enlarged, cristate midcaudals. There are 27–30 (av. 28) subdigital lamellae under the fourth toe counted from its plantar separation.

The patagia are strikingly reduced. The greatest width of the patagia, measured from the lateral chest, is 26–30% (av. 28%) of SVL.

In life female coloration averaged darker, grayer, and less brown than male. Females often showed more golden-yellow tints on the head, dorsal trunk, and limbs. The throat fan is tiny, obtuse, and was pale yellow with sooty spots. The lappets were washed with yellow ventrally.

The dorsal patagia in life were darker than in males with a different pattern. A slatey to sooty intercostate pattern contained bold, near-white and gray-greenish blotches. There were prominent light, ash to lead gray radials. There was a brown tinge postero-basally.

The ventral patagia were more boldly marked than in males, approaching black and white with a considerable yellow or yellowish-green postero-basal wash.

Of note is MCZ 173410 from Ivana, which showed the most yellow-gold tints seen in the species. This coloration was on the scale bases; the scale edges were gray. The yellow-gold tints were especially prominent as posterolateral components of the transverse markings on head, trunk, limbs, and even dorsal surfaces of the feet.

The only specimen taken in wet forest, on the west slope of Mount Iraya at Sitio Nacamaya, MCZ 173404, was not unusually colored. This is described in my notes as having a pale beige belly, most richly colored at the vent. Her dorsal patagia were near black with a plumbeous border, gray radials, and near-white frosty patches in her intercostate pattern.

USNM Paratypes. Fourteen specimens collected by C. A. Ross and colleagues were received after this work was in press. Most were shot, sometimes more than once, often precluding diagnostic measurements and counts. In all, the pattern is very well preserved except right around damaged tissues. All have been very useful in confirming the diagnostic pattern characters of *Draco jareckii*.

There are ten males. Two, USNM 266503–4, are too damaged for either SVL, head length measurements, or nuchal crest counts. Two, USNM 266501 and 266506, cannot yield SVL but do provide fan and nuchal crest characters. One, a juvenile, USNM 266508, was not used for head or STD measurements but is usable for patagia.

Thus in six males the patagia are 25–29% (av. 27.5 ± 1.7%) of SVL. In seven males the fans are 120–146% (av. 132 ± 11.4%) of head length, as great a variation as seen in the entire species. In six males there are 12–17 (av. 14 ± 1.8) midnuchal crest scales in STD.

There are four females. One USNM, 266500, was shot through head and body, precluding measurements and counts. One, USNM 266507, was shot through the trunk, precluding an accurate SVL measurement but STD and nuchal crest are measurable. One, USNM 266510, is a tiny but nearly perfect specimen, 34 mm SVL – the smallest examined. In pattern it is a replica of the adult females.

Thus, in two females the patagia are 25 and 30% of SVL and in two there are 17 and 19 nuchal crest scales in STD.

Two virtually undamaged specimens are especially notable, retaining beautiful patterns and rich brown, gray, and blue-gray colors, when examined 7 February 1991: USNM 266512, a female 82 mm SVL, and USNM 266513, a male 77.5 mm SVL.

A topotypic adult female is shown in Figure 8.

Comparisons. The only previous author to have considered specimens Field Museum of Natural History (FMNH) 100882–3, was Inger (1983). He placed them, *D. spilopterus* of Luzon, *D. everetti* and *D. ornatus* of Mindanao, and many other easily distinguished forms in the synonomy of *Draco volans* (see Ross and Lazell, 1991). In general, Inger's (1983) species are characterized by the sorts of broad-brush, if modal, morphological trends used by many other modern systematists (not me) to diagnose genera (e.g., Malnate and Underwood, 1988, for Philippine forms; Guyer and Savage, 1986, for anoles). Inger's species may correspond to species groups, or real species in a few very geographically restricted cases. His composite making *D. volans* was untenable, as shown by Musters (1983), who at least recognized sympatric species immediately distinct in major morphological, mensurable, and meristic characters. Nevertheless, the FMNH specimens are problematical and not paratypes of *Draco jareckii.* Both are from "Batanes I," but bear no more specific data. The Batanes group includes at least 10 islands large enough to support *Draco* on at least three different banks. Batan Bank alone has four islands. These specimens are described on the FMNH printout as "part of the Edward Taylor collection," but the collector is listed as "unknown." One specimen, FMNH 10082, an adult male 81 mm SVL, may well be a *Draco jareckii.* It has reduced patagia, their width 26% of SVL, and a prominent midnuchal crest of blade-like scales, only 13 contained in STD. In all other meristic characters it fits *D. jareckii* (or *D. spilopterus*). The throat fan seems very short, possibly from loss of elasticity or shrinkage in formalin. It extends only about 20 mm, 116% of head length and 25% of SVL.

In coloration FMNH 100882 is dark and muddy, also a likely result of strong formalin. The patagia are darkly pigmented in a roughly concentric pattern consistent with *Draco jareckii.* Given the present paucity of our knowledge, I cannot guess which island this specimen may have come from.

The second specimen is the more remarkable. FMNH 100883 appears to be a typical Luzon *Draco spilopterus.* The color pattern is reasonably preserved, the patagia pale yellowish with the dark spots in roughly concentric zones picked up by the radials, as in Manila region males. The specimen is badly damaged. Notably, a deep and broad laceration crosses the anterior nuchal region. Flesh and probably scales are missing, so this diagnostic count cannot be made. The specimen is an adult male 79 mm SVL. The throat fan is shredded, the hyoid skinned. Nevertheless, what remains extends to 24 mm, 157% of head length and 30% of SVL. The patagia are broad, 34% of SVL in width. I suspect this individual indeed came from Luzon and somehow got associated with the Batanes individual. The possibility of sympatry between the two species in nature seems remote to me.

Musters (1983) recognized only a single species on Luzon, *Draco spilopterus*, and expanded its range through the Philippines to include all of the mid-sized, generalized *Draco,* however disparate in coloration, pattern, or details of squamation. Because *Draco jareckii* is the geographically extreme member of the genus yet discovered in the eastern portions of the range, it must be derived from *Draco spilopterus* or a common stock, and requires close comparison to that species on Luzon.

Draco jareckii is immediately distinct from all known members of the genus in reduction of the patagia. Measured from the lateral chest, the patagia of all other *Draco* I have seen were at least 33% of SVL in greatest width. In 24 *D. spilopterus* from the type locality, Manila (5) and nearby central Luzon (19), the greatest width of the patagium is 33–39% (av. 36%) of SVL. The adaptive significance of this character is discussed under "ecology and behavior," below.

The male throat fan of *D. jareckii* is also reduced compared to that of *D. spilopterus*. While never longer than 30% of SVL or 142% of head length in *jareckii*, it is 33–40% (av. 37%) of SVL and 152–204% (av. 186%) of head length in *spilopterus*.

In squamation the two species are rather similar, but *D. jareckii* has a more prominent midnuchal crest. In both sexes these crest scales are relatively large, 13–19 (av. 16 ± 1.7) are contained in STD, counted from the anteriormost, obviously enlarged scale. In *D. spilopterus* the midnuchal crest is less conspicuous. In both sexes there are 20–27 (av. 24 ± 1.9) in STD.

The most spectacular distinctions between *Draco jareckii* and *D. spilopterus*, or any other Philippine *Draco* known to me, are in coloration and pattern. While at the British Museum (Natural History), I was able to compare topotypic Manila *spilopterus* directly to Wiegmann's (1835) plate 15, which serves as the type specimen. Of the series BMNH 82.8.29.72–74, an adult male, BMNH 82.8.29.73, is a near-perfect match for Weigmann's plate 15. All of these specimens, two males and a female, two males from Manila (MCZ 7768 and 170253), and two males from "near Manila" (MCZ 26173–4) are included within the range of pattern variation shown by a series of 17 collected, chronicled, and photographed alive by Ross, Jarecki, and me at Alaminos, Laguna Province, Luzon, on 4 March, 1988. This is ca. 47 km SW of the Manila.

Because *Draco spilopterus* seems never to have been depicted in life, I include both sexes in Figure 8. Even Taylor (1922) gave only a brief description of the male in life (and females only as preserved).

In life, adult males from Alaminos (MCZ 173451, 173453–4, 173456–7, 173460–1, 173464–5) were dorsally patterned in brown. They were warm, light, fawn brown on the napes, darker posteriorly, and with dark gray-brown transverse markings. Ventrally they were palest gray-green, nearly white. Their throat fans were brilliant yellow, shading to pink distally; the brightest pink was along the antero-distal fan edge.

The male dorsal patagia were bright yellow, shading rather abruptly through orange to red or orange-red along their bases. There was narrow costate pattern of gray-brown, especially distally along ribs two and three. There were boldly contrasting brown or gray-brown spots which appeared rather randomly scattered over the patagia. In some specimens these spots tended to form 8 to 10 roughly concentric sets. These spots often coincided with radials, and the radials may carry brown scales for varying distances. These spots amalgamated to form an anterodistal bracket.

The male patagia ventrally were paler with the spots showing through. The bracket was intensified, slate to sooty, and may overlay the costate pattern. The sides of the trunk along the patagia were blue-green.

In life, adult females (MCZ 173455, 173458, 173462–3, 173466–7) were duller than the males, conspicuously lacking the blue-green sides, orange or orange-red dorsal patagial bases, and bright yellow dominant dorsal patagial coloration.

Dorsally the female patagia showed a costate pattern of light gray-brown on a ground of dark gray-brown and slate. There was a yellow wash posteriorly and distally.

Ventrally the female patagia were little pigmented, so most of the somber dorsal coloration showed through, but paler. The posterodistal yellow was more conspicuous, and the sooty bracket especially prominent. There were scattered sooty spots. The richest colors of females tended to be yellow tones on the otherwise drab, gray-spotted, small throat fan, and the abdomen and underside of tail.

In both sexes the patagia of *D. spilopterus* are distinct from those of *D. jareckii*, but the distinctions in females are most obvious in the amount of ventral pigmentation in *D. jareckii*.

Ecology and Behavior. Batan Island appears brutally cutover, virtually sheared bald. Except around the volcano, Mount Iraya, in the extreme northeast, there is not even remnant forest. There are only scattered trees in ravines, for shade around dwellings, and in pathetic, obviously ineffectual windbreaks straggling across the agrarian scene. It is not unusual to see several *D. jareckii* in a single tree, although it may be a long hike to the next such tree. Interestingly, this species does not seem to be more common in the forest on Mount Iraya, although regularly seen there too.

Draco jareckii regularly perch, often head down, on trunks of trees and palms at 1.5 to 6 m. This is notably lower than most *Draco* perch elsewhere in coastal zones where I am familiar with them. In part, low perch height corresponds to the battered trees, scattered hat-racks in the wind. However, many trees are tall enough for *Draco* to perch higher regularly and it is never necessary for them to perch so low. They escape by climbing up and do not show much reluctance to enter tree crowns, despite the presence of arboreal snakes on the island (but not necessarily in the trees).

We repeatedly observed male *Draco jareckii* display with throat fans and lappets, but never saw one fan the patagia. For me this truncated behavior fits into a larger pattern.

The reluctance to spread the patagia, the reduced size of the patagia, the presence of broken patagial ribs or patagial holes in about 10% of individuals, and the ubiquitous presence of *D. jareckii* in sparsely vegetated terrain suggest that a novel adaptive realm has been entered. I submit we are seeing here the reversal of the evolutionary trend which set *Draco* apart from other lizards; we are going back to a flightless *Draco*. Under the heel of hardship, brutal natural selection is operating in these blasted isles.

PREDICTIVE BIOGEOGRAPHY

A major goal of science is accurate prediction. Since the Lesser Antilles have been long studied in great depth in terms of biogeography and the evolutionary relationships of their faunas, comparison to the Far Moluccas and Typhoon Islands provides an unparalleled opportunity for complex prediction. Just how close are the similarities between these remote island realms?

The Lesser Antilles are the largest of the three archipelagos, spanning seven degrees of latitude. They spread over about 725 km north-south, and 310 km east-west. Their western arc is called the "first cycle" because its islands have not been deeply submerged and capped with oceanic limestone. St. Croix, at the northwest extreme of the westen arc, is geologically distinct from the simple volcanoes which make up the rest. The eastern arc, from Sombrero to Barbados, is the "second cycle." The volcanic foundations of these islands have been largely or completely overlain with limestone dating from perhaps the Miocene (ca. 25 million years ago), when ocean levels were much higher than today.

The Lesser Antilles are in the Trade Wind zone, where the winds blow almost incessantly from the east or northeast. This constant windstream has dramatically influenced life on the islands. There are sharp distinctions between windward and leeward; at about 650 m above sea level even the most arid land shifts abruptly to rain forest. All Lesser Antillean islands high enough to support rain forest are in the western arc. There are nine over 650 m, and five over 1,000 m.

One immediately wants to know how many islands are included in each archipelago. The Lesser Antilles are well-mapped, so a count is theoretically possible. But just what is an island? How high above water must it rise? How far must it be distant from other things (like boulders) protruding above the sea? The Lesser Antilles lie between the Puerto Rico Bank (north) and the continent of South America (south). There are 16 separate Lesser Antillean banks supporting islands today. The concept of "bank" is more useful than that of "island." A bank is a submarine platform whose edges correspond closely to sea level during a glacial maximum – when sea level was about 100 meters lower than it is today. Oceanic islands lie on banks disjunct from the continental shelf, which was also dry land at glacial maximum. The last glacial maximum, the Wurm, was about 70,000 to 10,000 years ago. In counting the banks of the Lesser Antilles I have not included La Blanquilla, a southwestern outlier just off the South American Shelf. It is perhaps an analog of the Nain Bank, which lies just north of Manado and the Sulawesi Shelf, or Lu Tao Bank, which lies just east of Taiwan.

Omitting Nain, the Far Moluccas also comprise 16 banks. The best maps show about 54 islands, total, but I know that count is too low because I have seen islands – large and well-vegetated – that are not mapped.

At their northeast ends both the Far Moluccas and the Lesser Antilles approach a major island on a large and complex bank. The Far Moluccas nearly reach Mindanao on the Greater Philippine Bank. This vast bank includes most of the major Philippines to and including Luzon. The closest Far Molucca Bank is Sarangani, closer to the southern tip of Mindanao than to its next nearest neighbor, Kawio, to the south. Thus, the Sarangani Bank (politically part the Philippines) is reminiscent of the St. Croix Bank in the Lesser Antilles. The Far Moluccas' tiny Miangas, away to the northeast, reminds one of the Lesser Antilles' Sombrero.

However, the comparison is not perfect. The Greater Philippine Bank is much larger and more complex than the Greater Puerto Rico Bank of the Antilles. There is no deep water channel like the Anegada Passage between the Philippines and the Far Moluccas. With lower, glacial maximum sea levels, over-water dispersal might be easier between the Philippines and the Far Moluccas than between Puerto Rico and the Lesser Antilles.

At their southern ends the comparison is even less close. The Far Moluccas approach the Sulawesi Bank, another huge oceanic island system. The Wallace Line runs through the deep water channel that separates Borneo and Palawan – continental shelf islands solidly part of the mainland at glacial maximum – from Sulawesi, an oceanic island with a depauperate, largely endemic fauna derived from a few stocks able to cross water. The Lesser Antilles approach the South American continent with its large shelf islands of Trinidad and Tobago, which are a vastly richer source for potential colonizers, but ones not pre-selected for over-water dispersal.

The Far Moluccas span about four degrees of latitude, from just below 2°N to just below 6°N. That is about 405 km, or 56% of the linear distance of the Lesser Antilles. Linear north-south distance is what over-water dispersing animals must cross to colonize the islands. At 262 km wide, east to west, the Far Moluccas are better than 80% of the width of the Lesser Antilles. This provides a good, broad spread for dispersers to hit.

I do not have the sort of richly detailed, comprehensive geological evidence available for the Far Moluccas that I had for the Lesser Antilles. However, Hamilton

(1979:191–197) provides a historical scenario and some specific data for the Sangihe, Talaud, and Nenusa Banks. The western arc or Sangihe Ridge is said to be of Miocene age with numerous active to barely dormant volcanoes along it, quite like the first cycle of the Lesser Antilles. Sangihe itself is said to be all Quaternary igneous extrusives on the surface. The land areas on Sangihe Ridge are the subaerial extensions of the volcanic region of northern Minahasa, Sulawesi.

The large islands of the Talaud Bank are older, like the eastern, second cycle islands of the Lesser Antilles. Hamilton (1979) describes them as a "polymict melange" of "broken formations" of Tertiary age. He notes extrusives such as basalt and sedimentary formations trending towards metamorphosis such as clay, shale, sandstone, and chert. In keeping with their greater age (and in congruity with the Lesser Antilles) these eastern arc islands are lower than the younger western arc; the highest peak on Karakelong – largest of the group – is a mere 660 meters. The Talaud Bank is geologically kin to the San Agustin Peninsula east of Davao Gulf, southeastern Mindanao.

Interestingly, Hamilton (1979) describes the Nenusa Bank islands, geographically intermediate between the Tertiary lands of Talaud and San Agustin, as Quaternary and entirely sedimentary: "raised reefs" on "marl and sandstone." There are Lesser Antillean islands with only oceanic limestone at their surfaces: Anguilla, Sombrero, and Barbuda. These islands are also in the northwest of their archipelago. How much further one might carry geological analogy to the first and second cycle generic sorts of Lesser Antillean islands is presently unknown to me.

There is no arc-joining bank in the Far Moluccas corresponding to the Guadeloupe Bank of the Lesser Antilles. However, the large and complex Sangihe Bank offers tempting parallels. Sangihe itself, like La Guadeloupe, is a high island for its entire archipelago: 1,320 m versus 1,354 m, respectively.

Sangihe and La Guadeloupe are just about the same area, too. Both are attended by several lower islands that would unite with them at glacial maximum. The largest island in the Far Moluccas, Karakelong of Talaud, is at least as big as Martinique, largest of the Lesser Antilles (note that the two parts of Guadeloupe – La Guadeloupe proper and Grande Terre – are actually separated by sea water today). However, Karakelong is very low compared to 1,397 m Martinique. Also, the Talaud Bank is a complex of large islands; Martinique has only tiny coastal cays on its bank.

The resemblance of Sangihe to Martinique is striking. Both have a high northern massif, 1,320 m and 1,397 m respectively. Both have low peninsulas south and east. Because these peninsulas break up into islands during interglacials (as at present) on Sangihe, there may be chances for a combination of relatively weak ecotypic selection to combine with isolation and produce distinctive subspecies on the Sangihe Bank.

As noted above, one striking difference between the Far Moluccas and Lesser Antilles results from their positions relative to the equator. Both are tropical archipelagos, but the Far Moluccas are so close to the equator as to be in the equatorial doldrums: there is little breeze. The Lesser Antilles are far enough north to be plied by the trades. The lowlands of the Lesser Antilles are dried by the ceaseless winds; the highlands, above 650 m, are soaked by frequent rains and cumulus clouds carried by the winds; the largest islands have dramatic ecological zones: rain forests high and to windward, desert rain shadows to leeward. Ecological zonation will be weak in the Far Moluccas.

To date we know far less about the animal life of the Far Moluccas than we did of the Lesser Antilles in 1920. A few ornithologists and entomologists (or at least professional collectors representing those disciplines) have visited the larger islands of Sangihe and Talaud. I may have been the first herpetologist to ever visit the Far Moluccas. In 1986 I went north from Manado by small boat only as far as Biaro (Lazell, 1987b), and in 1988 flew north to Sangihe.

There are 17 separate island forms of *Anolis* in the Lesser Antilles. There are 19 other intergrading, ecological subspecies on those big islands with Trade Wind caused zonation; since the Far Moluccas lack such zonation it seems unfair to include them in a comparison. The 17 forms tend to be exclusive on individual banks, but five banks (Anguilla, St. Kitts, Antigua, St. Vincent, and Grenada) each have two full species. The Guadeloupe, Iles des Saintes, and Marie Galante Banks share one highly varied species. The northern Lesser Antilles, south through Dominica, have *Anolis* of Greater Antillean origin. The southern islands, north through Martinique, have *Anolis* of South American origin. As one might predict, *Draco biaro* is most closely related to Sulawesi forms (Lazell, 1987a).

There are three roughly distinguishable ecomorphs of Lesser Antillean *Anolis:* generalized trunk perchers, big tree giants, and rock and brush dwarfs. Few generalized trunk perchers attain large size. Of eleven species, only three – *nubilus, oculatus,* and nominate *marmoratus* – regularly exceed 80 mm SVL. Only one subspecies, *Anolis marmoratus ferreus,* reaches giant size, exceeding 100 mm SVL. Most generalized trunk perchers live alone, without sympatric congeners. Two however, *trinitatis* and *aeneus,* occur with big tree giants. One, *gingivinus,* is sympatric with a rock and brush dwarf.

No analog of rock and brush dwarf *Anolis* has ever been found in *Draco,* the flying lizards. Indeed, their lifestyles call for gliding, which in turn requires relatively high perches like tree trunks. I discount rock and brush dwarf *Anolis* from my predictive comparisons. I believe *Draco* are the analogs of generalized trunk perching and big tree giant *Anolis.*

Much of the diversity at subspecies level in Lesser Antillean *Anolis* derives from the striking ecological zonation of the highest islands. This sort of zonation is reduced or absent from the Far Moluccas and Typhoon Islands for meteorological reasons. Eliminating ecological zone subspecies dramatically reduces the number of kinds of *Draco* I must predict for the Asian archipelagos if the notion of *Anolis* analogy is correct.

In the Lesser Antilles there are a total of eleven species of generalized trunk perchers. All but two, *Anolis marmoratus* and *A. gingivinus,* are endemic to a single Bank. *A. marmoratus* occupies three banks, but two are close satellites of the much larger third. *A. gingivinus* occupies one large bank and its tiny satellite. There are three species of big tree giants. One, *Anolis bimaculatus,* occupies two banks. The others are endemic to single banks. One bank, Saba, harbors only a rock and brush dwarf.

There are 16 Lesser Antillean banks. Of these, 14, or 88%, harbor *Anolis* that might have *Draco* analogs. Only two, 12%, harbor two relevant sympatric species. One striking fact about *Anolis* sympatry in the Lesser Antilles is that it never naturally involves a member from each of the two colonizing groups. The South American group invaded as far north as Martinique. The Greater Antillean group invaded as far south as Dominica. They do not overlap. All five cases of Lesser Antillean sympatry on any bank involve a second invasion by a close relative or the same ancestral stock. Since I discount rock and brush dwarf anoles as *Draco* analogs, only two Lesser Antillean Banks have relevant sympatry, the two southernmost, Grenada and St. Vincent.

Colonizers may enter the Far Moluccas too from both north and south. We have seen that Sulawesi derivatives reach at least as far north as Sangihe. Sulawesi has far fewer species, however, than Mindanao. Only one, *D. spilonotus*, is certainly known from Minahasa, the northern peninsula of Sulawesi. Even if the different sorts I have found there (and tacitly assume to be geographic variants of one species) prove distinct at species level, the result would still be half the number demonstrably sympatric on Mindanao (*mindanensis*, *bimaculatus*, *ornatus*, and *everetti:* Ross and Lazell, 1991; Taylor, 1922).

I predict that the shorter distances in the Far Moluccas will have facilitated independent colonizations, but the very low banks and tiny islets on three of the northernmost five will preclude sympatry on them: Miangas (Palmas), Kawio, and Nenusa.

Thus I predict two species sympatric on the other two northernmost Banks: Sarangani and Talaud. Sarangani Bank, however, is so close to Mindanao that little opportunity for full species differentiation will have occurred: colonizations will have been too frequent.

I predict the two Sarangani forms will be subspecifically related to Mindanao, Philippines species, therefore less distinct than the single St. Croix (Lesser Antillean) *Anolis* is from its Puerto Rico Bank (Greater Antillean) relatives. One Sarangani species will, I predict, be a giant (greater than 100 mm SVL.)

I predict that, because of the short distances involved, Sulawesi and Philippine *Draco* stocks will overlap in sympatry, fully evolved as endemic species, on the one other bank with two species: Talaud. One Talaud species will, I predict, be a giant.

Because the Lesser Antilles' 17 relevant forms are in 14 full species spread over a linear (travel) distance 44% larger than the Far Moluccas, I predict the *Draco* forms will not be as well differentiated. Because Far Moluccas' travel distances are shorter, colonizations and genetic interchanges will have been more frequent. Thus, I predict as many recognizable forms (subspecies as well as full species) – 17 – but only 56% as many full species: eight.

I predict full species on the Miangas (Palmas), Kawio, and Nenusa banks. I predict two more species on Talaud. I have already described *D. biaro* and *D. caerulhians;* I predict they will divide the banks between Kawio and Biaro that support *Draco*. I predict only one of the three, small, western, single islet banks will support a *Draco*, even as Aves and Saba support no relevant *Anolis*, but little Redonda does. I will not guess which one.

Two of the nine remaining subspecifically differentiated forms will, I predict, be the Sarangani Bank derivatives of Mindanao. I realize these are predicted by me to be distinct at species level from all other Far Moluccas forms, but I count them at the postulated rank of subspecies herein because they may not be endemic at species level to the Far Moluccas.

Four of the remaining subspecies I predict will be derivatives of *Draco caerulhians* on Sangihe and satellite banks. The other three I predict will be derivatives of *Draco biaro* on the three southernmost banks.

The Typhoon Islands are the smallest archipelago. They span a little more than three degrees of latitude from 19° 10'N to 22°N, a distance of ca. 390 km. They are about 120 km wide, east to west. They are rather like the Lesser Antilles or Far Moluccas viewed upside-down (Fig. 2). When viewed as we normally do, their oldest (equals lowest) components are on the westernmost Bank, Fuga (four islands). The highest elevation on this bank is only 290 m, on Dalupiri. The next bank north in the western group, Calayan, is only 517 m high.

The eastern line of the Typhoon Islands, from Camiguin Norte to Lanyu (and Lu Tao), resembles the western lines of the Lesser Antilles and Far Moluccas, but is lower. The highest peaks, obvious volcanic cones, are 1,088 m on Babuyan and 1,009 m on Batan. There has been very recent volcanic activity in this chain, for example at Didicas, just northeast of Camiguin Norte (Gonzales, 1966, p. 85).

It is difficult to guess the real number of banks. Maps available to me show a 200 m submarine contour; a 100 m contour would be far more useful. Even using 200 m, there is disagreement. A Bartholomew map of 1985 shows 11 banks; a National Geographic map of 1986 shows 12. The discrepancies involve the satellite isles of Itbayat. Are the northern islets of Mabudis and Siayan on their own, separate bank? It may not matter here, because I believe they are too small and remote to support *Draco*. Of greater concern is the great volcanic spire of Diogo or Dinem, just east of Itbayat, discussed below.

There are no *Draco* on Taiwan or in southeast China, so colonization can only have come up from the Philippines proper into the Typhoon Islands. These islands are all rather steep, with narrow banks, and therefore presented scarcely larger targets at glacial maximum than they do now. We can believe that no *Draco* has penetrated as far north as Lanyu because this island has been well studied herpetologically by Ota (1987, and references therein) and visited by C.A. Ross (pers. comm.). However, we know *Draco jareckii* exists on Batan, about 60% of the way up the chain.

I predict that lack of colonization from the north, combined with only one known parent species on Luzon (*D. spilopterus*) will limit the possibilities for species presence in the Typhoon Islands. I believe their situation is similar to the northern Lesser Antilles. None of these banks, populated by species derived from the Puerto Rico Bank (the analog in this case of Luzon), supports more than one species of relevant *Anolis* (I discount *Anolis sabanus* and the *A. wattsi* complex as irrelevant rock and brush dwarfs).

I predict only six banks in the Typhoon Islands will support *Draco*, from south to north: Camiguin Norte, Fuga, Calayan, Babuyan, Batan, and Itbayat. I believe five banks will each harbor a single full species, all five distinct from each other and as distinct from Luzon *D. spilopterus* as St. Croix *Anolis acutus* is from any Puerto Rican species. The difficulties of colonization in the Typhoon Islands will, I predict, have provided ample isolation for speciation despite the small distances between banks.

On the six comparable, proximate Lesser Antillean banks – St. Croix, Sombrero, Anguilla, St. Kitts, Antiqua, and Redonda – there are two cases of species occupying different banks: *A. gingivinus* on Sombrero and Anguilla; *A. bimaculatus* on St. Kitts and Antigua. Only the latter are subspecifically distinguishable. Even if one substitutes Montserrat for tiny Sombrero or Redonda, there are still a maximum of five full species – one with two subspecies. I believe this pattern will hold for the Typhoon Islands: five full species, one with two subspecies, on six banks.

The most intriguing area for prediction, I believe, offered by the Typhoon Islands derives from the evolution towards flightlessness described for *Draco jareckii*. I predict that patagial, gliding, and display reduction will reach their extreme on the Itbayat Bank.

Itbayat itself is low, ca. 280 m at the highest point, but entirely flanked by sheer cliffs 30 m high (Gonzales, 1966, p. 6). I could rarely glimpse it across the tumultuous sea from Batan, but neighboring Diogo (called Dinem in the Batanes) is a grand cone towering 513 m and clearly visible. These must surely be the most awful lands on Earth inhabitable for an aerial lizard, yet I believe one will be found there.

Glacial maximum sea level drop will, I predict, have provided relief from cruel selection against patagia on the Itbayat Bank. In contrast, interglacial sea level rise will have been a grim reaper indeed. Contemplating

Diogo from Batan, I could imagine Draco stranded there repeatedly by sea level rise. The opportunity to survive anti-patagial selection will have followed each glacial maximum. Should the process ever have succeeded, a cliff dwelling *Draco*, perhaps reminiscent of *Anolis agassizi* on far Malpelo in the eastern Pacific, might well be the result. I predict it would succeed upon recolonization of main Itbayat just as I envision dry island *Anolis* succeeding in invading main Jamaica following interglacials (Lazell, 1966).

Some of my predictions, above, are certain to come true. I have already examined two specimens of *Draco* from Camiguin Norte in the Typhoon Islands, in USNM, with color photographs, and they are wonderfully distinct from any described form.

If any significant number of my predictions prove true, if I have predicted even the broad outlines and approximate levels of differentiation and diversity, I will be discomfitted. A half century of observing and hunting animals has yielded no picture of the order of nature – quite the opposite. The nature I know is as chaotic as the constraints of physics allow. Nature appears to me to sidestep deftly Occam's razor and never follow the shortest distance between two points. I see grave uncertainty conspicuously perched on every tree. So far, my pursuit of *Draco* has been a remarkable and exuberating repeat of my experiences earlier on the opposite side of the Earth. If, however, I never find another new species of Draco on these islands where I predict them, I cannot be disappointed. I will not find empty archipelagos.

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