Cape Fear Serpentarium

THE BUSHMASTERS

MORPHOLOGY IN EVOLUTION AND BEHAVIOR

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The Bushmasters
(Genus *Lachesis* Daudin, 1803)
Morphology in Evolution and Behavior

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Chapter I: Geographic Variation in Bushmaster Morphology

IN THE PAST, the bushmasters were seen in a polytypic context, and locality, not morphology, answered for the first major divisions. Cope's (1876) *Lachesis stenophrys* appears based on nothing more than a specimen locality for the bushmaster in Middle America, and Boulenger (1896) acknowledges its existence uncritically. Taylor (1951) sinks it into *Lachesis muta*, retaining *stenophrys* as the trinominal. Peters and Orejas-Miranda summarized differences in scale number and color among the (then) three known taxa, but it was not until 1986, when Solórzano and Cerdas described *L.* (*muta*) *melanocephala* as a new subspecies that *L. stenophrys* was rigorously examined, and this inadvertently through these authors' attempts to justify allopatry in the former. Thus, almost a hundred years after it had been named, this previously little-differentiated form began to emerge for the first time in a truly distinctive light. Meanwhile the guidelines for separating *L. muta rhombeata* from the nominate *L. muta muta* remained as cloudy as ever—a condition my data can only emphasize.

As the bushmasters in this article are treated as "species", I am for the first time exploring morphological variation within the binominals themselves. Although, in Ripa (1994), *L. muta muta* of Mata Grosso, Brazil were held analogous to *L. muta rhombeata*, of the Brazilian Atlantic Forests, a variation was described in Guianaese examples; but these ideas were not pursued very far. The following provides an overview, from a phylogeographic perspective, of the trends exemplified by each species. This will hopefully show a truer picture of the evolutionary relationships of the bushmaster forms, and reveal paths for their divergence. This section should be read in conjunction with Tables 1-3, which covers these data in greater detail; and with Table 4, which reviews these snakes' distribution and habit.

Certain conclusions are inevitable: the South American taxa show clinal variation from north to south; the originally nominate form (*L. muta muta*), recognized today as one of two subspecies, is geographically variable within itself, resulting from an ancestral disjuncture potentially older than the rise of the Andes and those other biogeographic alterations which later separated the Amazonian from those of the Brazilian Atlantic Forests; it might therefore be regrouped accordingly with respect to what is now called *L. muta rhombeata*, and the range of the latter extended into western Brazil (e.g., Mato Grosso) and beyond, into those other regions where similar traits are also observed. Hence I have reduced the distribution range of *L. muta muta* and extended that of *L. m. rhombeata*, accordingly (Figure 22 - 23). The Central American *L. stenophrys* is embraced by two weakly differentiated geographic variations, both of which are intergrading and should not be viewed as taxonomically distinctive; *L. melanocephala* is without region variation; and a fourth bushmaster, the Chocoan one (from eastern Panamá and northwestern South America) has been sufficiently isolated from all others as to evolve distinctively as a species in its own right (Figure 24).

The wider its distribution, the more a species can be expected to vary. Hence *L. muta muta* with its vast distribution in equatorial South America varies considerably from north to south, while *L. melanocephala* with its tiny, almost insular range in southeastern Costa Rica, exhibits little or no geographic variation whatsoever. From the available specimens, the South American *L. muta muta* appears to embody at least two moderately distinct forms, a Northern form, endemic to the Guiana Shield and contiguous regions, and a Southern, which I am tentatively

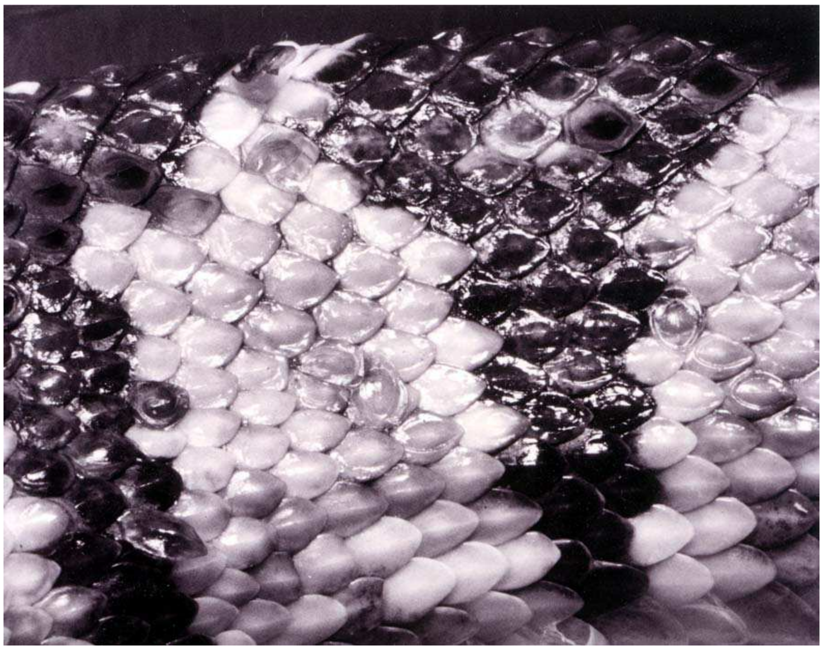


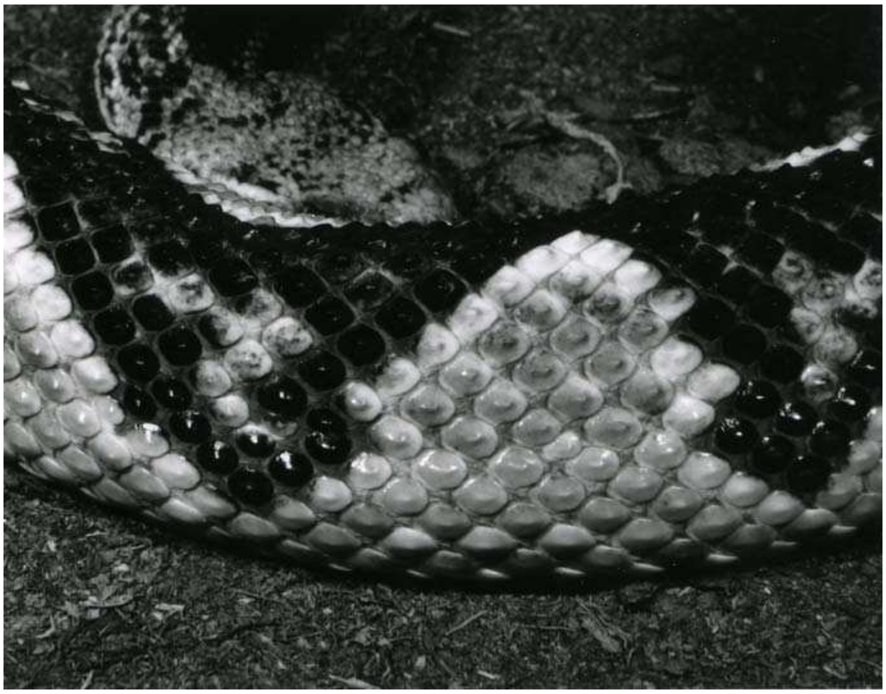
Figure 19. This Chocoan bushmaster reveals a dorsolateral scalation similar to the two Central American forms: imbricate, with a blunt basal end, and obtuse keeling that tends away from the midline of the scale and may reach a free apex. The tubercular center rests upon a flat outer surface. The pattern tends to vertical bars that may reach the ventrals, a characteristic typical of Central American forms, and in the Amazon Basin (but not Guiana Shield) form of *L. muta muta*. Modified from Ripa (1999; 2000).

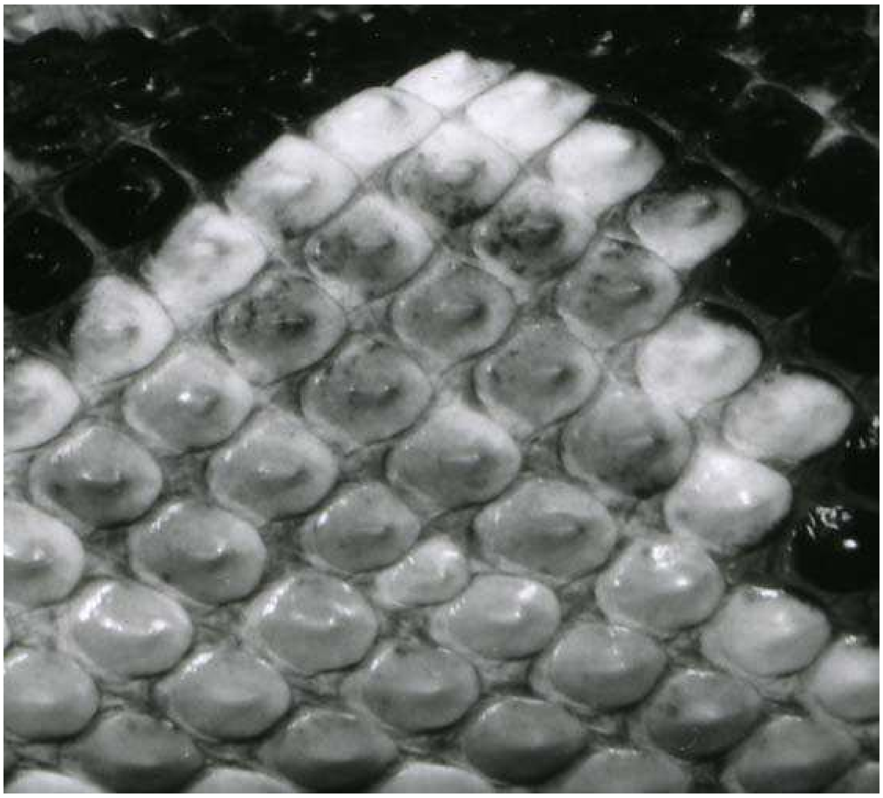
identifying with the Amazon Basin (called Western Amazon form in Ripa, 1999).

The Northern, or Guianaese (Guiana Shield) form is endemic to French Guiana, Surinam, Guyana, Trinidad, eastern (and possibly southern) Venezuela, and proximate areas of extreme northern Brazil; in short, throughout the contiguous Guiana escarpment. This form usually has a thinner, sharper, anteriorly narrower head, and a more slender body conformation. The dorsal scalation is extremely beaded, with the medially biased tubular keel strongly centered along the midline of the scale (apically biased in the Amazon basin). The internasals, canthals, and prenasals are larger, giving the snout a more elongated aspect. The head markings are much less advanced and usually take the form of a series of numerous (up to 40) small speckles that may or may not conform to a latent pattern. The eyestripe is typically narrow. The dorsal body blotches may be strongly rhombic or simple ovoids. They are fewer in number than in the Amazon Basin, and more widely interspersed with ground color. They are not always black, being of umber, sienna or other dark brown hues. (Figures 13-21). The ground ranges from brownish tan, to yellowish tan, to pinkish-tan.

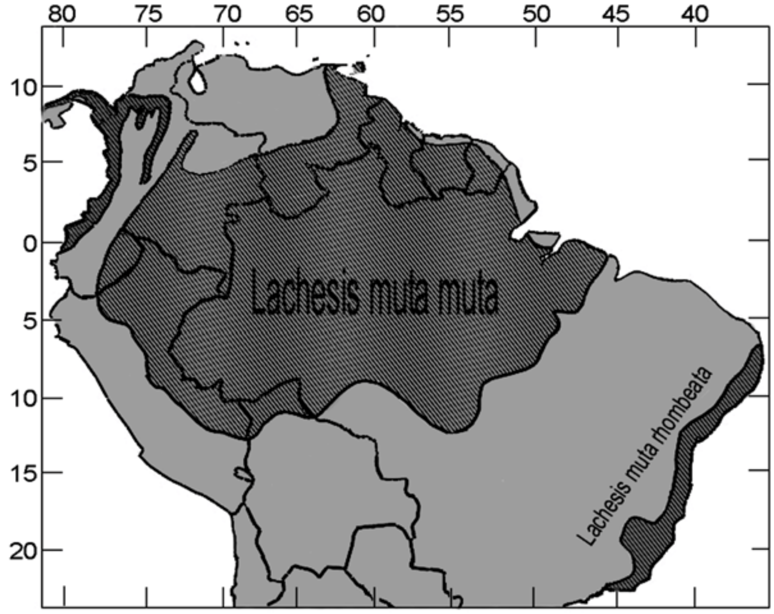
In Southern, or Amazon Basin form, holds a north–south affinity in the western Amazon Valley following the Andean versants from northeastern Colombia south through eastern Ecuador and Peru, into northeastern Bolivia, contiguous areas of Brazil, and east into Mato Grosso State, Brazil. The presence of this form in the Amazonian lowlands needs further study, but the continuance seems probable. It is factually the form found in the Atlantic Forest area of eastern Brazil, what is now called *L. muta rhombeata*.

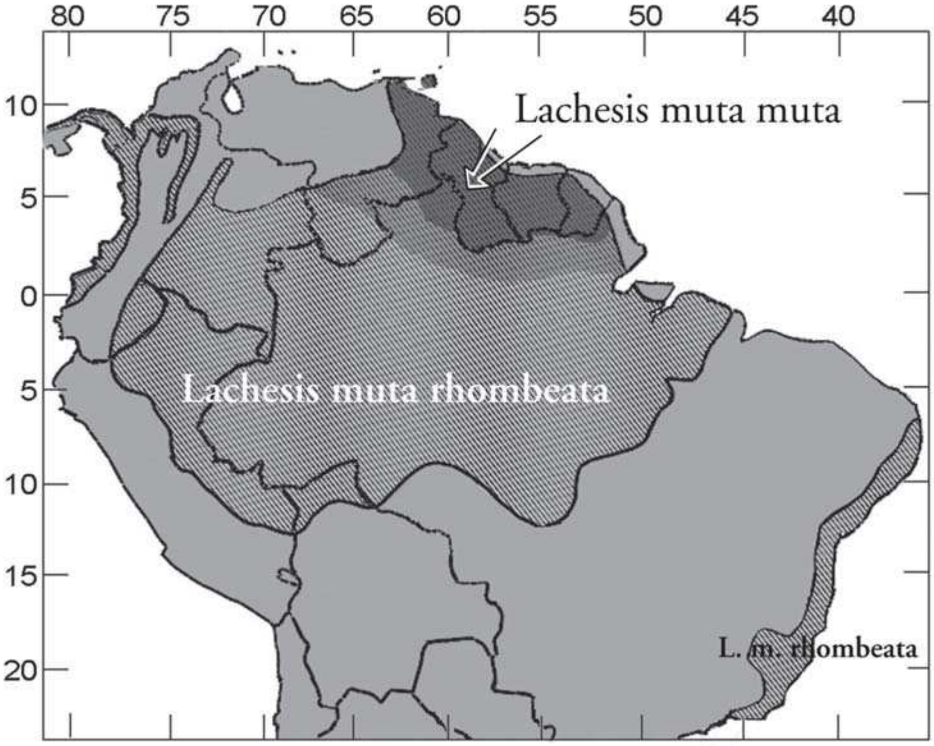
The southern (Amazon Basin) form will be immediately distinguished from the northern (Guiana Shield form) by the striking and vivid head markings, which suggest an “arabesque” or asterisk-like pattern. A blunter anterior head with a somewhat more robust body conformation, flatter (less beaded) dorsolateral scales with an apically biased tubular keel, and dorsal rhombic markings tending to greater vertical barring are other traits that may vari-





Figures 20 - 21. Dorsolateral scalation of *L. muta muta* showing the large, beaded, diamond-shaped scales of the bushmasters of the Guiana Shield. There is little or no free apex; the cranial end is rounded (V- or U- shaped) at the point of emergence from the interstitial skin. The tubercular center rests upon an embossed outer surface. The pattern is strongly rhomboidal. Adapted from Ripa (1999; 2000).





Figures 22 - 23. Map of South American distribution of *L. muta muta* and *L. muta rhombeata*. Figure 22 shows the standard demographic arrangement of *Lachesis muta* in South America, with *L. muta muta* occupying nearly all of the Amazonian regions; and the debated subspecies, *L. muta rhombeata* restricted to Brazil's Atlantic forest belt. Figure 23 shows my recommended revision of this distribution based on morphology: *L. muta muta* becomes restricted to Trinidad, the Guyana Shield and contiguous regions; and the range of *L. muta rhombeata* expanded to include the Amazonian basin and contiguous areas. There is obviously a high degree of overlap, not unexpected in trinominal classification. This is a true clinal variation within a single species of snake, and subspecific classification best addresses these morphological differences accordingly.

ably appear within the south. In some regions, such as along the Rio Pucayacu in Pastaza, Ecuador, the dorsal head markings may be so elaborate as to render the entire head dorsum almost completely black. The extreme southern populations, in Mato Grosso, Brazil, typify this form in most often having the elaborate head pattern (Figure 13). The ground color, when light, may be yellowish-tan, but unlike the Northern form, is rarely pinkish or salmon colored.

Where and to what extent the Amazon Basin form gradates with the forms of the Guiana Shield form, is not easy to determine; but intergradation is a certainty—a case of reproductively compatible populations renewing contact after probable periods of geographic separation. A wider investigation than is in the scope of this chapter would be relevant to discovering their phylogeographic history. Given the difficulty of finding new specimens in already ravaged rainforests, such a task presents almost insurmountable difficulties in the modern day.

The Brazilian Atlantic Forest bushmaster, *L. m. rhombeata* (Wied-Neuwield, 1824; Hoge, 1965) is an apparent homologue of the Southern, or Amazon Basin form of *L. muta muta*. Its justification as a subspecies rests on little more than geographic isolation and tradition; from a purely morphological perspective, subsuming the Amazon Basin form within this trinomial seems a more appropriate systematics. While contemporaneously isolated by vast barriers of unsuitable habitat, its identical physical appearance with these southern Amazonian populations

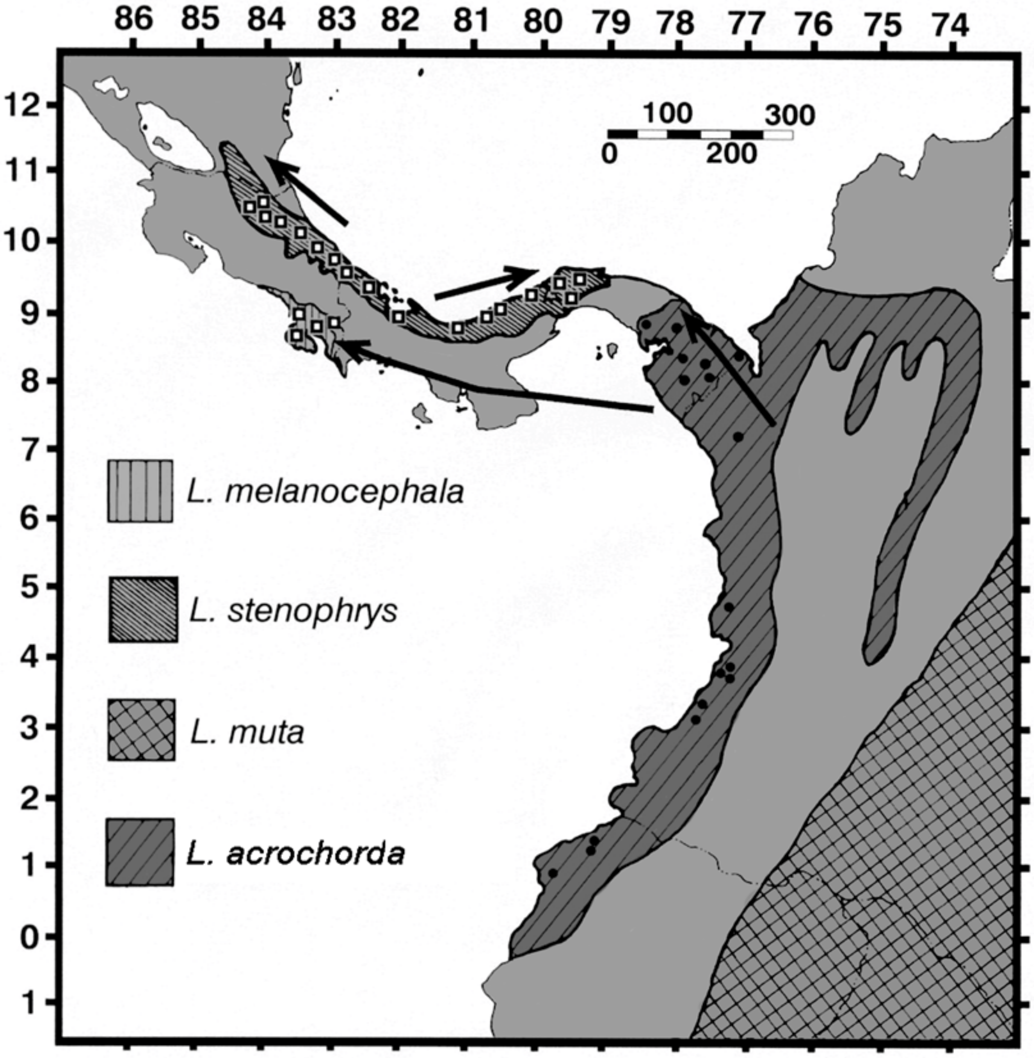


Figure 24. Geographic distribution of the bushmasters of Nicaragua, Costa Rica, Panamá, and eastern Panamá -northwestern South America.

Distributions of *Lachesis stenophrys* and *Lachesis melanocephala* are shown west of longitude 79° W. Distribution of the western Andean form, *Lachesis acrochorda*, is shown east of 78°50 W, and extending south to just below the equator. Despite close proximity to L. stenophrys in Panamá, *L. acrochorda* retains its own identity southwest of the Tropical Dry Forest barrier that divides them, indicating low genetic flow between ancestors. Intergradation between the two populations, in the narrow San Blas corridor, is unlikely due to habitat requirements.

Arrows indicate probable dispersal routes based on morphology. *L. stenophrys* followed a Talamancan fauna dispersal route (sensu Savage, 1966), advancing along a northwestern route into Nicaragua, where it was held back by the Nicaraguan depression. Advancing southeastward across the lowlands of Caribbean Costa Rica and northeastward into an emerging middle Panamá, it was held back by another marine barrier from penetrating eastern Panamá. During this period, the ancestral Chocó bushmaster was possibly already endemic to eastern Panamá on an enduring land mass called the "Panamá Spur" (sensu Lloyd, 1963), perhaps the original source of the westward invasion into Pacific coastal Costa Rica (or western Panamá during a climatically different glacial period). When the Panamanian portal closed in the late Miocene or early Pliocene, areas of unsuitable habitat (Tropical Dry Forest) persisted to bar further eastern colonization by *L. stenophrys*, and western colonization by the northwestern South American form. Today these two allopatric and morphologically distinct snakes exist within 100-150 km of each other, separated only by this vegetation barrier. The occurrence of *L. acrochorda* in the inter-Andean valleys of Colombia is inferred on the basis of Campbell and Lamar's (1989) report of bushmasters occurring in those regions, and from the lack of barriers to prevent it.

betrays recent ancestral ties. Like the latter, the head dorsum is marked with a distinctive "arabesque" pattern (see photographic depictions). Variably, it may have a brighter, more contrasting dorsal body color than the Mato Grosso snake, tending toward yellow rather than orange or reddish-tan. The eye-stripe is usually broad. The scales are often very rugose, seemingly more so than for *L. muta muta*. However, these traits, which appear statistically, may not reflect every case.

It seems likely that *L. m. rhombeata* and the southern (Mato Grosso) populations of Amazon Basin *L. muta muta* once formed a continuous distribution, probably occurring australly across the Brazilian Shield, where recent glacial events resulted in the disjunction of the two populations, creating the habitat barriers that exist today (sensu Dixon, 1979). Zamudio and Greene (1997) place the divergence of the Atlantic Forest snakes from the Amazonian as occurring not more than 300,000 to 800,000 years ago. It seems likely that geologically older events in the Amazon basin conspired to diversify these populations within the Amazon much earlier, and that the Guiana Shield, remaining relatively stable, made for a stable population, so that *L. muta muta* did not follow the trajectory that occurred in the south. Figure 22 - 23 attempts to plot this area and re-describe the distribution for these two forms.

The Central American bushmaster (*L. stenophrys*) is distinguished from all other bushmasters by the lower range of ventral scales, smaller internasal and prenasal scales, ground color (obscure), absence of (or lesser) head markings, increased vertical barring of body blotches, head shape (blunter, from shorter quadrate bones), body conformation (taller, heavier, with higher vertebral ridge), among other traits (see Tables 1-3). Males of this species are usually more darkly colored than females, a less reliable character difference in South America. *L. stenophrys* has two weakly differentiated forms, a Western form (endemic to Caribbean Costa Rica and Panamá west of the Canal) and an Eastern, or Middle Panamanian form (vicinity of the Panamá Canal Zone east to approximately 79° W, but not extending into eastern Panamá). The Middle Panamanian form reaches the Pacific Coast in Panamá, a radiation that *L. stenophrys* achieves nowhere else in Central America.

Differential diagnosis of the Middle Panamanian form can be made by its pattern, with the dorsal rhombs having greater triangulation with less lateral barring, medially spaced with wider areas of ground color and often bordered by a whitish-tan throughout (in the Western form this light border rarely occurs except posteriorly). Pacific coast Panamanian males (a population survives in the Cerro Azul area) may show increased head-markings, a diagnostically reliable sexual dimorphism in all *L. stenophrys*. Ventral scale counts of both forms are consistently low, but examples from the Pacific extremity of the eastern Canal Zone range have been lowest of all: 190 ventral scales were seen in an example from Cerro Azul. This is significant in view of the near but historically disjunct proximity of the Cerro Azul to the eastern Panamanian (Chocoan) form, whose ventral scale range is always higher [211-226] as in *L. muta*. The Pacific coast population also represents the southeastern most extremity of its range, and borders the broadest aspect of the Dry Forest barriers that disrupt bushmaster distribution on the Pacific coast until replaced with the forms of the Darién and Chocó regions of eastern Panamá. Both Western and Middle Panamanian forms of *L. stenophrys* comprise a single population; their varying character is due, if anything, to the extreme attenuation of their very linear range, with episodic separation during the evolving isthmus resulting in periodic refugia (but see below) and/or previous intergradation with populations from northwestern South America.

The close-lying but distinctive "Chocó" bushmaster ranges from eastern Panamá into northwestern Columbia and Ecuador (see Figure 24). Sharing the somewhat heavier body conformation of the two Central American forms (distinct from Guiana Shield *L. muta muta*, however, a morphology already appearing in the Western Amazon), this snake is distinguished from *L. stenophrys* by its elaborate "arabesque-like" head markings, typically narrow eye-stripe, ground color (which ranges to orange-tan and orange-pink), and high ventral scale range (comparable to *L. muta*), among other differences. In my previous papers (Ripa, 1999; 2000), I regarded this form as distinctive, meriting its own designation as "species", but did not take into account an available name for it, from Garcia (1896). In this text, Garcia's *Bothrops acrochorda* becomes *Lachesis acrochorda* accordingly. Chapters 3 and 4 discuss this area in greater detail.

While it is tempting to explain the Chocoan snake as an embodiment of "derived" traits of both South American and Central American origin (either as a recent intergradation, or a wide ranging relict hybrid), this interpretation ignores geologic evidence of vicariance, and temporal estimates of the two better known Central American forms, which logically suggests that they cannot have coexisted as well as evolved separately. Moreover, the tremendous size of its distribution range, which exceeds many times that of both its Central American relatives, would minimize more recent Middle American influences (< 3.5 Mya; see further sections) radiating from across the narrow isthmian link. Morphology supports this, as consistent along the northern range extremity as in the extreme south (Pacific Ecuador). Their isolation would seem to be of longstanding history.

Paleogeographic models to date show that this form has been isolated from other bushmasters for millions of years—by the Andean chain on the east (preventing contact with *L. muta muta* today) and previously by open sea on the north (preventing contact with *L. stenophrys*). Only in more recent times (less than 3.5 Mya; sensu Coates and Obando, 1996) can an apparent juncture with *L. stenophrys* have taken place (see Chapter 3), but the results of this union (if it actually occurred) have not been significant to either group, owing to habitat barriers restricting contact between them. An interpretation based on existing data would place the ancestors of this form as the ancestors of the forms that later developed independently in Central America the results of this union (if it actually occurred) have not been significant to either group, owing to habitat barriers restricting contact between them.

Ad hoc explanations that episodic contact with the Amazonian forms through narrow mountain passes have merely diluted what was once an ancestral population of *L. stenophrys* are inconsistent with the evolutionary history of *L. stenophrys* as it has been portrayed—a species tied to the development of the Talamancan chain, and not the Andean, which are not now nor have ever been, so far as is known, in direct contact. A comparative look at this form is provided in Tables 1- 3. Its meristic characters are subjected to a variance analysis (MANOVA), showing the low probability (Pr > F 0.0001) of this suite of characters being repeated in any other group.

Viewing this population as an intergradation of both widespread forms (i.e., *L. stenophrys* and *L. muta muta*) says nothing about its morphology in present time; all species are continually modified by sympatry. We need to know the state of the population in its present stage of evolution before we can beg its history. The polytypic classification of former times was a haphazard construct even less useful than our newly invented monophyly. Taxonomy, which initially demands as much of a subspecies as it does of a species (one must set about describing it), ultimately expects far less of a subspecies: the possibility of intergradation remains an inherent part of the trinominal rank. Hence, nothing is stated. Within the older usage, one did not argue that *L. muta stenophrys* must inevitably bleed into *L. muta muta* somewhere; it was assumed that it must. But with the latest treatment of the bushmasters as three distinct species (e.g. Ripa, 1994; Zamudio and Greene, 1997), where does the enigmatic "middle" population "fit"? A subsequent chapter (derived from Ripa, 1999, and 2000) offers a comprehensive look at this unresolved taxon, revealing its nearer resemblance to the Amazonian South American lineages than to the Central American *L. stenophrys,* however, showing how difficult it is to bring it into either group. This, with the available paleogeographic evidence suggests that the Chocoan bushmaster represents a widespread, distinct and allopatric population that has been separated from the other bushmaster species for millions of years. Thus *L. acrochorda* meets Wiley's (1978; modified from Simpson, 1961) definition of a distinct evolutionary species, as a "single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate."

Geographic variation in the South American bushmasters (*L. muta muta* and *L. muta rhombeata*) might reflect paleoenvironmental and climatic changes as recent as the Pleistocene (sensu Potts and Behrensmeyer, 1992; Van der Hammen and Absy, 1994), or paleogeographic events going back much further in time. (Zamudio and Greene [1997] refute a "forest refugia" hypothesis as the cause of speciation in *Lachesis*, with a temporal estimate of divergence having a deepest branching in the Tertiary). Certainly the shared traits of the two Central American forms seem derived from the Amazon Basin populations rather than from the geographically more distant forms of the Guiana Shield. Interpreting the two Central American species to be evolutionarily "newer" than the Amazonian (diverging 11–6 Mya; Zamudio and Greene, 1997), and these being less dissimilar, the Amazon Basin form is logically the more recently evolved of the two phases of *L. muta muta.* This implies an initial radiation from an eastern rather than a western origin.

The Guiana Shield, a "stable positive unit since the Middle Precambrian" (Stuart, 1966) is the oldest large, stable landmass in northern South America currently inhabited by bushmasters. While the age of a landmass does not ensure the origination of a species in that landmass, the unstable orogeny of the frequently deluged Amazon Valley during its early history does not offer many good opportunities for the development of a highly specialized fauna with habitat requirements like the bushmaster. Northwestern South America was intermittently flooded until the mid-Miocene, while the eastern Andean area was underwater at various times until the Paleocene (Nygren, 1950; Harrington, 1962; Jacobs et al., 1963). The receding North Andean geosyncline would probably have left the western Amazon Valley a vagarious habitat of partially submerged swampland for an indeterminate period during the Tertiary (pers. interpretation of the literature); and as further subsidence of the Amazon Valley drowned the drainages of the Magdalena, the Cauca, and the Orinoco during the Tertiary (Van der Hammen, 1961; Hoorne, 1994), and it is reasonable to suppose that unsuitable habitat conditions for bushmasters (which have specialized moisture requirements and avoid swamps), might have prevailed for a considerable period afterwards. The Guiana Shield provides an ecologically more reliable place for evolutionary development.

Similar events seem to have taken place in Central America, although more recently. From the available geological data, the Talamancan orogeny appears to have arisen from northwest to southeast, culminating in the closure of the Isthmian Link about 3.5 Mya (Savage, 1982; Coates and Obando, 1996). *L. stenophrys* appears to have followed a Talamancan route of dispersion such as is seen in other fauna assemblages (sensu Savage, 1966), colonizing these new middle Panamanian lowlands as the portal closed.

Thus, while bushmasters are now endemic to the Amazon Valley, unsuitable conditions persisting there long after the emergence of the first land bridges might have presented barriers to bushmaster ancestors within that region. During a long westward immigration through these developing lowlands, the ancestral Amazon Basin forms may have differentiated (from the Guiana Shield forms) even before the next Andean uplift would further segregate this population into East Andean (Amazon Basin) and West Andean (Chocoan) forms. Based on morphology, I have no trouble viewing the two forms of *L. muta muta* as distinct races (or "subspecies") of a single taxon, a useful systematics. Modifying their present range to show their overlaps will be even more useful, however. The southern bushmasters (Atlantic Forest, Mato Grosso, etc.,), appear to form a separate clade from those of the north (Guiana Shield). *L. muta rhombeata* seems basically a southern Amazonian (Amazon Basin) form while the northern populations of the Guianas and Trinidad form a good unit within themselves (see Figure 22 - 23). The former almost always show the strong head markings usually lacking in the north, and there may be other color variations. Thus I recommend making use of the subspecific *L. m. rhombeata* rather than abandoning it, however extending its range into those western (Amazonian) regions where morphology supports it. Owing to present day juncture and probable widespread intergradation of what are no longer distinct populations, the search for exact divisions will be difficult and perhaps fruitless. But systematics, an abstract concept, does not demand exact determinates among populations presumed to intermingle. There is no genetic basis for subspecific classification that cannot better be answered by specific classification, when such can be shown. When it cannot, a triname forms a useful and descriptive purpose.

The blackheaded bushmaster (*Lachesis melanocephala*) of Southeastern Costa Rica is unique for a jet-black cap that masks the entire dorsum of its head, from snout to nape, including the eyes and ocular stripe. No other viper in the Americas has this distinctive appearance. Its high ventral scale count distinguishes it from *L. stenophrys* (Solórzano and Cerdas, 1986), being comparable to *L. muta* and the Chocoan form (Ripa, 1999; 2000). Other differences include an anteriorly shortened snout, the dorsal height of which may be equal to or elevated above frontal; significantly smaller scales than any other bushmaster; a very pale yellowish-white ground color; and a darker interstitial skin causing the scales to stand out markedly, lending the scales a uniformly speckled or braided appearance, especially in males (Ripa, 1994). Significantly, the ventral scale counts favor *L. muta* rather than the close-lying *L. stenophrys*. The Talamancan mountain chain has prevented contact between these two species for millions of years.

Lachesis stenophrys is an essentially coastal species of lower Middle America. With its blunt snout, lower ventral scale count, stockier body conformation, dull greenish-gray coloration, and usually nearly patternless head, it is the least like the other members of the genus. It seems to have evolved alone and separately from the other bushmasters in the Talamancan orogeny, thence following the developing isthmus toward the southeast. It is logical that the Eastern (Middle Panamanian) phase of *L. stenophrys* (with its larger prenasals and occasional headmarkings, both similarities to *L. muta* and the Chocoan *L. acrochorda*) is the more recent arrival from an invasion initiated within the northwestern Talamancan regions of Panamá and Costa Rica. Barriers of unsuitable habitat and/or a preexisting marine barrier reduced if not entirely prevented its contact with the populations of the Chocoan refuges farther east. The whole assemblage (of *L. stenophrys*) can be viewed as a strong taxonomic unit if described according to the proposed distribution range given in Figure 24. To muddle it with the Chocoan form undermines the present determination of "what is" *L. stenophrys*, ultimately disrupting the present and very useful species concepts now evolving in this genus.