

**A Translation  
of  
Mertens, R. 1956. Das Problem der Mimikry bei  
Korallenschlangen.**

*Zoologische Jahrbucher, Abteilung für Systematik, Ökologie und Geographie der Tiere 84:541-576*



**Andrew M. Durso**

Department of Biological Sciences  
Florida Gulf Coast University

**SMITHSONIAN  
HERPETOLOGICAL INFORMATION  
SERVICE  
NO. 160**

**2023**

## SMITHSONIAN HERPETOLOGICAL INFORMATION SERVICE

The first number of the SMITHSONIAN HERPETOLOGICAL INFORMATION SERVICE series appeared in 1968. SHIS number 1 was a list of herpetological publications arising from within or through the Smithsonian Institution and its collections entity, the United States National Museum (USNM). The latter exists now as little more than the occasional title for the registration activities of the National Museum of Natural History. No. 1 was prepared and printed by J. A. Peters, then Curator-in-Charge of the Division of Amphibians & Reptiles. The availability of a NASA translation service and assorted indices encouraged him to continue the series and distribute these items on an irregular schedule.

The series continues under that tradition. Specifically, the SHIS series distributes translations, bibliographies, indices, and similar items judged useful to individuals interested in the biology of amphibians and reptiles, and unlikely to be published in the normal technical journals. We wish to encourage individuals to share their bibliographies, translations, etc. with other herpetologists through the SHIS series. If you have such an item, please contact George Zug [zugg @ si.edu] for its consideration for distribution through the SHIS series.

Our increasingly digital world is changing the manner of our access to research literature and that is now true for SHIS publications. They are distributed now as pdf documents through two outlets:

**BIODIVERSITY HERITAGE LIBRARY.**

[www.biodiversitylibrary.org/bibliography/15728](http://www.biodiversitylibrary.org/bibliography/15728) All numbers from 1 to 140 [1968-2009] available in BHL.

**SMITHSONIAN LIBRARY'S WEBSITE.** <https://repository.si.edu/handle/10088/842>

2023 – Division of Amphibians & Reptiles  
National Museum of Natural History  
Smithsonian Institution  
ISSN 2331-7515

Cover Image: *Micruroides euryxanthus*  
By Andrew M. Durso

MERTENS, R. 1956. DAS PROBLEM DER MIMIKRY BEI KORALLENSCHLANGEN.  
*Zoologische Jahrbucher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 84:541-576  
 Translated by Andrew Durso.

## Contents

- I. Introduction
- II. Morphology & Taxonomic Overview
  - 1. Coral Snake Phenotype
  - 2. Snakes with a Coral Snake Phenotype
- III. Explanations Other Than Mimicry
  - 1. Coral Snake Phenotype as a Shared Derived Character
  - 2. Coral Snake Phenotype and Randomness
  - 3. Coral Snake Phenotype and the “*Genius Loci*”
  - 4. Coral Snake Phenotype as a Result of Directed Evolution (Orthogenesis)
  - 5. Coral Snake Phenotype as Cryptic Camouflage
- IV. Coral Snake Phenotype as an Example of Mimicry
  - 1. General
  - 2. Ecological Importance of the Coral Snake Phenotype
  - 3. Snake Predators and Their Ability to Perceive the Coral Snake Phenotypes
  - 4. The Mimicry Postulates of Wallace
  - 5. Relative Abundance of “True” and “False” Coral Snakes
  - 6. Defensive Abilities of Models and Mimics
  - 7. The Evolution of Coral Snake Mimicry
- V. Concluding Remarks
- VI. Summary
- VI. Bibliography

Dedicated to the one who knows coral snakes best, Dr. Karl Patterson Schmidt, on his 65th birthday on the 19<sup>th</sup> of June, 1955.

## I. INTRODUCTION

If the literature on snake mimicry is to be enriched by this treatise, it is because the author acquired a new viewpoint on this interesting topic during a 10-week stay at the Butantan Institute in São Paulo at the end of 1954. This led to a critical examination of the phenomenon of the exclusive occurrence of coral snakes in the New World, at the end of which lies the mimicry question. The main focus of the discussion has not been placed on the often-discussed morphological or taxonomic aspects, but on the ecological-evolutionary aspects.

For enabling the Brazil trip, I thank the German Research Institute, and for the kind invitation to work at the Butantan Institute, I humbly thank its director, Dr. Afrânio do Amaral. My colleague and friend, Mr. A. R. Hoge, the head of the snake department, made my stay at Butantan very pleasant in every respect through his constant help, procurement of materials, and warm hospitality. He and his staff are sincerely thanked. I also must thank the gentlemen Arthur Loveridge (Museum of Comparative Zoology, Cambridge, Mass.) and Dr. Heinz Wermuth (Zoological Museum, Berlin) for loaning some coral snakes from their collections. Dr. K. Max

Hecht allowed me to inspect the manuscript on the mimicry problem written by him and Daniel Marien prior to publication (see bibliography). Finally, it should be mentioned that the author presented the main results of this work at the “evolution colloquium” in the Zoological Institute of the University of Hamburg on December 4, 1955, and owes several suggestions to the ensuing discussion with Prof. Koehler, Prof. Kosswig, Dr. Meise, and Prof. Remane.

By the beginning of the last century, it had already been noticed by herpetologists that very different snakes from tropical America have a very similar and striking color pattern consisting of red, black and yellow (or whitish) rings or cross bands. For example, Weid (1820) pointed out that the snakes referred to in Brazil as “coral snakes” belong to quite different genera. Around the same time that Bates first used the term “mimicry” and illustrated the concept using South American butterflies, Cope (1860) gave the phenomenon of coral snakes renewed attention: he mentioned the venomous genus *Elaps* (= *Micrurus* after the current nomenclature) and the sympatric harmless species in the genera *Oxyrhopus* (*Pseudoboa*), *Erythrolamprus*, *Pliocercus*, and *Lampropeltis*. It was Wallace (1867) who believed he had found an explanation for this similarity, namely mimicry. Since that time, coral-patterned snakes have often been cited as an example of true mimicry (as distinct from mere “lookalikes”)<sup>1</sup>, in which the genus *Micrurus*, *i.e.*, the “true” coral snakes, all of which are highly venomous, have been presumed to be the models, and the harmless or “false” coral snakes<sup>2</sup> to be imitators or mimics.

However plausible this explanation may be, this view has also found outspoken opponents. Among the reptile researchers who denied coral snake mimicry especially emphatically are Gadow (1908, 1911) and Werner (1907, 1917). The former was a proponent of goal-oriented evolution or orthogenesis<sup>3</sup>, such that red-black-yellow snakes without mutual relations should inevitably become similar to each other. For Werner, however, snake mimicry was nothing more than a purely fortuitous convergent phenomenon. I once (1946) held a similar view: the number of different snake species and subspecies (a total of about 3000) is so disproportionate to the possible variations in color, that it would be quite conceivable that similar colors and patterns could evolve in completely different, distantly-related species of snakes, without invoking that the color of venomous snakes could play a role in that of harmless ones (*i.e.*, mimicry). In contrast to such views, Sternfeld (1913), a student of Weismann and therefore a firm believer in the theory of natural selection, tried in a spirited way to refute all the arguments of Gadow and Werner, where he extends the mimicry theory without limitation not only to coral snakes, but rather uncritically to many other species of snakes. Recently, Dunn (1954) pointed out that the problem of coral snake mimicry still existed, in support of which he presented some data from Panama. Dunn’s view was convincingly corroborated by Hecht and Marien (1956), whereas Brattstrom (1955) has spoken out very firmly against the mimicry hypothesis in coral snakes.

## II. MORPHOLOGICAL & TAXONOMIC OVERVIEW

### 1. The coral snake phenotype

“*There is no prettier and more conspicuously colored object than a live Coral Snake*” (Gadow). The color pattern of coral snakes is most striking indeed. These animals generally have a red background color, which varies from a luminous cinnabar or coral to deep carmine or burgundy and is interrupted by black and yellow (or white) rings or cross bands in a particular arrangement. The red interspaces, the scales of which often have black tips, are wide or narrow, sometimes so

narrow that they can also give the impression of being rings. The black rings have sharply-defined edges and can be individual or arranged in groups of two, three, four or even five. The distribution of these color zones can be broadly classified into the following four types of patterns (the examples are confined to toxic or slightly toxic species).

I. red-yellow-black-yellow-red; the black bands stand alone (monads<sup>4</sup>). Examples: *Micrurus corallinus* (Plate 10, Fig. 19), *Micrurus nigrocinctus* (Plate 11, Fig. 24) and other members of the genus, *Micruroides euryxanthus*, *Erythrolamprus mimus* (Plate 10, Fig. 22), *Rhinobothryum bovallii* (Plate 7, Fig. 9), *Pliocercus elapoides* (Plate 11, Fig. 26), *Sibynophis venustissimus* (Plate 9, Fig. 18), *Chionactis palarostris*, *Hydrops martii* (Plate 8, Fig. 14), *Procinura aemula*, *Dipsas anthracops*.

II. red-black-yellow-black-red; the black rings form groups of two (dyads). Examples: *Erythrolamprus aesculapii venustissimus* (Plate 7, Fig. 5), *Cemophora coccinea*, *Sonora michoacanensis*, *Lampropeltis doliata polyzona*, *Lampropeltis d. micropholis* and other races (Plate 7, Figs. 6-8), *Sibynophis cyclurus* (Plate 9, Fig. 16), *Lystrophis semicinctus* (Plate 12, Figs. 28, 30), *Tantilla annulata*.

III. red-black-yellow-black-yellow-black-red; the black rings form groups of three (triads). Examples: *Micrurus lemniscatus*, *Micrurus frontalis* (Plate 6, Figs. 1, 2) and many other species of this genus, *Pseudoboa trigemina* (Plate 6, Fig. 4), *Simophis rhinostoma* (Plate 6, Fig. 3). *Simophis rhinostoma* exhibits individual variation such that in some individuals, there can be so much black pigment in the middle of the yellow rings that the impression of a narrow secondary black ring is given; in some individuals, it may appear that the black rings can form groups of five (pentads) (though this is not very conspicuous; e.g., Plate 14, Fig. 39). *Micrurus smithi*<sup>5</sup> can also have black rings in such groups of five.

IV. red-black-yellow-black-yellow-black-yellow-black-red; the black rings form groups of four (tetrads). Examples: *Erythrolamprus aesculapii tetrazona* (Plate 14, Fig. 38), *Atractus latifrons* (some variants).

Among the *Micrurus* species that have three-colored patterns, the black rings are either individual or in groups of three or five, alternating with yellow or white. No *Micrurus* have black rings in pairs or in groups of four. Pairs occur in the “false” coral snakes most often because they simply arise when a black transverse spot or ring divides a lighter area through the middle. Triplets are far less common in the “false” coral snakes. Some harmless coral snakes are confusingly similar to *Micrurus* species, such as *Pliocercus elapoides* to *Micrurus nigrocinctus* in El Salvador (Plate 11, Figs. 24-27); *Erythrolamprus mimus micrurus* is identical in color and pattern with *Micrurus clarki* in Panama (Plate 10, Figs. 21, 22.); a variant of *Erythrolamprus aesculapii venustissimus* (Plate 10, Fig. 20) can barely differ from *Micrurus corallinus* (Plate 10, Fig. 19). *Simophis rhinostoma* (Plate 6, Fig. 3) or *Pseudoboa trigemina* (Plate 6, Fig. 4) resemble *Micrurus frontalis* or *Micrurus lemniscatus* (Plate 6, Figs. 1, 2).

The observation of living coral snakes shows, moreover, that it is hard to recognize how the black rings are arranged on a fast-moving, forward-crawling snake. The general impression of the color and pattern is always the same, no matter which genus the snake belongs to; in any event, one is always surprised by the striking appearance of these snakes, regardless of whether they are toxic or not (some color pictures of these animals are published in Mertens [1956, 1957]). The extent of the similarity between “true” and “false” coral snakes, especially preserved specimens, is underscored by the fact that researchers have described harmless species as members of the genus

*Micrurus* (or *Elaps*). As late as 1927, Ernst Ahl, the first herpetologist at the Zoological Museum in Berlin, described the completely harmless *Atractus latifrons* (Plate 13, Fig. 36) as a new species of *Micrurus* (“*Elaps herthae*”)!<sup>6</sup> In fact, the similarity between “true” and “false” coral snakes extends not only to the coloration and pattern, but also to the body form and proportions, and one even notices similarities in certain details of the behavior, to which we will return.

The pattern on the underside of coral snakes is quite striking. In the “true” coral snakes (*Micrurus*, *Micruroides*), the pattern on the venter is about the same as on the dorsum<sup>7</sup>: that is, the rings and the red zones are continuous (Plate 11, Fig. 25). This is also the case for many “false” coral snakes (Plate 11, Fig. 27), but not all. There are, for example, those who have the coral snake phenotype<sup>8</sup> only on the dorsal side, whereas the underside is monochrome white or gray and bears no trace of a coral snake pattern. This is the case in, for example, the small harmless *Cemophora coccinea* in the southeastern United States, in *Sibynophis venustissimus* (Plate 9, Fig. 18) from Central America or in *Lystrophis semicinctus* (Plate 12, Figs. 29, 31) from South America. The South American species *Pseudoboa trigemina* is very curious in this respect: they have black rings arranged in triplets against a coral red background. Specimens from northern Brazil have porcelain-white venters, whereas those from southern Brazil have a marked tendency for the coral snake pattern, including the dark transverse bands, to extend onto the venter (Plate 13, Fig. 33). If mimicry really exists, the southern form of *Pseudoboa trigemina* would represent a more advanced form. In addition to snakes with this “typical” coral snake phenotype, which is always tri-colored, there are also many species that are two-colored, having only a black-red or black-yellow (or white) banding pattern, including some species in the Old World. These include *e.g.*, *Anilius scytale*, *Pseudoboa clathrata*, and *Tropidodipsas fasciata* in the New World, and various other snakes, including elapids, in the Old World. There are also such species within *Micrurus*. In the following, such snakes are not considered, even though they are phylogenetically of significance as primitive forms of the three-colored coral snakes. Among these there are some species in which the banding is tri-colored, but the third hue appears only on the flanks: for example, the Central American *Scolecophis atrocinctus* (Plate 8, Fig. 11), which has black and orange crossbands on the back, but with the orange replaced by ivory on the sides. *Pseudoboa rhombifera* is exactly the opposite: the banding on the back is black and yellow, but black-red on the flanks. *Micrurus mipartitus* (Plate 8, Fig. 10) has a vivid black and white banded body, but the head has a sealing-wax red spot, and the three caudal bands are not white, but sealing-wax red. None of these snakes give the impression of tri-colored rings or bands, as with the “typical” coral snake phenotype.

## 2. Snakes with a coral snake phenotype

The coral snake phenotype is present in a narrow sense in the following 18 snake genera:

1. *Micrurus*. About 60 species in this genus of “true” coral snakes are known at present, which can be divided into many geographical races. Of these, more than two-thirds have a characteristic coral snake phenotype of black transverse bands with sharply-defined edges, either as monads (“*corallinus*” group, Plate 10, Figs. 19 & 21; Plate 11, Fig. 24) or arranged in groups of three (“*frontalis*” group, Plate 6, Figs. 1 & 2). It is noteworthy that the latter group is discontinuously distributed, both in South America (into Panama) and in Guatemala and southern Mexico. Recently, Marianne von Harnack (1953) quite extensively analyzed *Micrurus* patterns and their variation, but unfortunately little attention was paid to the snakes’ nomenclature; their “*nigrocinctus*” group corresponds to our “*corallinus*” group, their “*ibiboca*”<sup>9</sup> group to our

“*frontalis*” group.

2. *Micruroides*. This North American genus is closely related to *Micrurus* and contains only a single species (*Micruroides euryxanthus*), which is characterized by very wide yellow rings on either side of solitary black ones. The third genus of Neotropical elapids (*Leptomicrourus*) contains no species with a coral snake phenotype.

3. *Erythrolamprus*. All species of this South and Central American genus bear a pronounced coral snake phenotype<sup>10</sup>. The ancestral pattern is apparently single sharply demarcated black rings, as in *Erythrolamprus mimus* (Plate 10, Fig. 22), equivalent to the “*corallinus*” group of *Micrurus*. These rings can be divided in two or even four by lightening in the middle: within a single species, *Erythrolamprus aesculapii*, all stages from solitary spots (“*monozona*”) to groups of two (Plate 7, Fig. 5) or groups of four (Plate 14, Fig. 38) are present. The most common forms in South and Central America have black bands in groups of two: *Erythrolamprus a. aesculapii*, *E. a. venustissimus*, and *E. a. bizona*. Forms with triplets, *i.e.*, similar to the “*frontalis*” group of *Micrurus*, are not present in the genus *Erythrolamprus*.

4. *Sibynophis*. Within this ancient snake genus, *Sibynophis venustissimus* (Plate 9, Fig. 18), with its characteristic *Micrurus*-costume stands out: black, sharp-edged crossbands, alternating with wide red ones. In contrast, in *Sibynophis cyclurus* (Plate 9, Fig. 16) the black bands are divided in the middle by a yellow band, so that they appear arranged in pairs against a red background. Other species are remarkable in that they have crossbands only on the front of the body. The genus *Sibynophis* is distributed in Central America, Asia and Madagascar; the Neotropical species have recently been separated as a distinct genus (*Scaphiodontophis*), but it is only assigned the rank of subgenus.

5. *Atractus*. This species-rich genus is also Neotropical. Of the many species, only two have a coral snake phenotype: most pronounced in *Atractus latifrons* (Plate 13, Fig. 36), less so in *Atractus elaps*. In *latifrons* the black bands are arranged in pairs or in groups of four but can also stand alone.

6. *Pliocercus*. Small, Central American snakes within which *Pliocercus elapoides* (Plate 11, Fig. 26) is characterized by a tendency to form geographical races. This snake has a typical coral snake phenotype, which is made up of red and sharp-edged black rings, which can be arranged in triplets.

7. *Chionactis*. Like *Sonora*, these are small, ground-dwelling snakes, some of which have a significant coral snake phenotype; *e.g.*, *Chionactis palarostris*, *C. occipitalis annulata* and *C. o. klauberi*. These are reminiscent of the simple, three-color *Micrurus* pattern (with solitary black bands), which also occurs in the sympatric *Micruroides euryxanthus*.

8. *Procinura*. This is a monotypic genus; the few known specimens of the single species, *P. aemula*, have a coral snake phenotype similar to that of *Micrurus fulvius*, *i.e.*, the black rings stand alone.

9. *Rhinobothryum*. This genus includes *Rhinobothryum bovallii* (Plate 8, Fig. 9), a large, well-known snake from Costa Rica, Panama and Colombia with very eye-catching black-white-red banding, with white bands that stand out by their width and the black standing alone.

10. *Dipsas*. Among the many Neotropical species of snail-eating snakes, there are some whose color pattern at least very closely approximates the coral snake phenotype. For example, *Dipsas anthracops* has black and brick red cross bands that are separated from each other by yellow zones—thus, a simple form of a *Micrurus* pattern (without triplets). Like *Sibynophis*, *Dipsas* is of

theoretical importance to the mimicry question.

11. *Hydrops*. Among the species of this South American snake genus is *Hydrops martii* (Plate 8, Fig. 14), a snake which is characterized by a dark red ground color with many black cross-bands; these are delimited from the red color by whitish spots in front and behind.

12. *Lampropeltis*. A very diverse snake genus from North and Central America that enters northernmost South America (Colombia, Ecuador). This genus contains many very handsome "false" coral snakes, such as the different subspecies of *Lampropeltis doliata* (Plate 7, Figs. 5-7). Other examples are *Lampropeltis pyromelana* and *L. zonata* in western North America. The black bands of these snakes are arranged in more-or-less distinct pairs.

13. *Cemophora*. The only species of the genus (*C. coccinea*) is North American and has a pattern reminiscent of *Lampropeltis doliata* in the southern United States, since the black cross bands are in groups of two, each band separated from its partner by a yellow zone.

14. *Sonora*. Within this genus, the Mexican species *Sonora michoacanusensis* has a pronounced coral snake phenotype (the black bands are in groups of two), but the other species also show a tendency towards this coloration.

15. *Lystrophis*. This genus is restricted to southern South America (southern Brazil, Argentina) and contains a very significant coral snake form: *Lystrophis semicinctus*, with black-white-red bands on the back, but not on the ventral side, the black bands forming groups of two. It is noteworthy that the pattern of this snake varies quite considerably, probably representing subspecies (Plate 12, Figs. 28, 30).

16. *Tantilla*. Dunn (1954) listed *Tantilla annulata* from Central America as among the three-colored coral snakes, although their black and yellow banding against a reddish-brown background is less well-developed than the other examples mentioned here.

17. *Pseudoboa*. A genus that consists of about 20 species, which is split by some herpetologists (*Oxyrhopus*, *Clelia*). The distribution of *Pseudoboa* is approximately the same as that of *Erythrolamprus*. Species of *Pseudoboa* tend to have a transversely banded pattern, but in fact a pronounced coral snake phenotype is present in only one species, *Pseudoboa trigemina* (Plate 6, Fig. 4; Plate 13, Figs. 32, 34). In this species the ancestral uniformly black dorsal flecks are so light in the middle that groups of three are formed, creating a resemblance to the "true" coral snakes of the "*frontalis*" group. Often, the left and right halves of one or more dorsal blotches do not perfectly align, corresponding to the ancestral asymmetrical dorsal pattern. However, the similarity to *Micrurus* is not in any way thereby impaired.

18. *Simophis*. The neotropical genus *Simophis* is monotypic. Many subspecies of *Simophis rhinostoma* are distinguished; they are all characterized by a coral snake phenotype, in which the black rings are in groups of three. In each group, the middle ring is much wider than its two partners in the typical form (Plate 6, Fig. 3). Occasionally, the black rings can form groups of five (Plate 14, Fig. 39).

### III. EXPLANATIONS OTHER THAN MIMICRY

The following six hypotheses are possible explanations for the phenomenon of the exclusive occurrence of the coral snake phenotype in the Americas:

1. The coral snake phenotype is a shared, derived character inherited from a common ancestor.
2. The coral snake phenotype has evolved purely randomly.



3. The coral snake phenotype is attributable to the effect of some environmental conditions that exist only in the range of coral snakes (“*genius loci*”).
4. The coral snake phenotype is a result of goal-oriented evolution (orthogenesis).
5. The coral snake phenotype is the result of natural selection for camouflage.
6. The coral snake phenotype is a form of mimicry.

### 1. *The coral snake phenotype as a shared derived character*

The first assumption implies that all snakes with coral snake patterns are descended from a single common ancestor and are one another’s close relatives<sup>11</sup>. It should be noted that the formation of a coral snake phenotype in these various snakes should be due at least in part to the effect of the same genes. But a close kinship of all snakes with coral snake patterns obviously cannot be concluded from that fact alone. The 18 genera that include species with coral snake phenotypes include highly venomous, slightly venomous and non-venomous species, spread out over two families, Elapidae and Colubridae. Within the colubrids there are snakes with a coral snake phenotype in 4 subfamilies and among both the aglyphous and opisthoglyphous series. The taxonomic grouping of the snake genera in which a coral snake phenotype occurs is:

Elapidae: *Micrurus*, *Micruroides*.

Colubridae:

Sibynophinae: *Sibynophis*.

Colubrinae (aglyphous series): *Lampropeltis*, *Cemophora*, *Sonora*, *Chionactis*, *Simophis*.

Colubrinae (opisthoglyphous series): *Procinura*, *Tantilla*, *Rhinobothryum*.

Xenodontinae (aglyphous series): *Pliocercus*, *Hydrops*, *Atractus*, *Lystrophis*.

Xenodontinae (opisthoglyphous series): *Erythrolamprus*, *Pseudoboa*.

Dipsadinae: *Dipsas*.

If all these snake genera belonged to a single ancestral group, the problem would be solved easily and convincingly. One could, for example, imagine that most of the New World colubrids are more closely related to each other than to Old World groups of this family; the tendency to form a coral snake phenotype would then be a trait based on kinship. This is probably true for some Neotropical genera due to the long periods of isolation of the South American continent, but there are those that are certainly more closely related to genera in North America, where the faunistic influence of the Old World is much clearer. The elapid ancestors of the “true” coral snakes certainly came from the Old World, likely immigrating to the Americas from Southeast Asia across the Bering land bridge (see pp. 22-23). If it were possible to prove that the New World elapids were not descended from the Old World elapids, but instead evolved from the New World colubrids, the coral snake phenotype would be more easily interpreted as having a common heritage, and the solution of the mimicry problem would be much easier. But such a view is untenable; rather, it is certain that *Micrurus* and its New World relatives, like many groups of mammals, reached tropical America from the Old World.

Evidence of the coral snake phenotype as a sign of kinship does not exist at this time. Rather, we see again and again that relatives of “true” and “false” coral snakes in the Old World completely lack a coral snake phenotype. Among the latter, it is missing among the Oriental and Malagasy species of the genus *Sibynophis*, which usually have a coral snake phenotype in Central America. Significantly, within elapids a tendency toward a ringed pattern is in fact an ancestral trait, as evidenced by a handful of Asian and African relatives of *Micrurus* and *Micruroides*. I will

mention here the southeast Asian genus *Calliophis* and the African genera *Elapsoidea* and *Boulengerina*. The latter genus includes *Boulengerina annulata* (Plate 8, Fig. 12), a large aquatic elapid which is not coral colored, but rather has striking black rings arranged in groups of two against a brown background, so that each pair of rings is separated by a bright, narrow intermediate ring (a pattern that does not occur in *Micrurus*). Furthermore, in Australia, the center of diversity for elapids, there are obviously a number of ringed forms (e.g., *Rhynchoelaps*), although no species that has a true coral snake phenotype. The degree of similarity between Old World elapids and New World *Micrurus* species is not even close to that between *Micrurus* and some of their alleged mimics from other genera.

## 2. *The coral snake phenotype and randomness*

Chance is ultimately the basis of all evolutionary events, and so, one could interpret the coral snake phenotype as a purely randomly occurring phenomenon in New World snakes. In fact, the coral snake phenotype could have been distributed by chance among some distantly-related species of snakes, especially since this process, genetically speaking, seems not to be very involved and is perhaps based on the interaction of a few genes or even just a single gene. Alone against such an explanation speaks the important fact that at least 75 snake species in 18 New World genera have the coral snake phenotype, and then only in the tropical and subtropical zones. It seems that about a quarter of all snake species live in this area. But one does not encounter the coral snake phenotype among the remaining three quarters of snake species! So if only chance was at work in the formation of the coral snake phenotype, the question arises: why did chance produce nothing of the kind among the much more numerous species of snakes in Europe, Africa, Asia and Australia? As we have already seen, in the Old World only the venomous elapids have patterns reminiscent of a coral snake phenotype. A few other Old World snakes (e.g., *Oligodon albocinctus*; Plate 8, Fig. 13) also have pattern variations that approach the coral snake phenotype; even though none among them approaches a “true” coral snake phenotype in our sense, such cases are nevertheless of considerable theoretical importance.

For the reasons set forth herein the explanation of the coral snake phenotype only through the inheritance mechanism “without effective control by selection pressures of either their physical or biotic environment” (i.e., through genetic drift<sup>12</sup>) may also be satisfactory. Allee (1949: 226-227) apparently applies this statement only to *Micrurus*, but if he would have also taken into account the many “false” coral snakes, he would probably not have come to this conclusion.

## 3. *The coral snake phenotype and the “genius loci”*

Thirdly, the influence of some environmental factors which act only within the geographic distribution of coral snakes would be conceivable. This is essentially the famous “genius loci” idea<sup>13</sup>, which has conventionally been used to explain the coral snake phenotype. However, it is highly unlikely that the conditions of life in the New World have a special character that would promote the formation of a red-black-white color pattern in snakes. This color pattern is undoubtedly most common in the rainforests of the tropical zone, but it is not absent in the sparse bushlands or the cool mountains. There are even snakes with this pattern in dry, desert-like areas (Arizona, Peru), but only in the New World. Perhaps one might think that under the influence of a humid tropical climate, the evolution of elaborate color patterns is easier. For example, take the red hue of the North American genus *Lampropeltis*, which increases in intensity from north to south,

while in the South American snake *Leimadophis poecilogyrus* this same pattern occurs in reverse; the northern race from Rio de Janeiro has red spots, which are missing from southern Brazilian and northern Argentinean examples. But such a climatic "*genius loci*" nonetheless fails to explain the occurrence of the coral snake phenotype only in snakes of the New World continents. Heikertinger (1954) relies too heavily on the "*genius loci*" in his studies of insect mimicry; but even for him this concept retains "a vestige of the mysterious".

Recently Dunn (1954) called attention to a peculiar relationship: approximately 85% of Panamanian coral snakes (in the broad sense) feed exclusively or mainly on snakes. This is quite remarkable, and in fact has been known for some time for the genus *Micrurus*, although these snakes also eat lizards. A live *Micrurus frontalis* that I currently keep lives exclusively on lizards, while a magnificent *Erythrolamprus aesculapii venustissimus* is an exclusive snake eater and swallowed *Coronella austriaca*, *Natrix natrix*, and *Natrix maura* and other snake species in large quantities but refused lizards and mice (Mertens 1956: 104). Although some species of *Pseudoboa* are also snake-eaters, the species with the most significant coral snake phenotype, *Pseudoboa trigemina*, in my experience always spurns snakes and is instead particularly fond of eating newborn mice. On the other hand, Old World snake-eating species (*Naja hannah*, *Lioheterodon madagascariensis*, *Coluber fasciolatus*) possess no hint of a coral snake phenotype. Many smaller mimics among the coral snakes (e.g., *Sonora*, *Chionactis*, *Pliocercus*) do not tend to eat other snakes. Thus, it is very unlikely that the "*genius loci*" has something to do with the diet of coral snakes, or even that ophiophagy has somehow influenced the evolution of the coral snake phenotype through selection.

#### 4. *The coral snake phenotype as a result of directed evolution (orthogenesis)*

The fourth assumption, which is admittedly *a priori* improbable, namely the progressive and purposeful development of the coral snake phenotype, was explained in more detail by Gadow (1911) in a hypothesis that he called isotely. Isotely can be understood as a process by which species reach the same "goal" through similar consecutive steps. In this hypothesis, the formation of a coral snake phenotype would be pre-determined and represent a final stage in the evolution of snake patterns. In turn, it is the "*genius loci*" that is supposed to favor the appearance of isotely. Against such a view, Sternfeld (1913), among others, correctly pointed out that the coral snake phenotype is restricted almost exclusively to snake species of medium size, similar to the dimensions of *Micrurus* species. There are few *Micrurus* which exceed a length of 1 m—*Micrurus spixi* and *M. surinamensis* reach maximum lengths of 1.6 and 1.9 m. "As one can see," says Sternfeld, "the mysterious American Something, the '*genius loci*', loses its power to produce black-red banded snakes below 40 and above 100 cm. A strange genius!" As mentioned in the introduction, Sternfeld was a proponent of selection and of mimicry and thought—often certainly wrongly—he could attribute the similarity of a number of other snakes to mimicry, although critical examination of his work is outside of our scope.

#### 5. *The coral snake phenotype as cryptic camouflage*

Surprisingly, some researchers have interpreted the coral snake phenotype as a form of cryptic protective coloration. According to Gadow (1911), the body shape is blurred by the black-red coloration in the twilight. For Brattstrom (1955), the ringed or transversely banded pattern is more important than the red coloration: the pattern firstly serves as a distraction ("*deflective effect*"),

drawing the eyes of enemies to the individual rings or transverse bands, which become smaller and smaller with the moving snake, until the snake is gone; secondly, the pattern contributes to the disruption of the body contours ("*disruptive coloration*"). The red coloration is portrayed as quite insignificant, as Brattstrom considers most coral snakes to be nocturnal animals and their enemies colorblind. While for Gadow the coral snake phenotype as camouflage comes about through isotely favored by the "*genius loci*", for Brattstrom the protective coloration (in his sense) evolves through selection.

Hecht & Marien (1956) have dealt in detail with Brattstrom's objections to the interpretation of the coral snake phenotype and have pointed out that a feature may not necessarily have only a single function but can have multiple functions. Brattstrom's inability to explain why there are snakes with a pronounced coral snake phenotype exclusively in the New World weakens his argument. His examples of Old World snakes (such as *Coluber hippocrepis*, *Elaphe situla*, etc.) are by no means "coral snakes"! A researcher as familiar with animal colors as Cott (1940) quite rightly notes that if one is to interpret the color of coral snakes as a cryptic protective color, then snails must also be described as fast and earthworms as heavily armed!

#### IV. THE CORAL SNAKE PHENOTYPE AS AN EXAMPLE OF MIMICRY

##### 1. General

To the objective, critical-minded biologist, the assumption of mimicry as a selective force offers a thoroughly convincing explanation for the very astonishing similarity between the color patterns of very different snake species in the Americas. This assumption has the advantage that it does not have to rely on any unprovable forces, as would be necessary in order to invoke Gadow's hypothesis of isotely or the effect of the "*genius loci*".

Among vertebrates, cases of mimicry are likely to be extremely rare. I interpret the similarity of certain cichlids from Lake Nyasa (*Corematodus*) to their prey of the same family or the approximation of the nestlings of certain Cuckoos (*Eudynamis*) to their foster parents as manifestations of "Zoomimese" [= zoological mimicry]. Whether "collective mimicry" (described in the catfish *Plotosus*) actually exists must await further observations. Cases of mimicry also include some eel-like fishes, salamanders (*Plethodon*, *Desmognathus*), lizards (*Phrynocephalus*) and even some mammals, but most of these cases are not able to withstand a truly critical consideration. The situation is different for snakes and especially coral snakes.

The mimicry theory assumes that non-venomous snakes that have an external appearance similar to venomous coral snakes have a better chance of getting away with their lives than those that are not, because their enemies confuse them for a venomous snake and do not recognize them as harmless. Given the opportunity to transfer these protective characteristics to their offspring, these snakes could over many generations increase their similarity to the toxic, protected species, until this similarity can hardly be surpassed. From simple mimicry in the sense of Bates, a whole "mimicry ring", in the sense of the German-Brazilian naturalist Fritz Müller, could gradually arise. In fact, in most areas there are not just two species of snakes, one protected by venom and one unprotected, forming a mimetic relationship, but rather several models and imitators. They wear the coral snake pattern almost like a uniform from which all benefit, toxic and non-toxic alike.

The following simple fact speaks quite convincingly in favor of mimicry in coral snakes: we know that snake genera and species have only evolved a coral snake phenotype where they have

role models. For example, *Lampropeltis doliata* in the northeastern United States has a pattern which is made up of dark dorsal spots with no red hues. In the southern United States, however, where this snake co-occurs with *Micrurus* species, it has a pronounced coral snake phenotype (Plate 7, Figs. 6-8). The Old World (Oriental-Malagasy) members of the genus *Sibynophis* have no trace of a coral snake phenotype, barely even a banded color pattern; in the New World, however, where they live alongside various models, they are festooned in a most remarkable manner with coral snake colors and patterns (Plate 9, Figs. 16-18), which will be discussed in more detail (see p. 24). Essentially the same applies at higher systematic categories, for example in the small subfamily Dipsadinae: none of the Old World representatives have the slightest tendency toward a coral snake phenotype, whereas some New World species have an unmistakable tendency in this direction, even if it comes nowhere close to a *Micrurus* pattern (a black-red, yellow-lined cross-banded pattern is still a coral snake phenotype in our sense). If a New World "*genius loci*" causes the formation of coral snake patterns, then it must be solely due to the presence of models exclusively in America! Of course, in supporting the mimicry hypothesis one must not only be very critical, but also cautious. As we will see in the following, some difficulties remain to be dealt with before coral snake mimicry ceases to be a problem. Of course, it is not correct to interpret any extensive similarity to a coral snake as mimicry: for example, Fassl (1910) suggested that a 3 cm long geometrid caterpillar with white and black bands and a glaring red head and rear end is an imitator of *Micrurus*—probably *M. mipartitus*. That many snakes whose appearance one would like to interpret in terms of the mimicry theory in reality only seem to be mimics is beyond any doubt. To give just one example: one harmless (to humans) and handsome species of snake frequently found in southern Brazil is *Xenodon merremii*. This animal is plumply built, and some individuals have a dorsal pattern that is reminiscent of some species of *Bothrops*, which are the most common venomous snakes in the areas inhabited by *Xenodon merremii*. It is decidedly mistaken to assume mimicry here, as did Sternfeld, who was not familiar with live snakes: when a *Xenodon* is bothered, it immediately flattens its body horizontally, especially the neck and head, and in doing so appears almost twice as thick as in reality. Through this motion, however, the similarity with *Bothrops* is gone, because such behavior is not found at least in *Bothrops jararaca*, the most common species in central and southern Brazil.

## 2. Ecological importance of the coral snake phenotype

If one is prepared to accept coral snake mimicry, one must assume, as with cryptic protective coloration, that a coral snake phenotype must have a function to its bearer. Anyone who has even once seen live coral snakes in their natural environment will admit that the coral snake phenotype cannot be interpreted as a concealing costume. For me, there is not the slightest doubt that the garish coral snake phenotype, interrupted as it is by deep black and yellow rings, has nothing to do with camouflage; rather, it is a color pattern that stands out and thus could function only to shock, scare, or warn. The coral snake phenotype primarily has a warning function in the opinion of Hecht & Marien (1956) as well.

The function of warning coloration consists of discouraging enemies before they come into close proximity or contact with the bearer. Since the coral snake phenotype is very striking, it is obvious that its original function must be aposematism. To wit, Heikertinger (1954: 80), a well-known opponent of the mimicry theory, asserted that a "caterpillar-catching" bird cannot be afraid of a 60 cm coral snake "which it has never seen in its life and which absolutely cannot eat it because

of the small size of its mouth”. But only five pages earlier, the same author wrote that when birds “encounter any unfamiliar, eye-catching thing, they utter expressions of mistrust and fear. Any harmless object can scare them in the utmost. The amazement, the timidness of the unknown and unfamiliar, the mistrust potentially leading to fear, is a phenomenon known to every bird keeper...”. As far as the impossibility of being eaten due to the too-small mouth of *Micrurus* is concerned, it is indeed irrelevant to our problem, because it is sufficient that the bird should be bitten or otherwise injured, or even frightened.

It is clear that repeated encounters would attenuate the effect of warning coloration of completely harmless animals, but not of dangerous animals, such as “true” coral snakes. The argument could be made that highly venomous snakes are already well-protected by their strong venom and that they do not really need special protective coloration. However, it must not be overlooked that the venom apparatus of snakes has a defensive function only secondarily. The primary purpose of the venom glands and fangs of snakes centers around procuring food; that is, the paralysis and pre-digestion of the victim. The stepwise improvement of the primitive venom apparatus, which can be seen in many snake genera, clearly illustrates this feature of the fangs; there are of course a myriad of snakes whose venom apparatus is so weak that it cannot serve a defensive function, although it helps subdue the prey by paralysis well enough. Even the least venomous snakes can therefore probably not do without this important function of the fang. In order to maintain the fangs and associated venom glands in a state of readiness for prey capture at any time, many venomous snakes have other special protection devices that are directed at their enemies. Through this lens, therefore, the otherwise nonsensical phenomenon that such dangerous venomous snakes as cobras (*Naja*) have adopted the habit of flattening and uplifting the front part of the body (the “hood”) or that rattlesnakes (*Crotalus*) have developed a rattle organ on their tail can be interpreted. Other adaptations that may function similarly to the rattle organ by making a sound that scares the attacker include scale-rubbing behavior that generates a rattling sound in horn vipers (*Aspis*) and saw-scaled vipers (*Echis*), as well as the violent hissing of puff adders (*Bitis*), whereas the musk glands of other species exert a stimulus on the olfactory organs of the enemy. What feature do the coral snakes of the genus *Micrurus* possess that has the same effect on the enemy’s sense of sight as their aforementioned Old World relatives, the cobras? Why, their unusual flashy red-black-yellow or red-black-white costume!

In this costume, therefore, undoubtedly exists an aposematic property: it serves to amaze, or, if you will, to discourage and thus repel the enemy. In studying the manifold aposematic behaviors of reptiles one repeatedly encounters the phenomenon that many snakes and lizards are particularly strikingly colored on parts of their bodies that they display when they are threatened or even at the sight of their enemies, such as the colorful skin between the scales, which is visible through expansion or swelling of the body, the red or yellow colors on the underside of the tail, which are revealed by its being lifted up, throat sacs of various colors that are suddenly deployed, etc. The sudden appearance of unusual flashy colors through rapid physiological color change in some lizards also belongs in this category. It is easy to understand that when a predator is confronted with the unexpected appearance of a snake with such a striking color scheme as a coral snake, that predator is much more dazzled than when confronted by a snake whose color and pattern are barely distinguishable from the background, such as a green tree snake among some leaves, a sand-colored adder on the desert sand, or a nondescript brown or blackish snake against the soil.

The evolution of warning coloration does not necessarily have anything to do with mimicry

(*i.e.*, with the assumption of a relationship between the “true” and “false” coral snakes). Of course, a learning experience for the predators of coral snakes has nothing to do with the formation of warning coloration in harmless species. It may even have a negative impact, or perhaps be of decisive importance only for toxic species. The convergence of a coral snake phenotype with a warning coloration function in no way explains why it occurs only in New World snakes and is completely absent in the Old World. Far more plausible, therefore, is the assumption that the various coral snakes, the “true” and the “false”, have a special relationship to one another! The coral snake phenotype must therefore have yet another meaning.

The other importance of coral snake phenotype—so far the sole assumption of most of the supporters of the mimicry theory—lies in its "warning" properties, which in our opinion<sup>14</sup> have appeared only secondarily. By falling outside the scope of the ordinary, the coral snake phenotype appears to function as a warning signal to enemies, of course not in an altruistic, but rather in a selfish sense. The coral snake phenotype can be understood as acting as an easily memorable distinguishing feature that is aimed at snake enemies. The unpleasant experiences that the enemies have had with venomous coral snakes are transferred to the harmless species. In their red-black-yellow or -white disguises they give the impression of venomous animals and get away with it. The coral snake phenotype would therefore function both as a startling and as a warning signal, thus having value to the species and being positively selected.

### 3. Snake predators and their ability to perceive the coral snake phenotype

Chief among enemies of coral snakes in the New World, like snakes everywhere, are smaller carnivores and various birds, including many birds of prey such as *Milvago*, *Caracara*, *Buteo*, *Ictinia*, *Leucopternis*, *Herpetotheres* etc., as well as roadrunners, cuckoos, cariamas, storks, rheas and perhaps large passerine birds. In tropical America, most birds of prey do not feed on smaller birds, but primarily on snakes and lizards. Additionally, large reptiles and batrachians prey on small snakes. Moreover, snake predators also vary widely among habitats. It is clear, however, that snakes have plenty of enemies and thus are exposed to the effects of natural selection. As Carpenter (1936) observed, it is essential for the evolution of mimicry that enough other prey are available to predators in the habitat of the models and mimics, as naturally the value of the protective coloration is reduced when predators must subsist on relatively few prey species. This criterion is satisfied for coral snakes, because their habitats are usually very rich in other species of snakes (and lizards) that serve as alternative food for predators.

Of course, the coral snake phenotype—like any other warning coloration or protective feature—never protects its bearer completely but provides only relative protection. This should not be overlooked when one learns that even coral snakes occasionally fall prey to predatory animals. Hoge (personal communication) has observed a yellow-headed caracara (*Milvago chimachima*) depredating an *Erythrolamprus aesculapii* in central Brazil, and some coral snakes are also expected to fall prey to specialized snake eaters. Brattstrom (1955: 219) reports the discovery of a headless *Micrurus* in the stomach of a *Herpetotheres*. The Mussurana (*Clelia clelia*) is a well-known snake predator which presumably recognizes its prey by means of the sense of smell and is not reluctant to attack *Bothrops* species, is said not to go after *Micrurus*, according to Hoge's observations. It has been objected that all coral snakes have secretive, nocturnal habits, and thus that their bright coloration could not function as warning coloration. Under these circumstances, selection would have no power to act. Thus, I was very eager to observe a large number of coral snakes of various

genera and species alive. The results are briefly as follows: I kept a specimen of *Micrurus corallinus* for about a year in a terrarium. While at first it led a hidden life, it eventually came into the open during the day, even in the sunshine. I can now report the same about a beautiful *Micrurus frontalis*, which is currently in one of my terrariums. This magnificent creature is very often seen in daylight outside its hiding place. Is exactly the same for *Micrurus lemniscatus*, and reports of *Micrurus fulvius* are also similar in that it has been observed sunbathing in captivity as well as in the wild, flattening the whole-body up to the base of the tail in a ribbon-like manner (de Grijs 1898). Noteworthy are the hasty manner and unpredictable movements of *Micrurus* that I have observed. When harassed, they throw their body loops horizontally from side to side, making the coral snake phenotype appear particularly garish. In this case, however, the head was never raised, in contrast to the incorrect depiction of *Micrurus corallinus* by Mützel in "Brehm's Animal Life". *Micrurus frontalis* curls its tail tip and holds it vertically in defense (Plate 6, Fig. 2)—Old World relatives of *Micrurus* (*Maticora*) and some other snakes also exhibit or approach this behavior, but unfortunately it disappears after a few months in captivity. De Grijs (1898) observed that, when agitated, *Micrurus fulvius* expanded and contracted its abdomen several times in a row and vibrated its tail.

Among the "false" coral snakes, *Pseudoboa trigemina* seems to be a creature of the dark, as indicated by its transverse pupil. The large snake *Rhinobothryum bovallii* also behaves in this way. *Simophis rhinostoma*, a bright sealing-wax-red, black, and yellow striped burrowing snake, usually keeps hidden during the day, although I saw one creeping about in the grass in bright sunlight a few times in the Butantan Serpentarium; *Simophis* stands out in making similar nervous movements as *Micrurus*, and when confronted with danger mixes in tail vibration, a behavior that occurs in a remarkable number of Neotropical snakes. In contrast, *Erythrolamprus aesculapii* seems to be a completely diurnal animal: I saw many specimens of this beautiful creature in broad daylight, not only on the move but also hunting for their prey, mostly smaller snakes (*Tomodon dorsatus*). On 14 November 1954, I even surprised two mating pairs at 4:00 PM after a heavy downpour, but in full sunshine. A large female, which I maintained in captivity for a few months, usually comes out in the afternoon and remains outside until dusk, hiding at night. Dunn (1954) has found the related *Erythrolamprus bizona* in Panama on a trail in the blazing sun. The specimen of *E. aesculapii* that I kept raised its tail when disturbed (Plate 7, Fig. 5), similar to *Micrurus*, and flattened its body dorsoventrally, making the warning coloration particularly garish and impressive. In El Salvador, the very *Micrurus*-like *Pliocercus elapoides* also proves to be a diurnal animal; the same is reported of this snake in Tamaulipas, Mexico (Hecht & Marien 1956). Finally, in the terrarium I became familiar with the large *Lampropeltis doliata oligozona*, *L. d. polyzona* and *L. d. micropholis* as not quite exclusively nocturnal animals, as they are generally considered; incidentally, they also have the habit of tail vibration when agitated. All these observations definitely do not speak against the impossibility of the effect of selection; on the contrary, they confirm that snakes with a coral snake phenotype are sometimes active in full daylight and therefore their colors and patterns can be visible to their enemies.

This raises the question of whether the coral snake phenotype is perceived by birds and other snake predators in a similar way as by humans. This is definitely the case, since red, orange or yellow oil drops are found in the bird retina. As a result, only the long-wavelength (red, orange and yellow) rays, which are the only ones meaningful for our problem, are perceived, the short-wavelength (blue and purple) rays being attenuated. Thus, the avian eye is particularly sensitive to



red and orange, whereas blue-violet coloration could never have a warning effect. That nocturnal birds and mammals are more-or-less color blind is of minor importance for the coral snake mimicry problem, since even in twilight the red of the coral snake pattern loses its luminosity. In contrast to humans, owls are supposed to be able to detect red in dim light. It is also important that birds as well as mammals are quite capable of and indeed excellent at learning from experience. Moreover, it is quite possible that some birds have an innate aversion to the coral snake phenotype and instinctively avoid such creatures. That they cannot tell apart and sometimes confuse venomous and harmless coral-patterned snakes is probably not in doubt, if not even all herpetologists are able to do so!

Do birds distinguish between snakes with a coral snake phenotype and those with other colors? This question, essential from the viewpoint of the mimicry theory, has not yet been answered experimentally, although corresponding experiments with both older, more experienced representatives of some snake-eating bird species as well as younger, more naïve birds would be easy to perform in a South American zoological garden; certainly one cannot expect to get clarity over a phenomenon that is the result of a period of millions of years in a few weeks or even months! The few observations that I made in the Cologne Zoological Garden, with the kind help of its director, Dr. W. Windecker, are of course not sufficient to answer the question of coral snake predation. They showed at least that a South American bird of prey known to eat snakes (*Caracara plancus*) did not attack a large coral snake (*Pseudoboa trigramina*) placed in its cage, although the snake was in the cage for only 6 minutes. More interest in the same snake was shown by *Chunga burmeisteri* and especially *Cariama cristata*; but attempted attacks by these birds on the reptile were quickly abandoned.

Perhaps it is not absolutely necessary that—in contrast to the requirement of opponents of the mimicry theory, such as Werner (1917)—the enemy makes a clear distinction between a snake with a coral snake pattern and a differently-colored one and completely spares the former. Rather, every moment of perplexity or hesitation on the part of the predator that comes between becoming aware of a coral snake and the attack means a not-inconsiderable advantage for the snake; it has greater prospects of reaching a hiding place and thus saving its life! In this I see the positive selective value of the coral snake phenotype for the small, completely harmless snakes (*e.g.*, the genera *Chionactis*, *Atractus*, *Pliocercus*) for which no other means of defense is available, even more than for those species that, through their teeth or their muscle strength (*e.g.*, *Micrurus*, *Erythrolamprus*, *Lampropeltis*), can fight back. Although opponents of the mimicry theory (Werner) have asserted that the imitators are often very powerful creatures that do not require protection through mimicry, it may be objected that these snakes develop their full strength only as adults. As juveniles or young adults they are quite feeble creatures, for which the red-black-yellow pattern is a decided advantage. This is shown very nicely by *Lampropeltis doliata gaigae* in Panama, which are mimics of *Micrurus* as juveniles, but become plain black as they outgrow the size of a *Micrurus*. A similar ontogenetic melanism is shown by *Micrurus nigrocinctus yatesi*: the animal has a three-colored coral snake pattern in youth, but when it becomes larger, the red rings turn black, so that the animal has only two colors (Dunn 1954). The advantage of the coral snake phenotype should certainly not be underestimated, as it is not just warning coloration, but also an identifying feature: it announces a venomous snake to the attacker, or at least simulates one. The more perfect the resemblance of this costume to the color and pattern of truly-protected models, the more significant the increase in the selective value of the coral snake phenotype.

#### 4. *The mimicry postulates of Wallace*

From the above, it is clear that one can easily conceive the exclusive presence of snakes with a coral snake phenotype in the New World as an example of mimicry, provided that one stands on the solid ground of Darwin's theory of natural selection. Nevertheless, the whole problem still presents some questions that have to do with Wallace's well-known 5 postulates for the appearance of mimicry. Let us now reexamine the coral snakes in the context of the mimicry postulates referred to by Carpenter (1936) for butterflies, insofar as they may be contemplated for coral snakes and so far have not been taken into account.

Wallace stated that mimics must always occur in the same place as their models. Gadow (1911) has already pointed out that the distribution of the models (*Micrurus*) does not quite align with that of their alleged mimics. Sternfeld (1913) has largely exhausted this objection of Gadow's to the problem of mimicry in coral snakes. At the very least, it must be acknowledged that there is one edge region (California) where "true" coral snakes are absent, but "false" ones (*Lampropeltis zonata*) occur. In South America, the likely southern boundary of the geographic distribution of *Micrurus* more-or-less coincides with that of "false" coral snakes, although there may also be some small *Micrurus*-free areas along the edge there as well.

As for their habitats, the *Micrurus* species are not very picky as to the substrate and probably exclusively avoid only rocky ground and the extreme desert; most species prefer loose, moderately moist substrate. The mimics behave similarly. All *Micrurus* species are quite fossorial animals that especially like to burrow in loose soil. Amphibious species of *Micrurus* are not known<sup>15</sup>, although in captivity the water bowl is sometimes visited, as de Grijs (1898) reported of his *Micrurus fulvius*. Arboreality is not found in *Micrurus*<sup>16</sup>. With regard to habitat, the predominantly aquatic *Hydrops martii* (Plate 8, Fig. 14) differs from *Micrurus*. We know nothing about the habitat of the large snake *Rhinobothryum bovallii* (Plate 8, Fig. 9). However, in spite of its coral snake pattern, this snake is quite different in appearance from *Micrurus* and other coral snakes, so it might not fall into the category of mimics.

Wallace's next postulate is that mimics must differ conspicuously in their appearance from the majority of their close relatives. This requirement seems of minor importance because of course one cannot always expect that the coral snake pattern of a particular snake species could not be at least somewhat intimated in other members of the same genus. Thus, *Pseudoboa trigemina* has a pronounced coral snake phenotype with black cross-bands in groups of three, and some other species of this genus (e.g., *Pseudoboa ornata*, *P. rhombifera*) are also tri-colored and have cross bands, from which a more pronounced coral snake pattern could have developed. Likewise, the genera *Sonora*, *Lampropeltis*, and *Pliocercus* also contain both members with a coral snake pattern and others with patterns that can be considered to be precursors thereof. There are also genera (*Simophis*, *Erythrolamprus*) containing only snakes with a coral snake phenotype; however, there are also relatives of *Erythrolamprus*, such as species of the genus *Coniophanes*, that have no hint of a coral snake phenotype. Of interest in this context again are *Sibynophis* and the subfamily Dipsadinae, whose Old World species do not even possess a hint of a coral snake phenotype, whereas in the New World, this tendency is clear (see pp. 5-6, 10-11).

Next Wallace says that true mimicry should apply only to purely external features which are directed at the sense of sight and never extend to the inner structures. It is easy to show that this requirement applies to coral snake mimics. Namely, the models of the genus *Micrurus* are well-

known for their specially constructed skull, with large fangs and well-developed venom apparatus. In none of the supposed imitators is there even an approximation of these conditions: the construction of their skulls and their venom apparatus, if it exists at all, remains unaffected by the mimicry. Similarly, the scalation or squamation is little affected, and not in a visible manner. The 15 dorsal scale rows of the genus *Micrurus* are shared by some mimics (e.g., *Erythrolamprus*, usually also *Simophis*), but others have 17 (e.g., *Atractus latifrons*, *Pliocercus*, *Sibynophis*) to 19 (*Pseudoboa trigenina*, *Cemophora*), 21 (*Lystrophis semicinctus*) and even up to 27 (in *Lampropeltis*, which are very variable: 17-27). The resemblance is confined exclusively to visual features, which is especially impressive in such species where the coral snake pattern is restricted to the only visible dorsal side, but is not found on the ventral side, such as *Cemophora coccinea*, *Sibynophis venustissimus* (Plate 9, Fig. 18), *Lystrophis semicinctus* (Plate 12, Figs. 29, 31), and in the northern, white-bellied race of *Pseudoboa trigenina* (Plate 13, Fig. 35). However, in more advanced mimics the pattern is continuous, just like in *Micrurus* (Plate 11, Fig. 25), such as for example *Simophis rhinostoma*, *Erythrolamprus aesculapii*, *Pliocercus elapoides* (Plate 11, Fig. 27), *Lampropeltis doliata* and so on. The selective importance of the coral snake pattern extending onto the ventral side is clear: if the enemy seizes its prey and it comes to a fight, the underside of the snake is usually visible.

The last two of Wallace's mimicry postulates require a more detailed discussion, to which the next sections are dedicated.

##### 5. Relative abundance of "true" and "false" coral snakes

Wallace has correctly recognized that the number of mimics must be less than the number of models; the models must always be in the majority. Carpenter correctly remarked that a large number of mimics (Bates's meaning) must reduce the impact of such mimicry, which is why Müllerian mimicry, *i.e.*, a mimicry ring with several models, is in general the more common form. In fact, what occurs in most areas where coral snakes occur is mimicry within the meaning of Fritz Müller; for example, this is the case in São Paulo (Brazil), where *Micrurus*, *Pseudoboa*, *Erythrolamprus* and *Simophis* occur together. There are, in contrast, only a few areas where we can count just one coral snake model and one or a few mimics (e.g., *Micruroides* and *Chionactis* in the USA). However, it must be admitted that a clear distinction between Müllerian and Batesian mimicry in coral snakes is not possible at present.

A great deal of attention was paid to a further difficulty raised by a large number of mimics by Ludwig (1954). The enemy, such as a bird of prey, only becomes familiar with the inedible nature of the model through experience—provided that no innate behavior exists. Although mimetic coloration and pattern may benefit the imitators, it can at the same time damage the model, since it is able to devalue its inviolability; also, the predator can be harmed as it is forced to try again and again. "Just as the mimics are selected to become more similar to the models" asks Ludwig, "why do the models not likewise and at the same rate evolve in a different direction, away from the mimics, and the birds not gradually acquire better discernment?" That question, legitimate in itself, is probably unnecessary if the number of imitators in an area always remains in the minority with respect to the models. As far as the ability of birds to distinguish among coral snakes and their mimics is concerned, I think that it could hardly be further perfected, since a bird can at most recognize venomous species using the (usually only weakly developed in the bird kingdom) sense of smell, even if they are only barely distinguishable visually.

What is the abundance ratio of venomous and non-venomous individuals of snakes with a coral snake phenotype? Gadow (1911), an opponent of the mimicry theory, pointed to the relative rarity of the putative models (*Micrurus*) in Mexico. This was also mentioned earlier by the much-traveled reptile observer Schnee (1900). Also in El Salvador, south of Mexico, I found *Micrurus* to be an extremely rare reptile: despite my intense collecting activity and that of my collaborators, which extended to a total of 3 years, my Salvadorian collection contains not more than 3 “true” coral snakes (*Micrurus nigrocinctus*), but at least a dozen mimics (*Lampropeltis doliata* spp., *Pliocercus elapoides*). In another area of Central America, namely Panama, Dunn (1954) determined the opposite on the basis of a much larger collection of snake material: of snakes with a coral snake phenotype, around 62% proved to be members of the genus *Micrurus* and 38% represented slightly venomous or harmless species. If Dunn also counted bi-colored species of coral snakes and their mimics—not considered in this study (see p. 4)—the relationship changes only a little compared to when only tri-colored species are concerned. Panama is a small country. What is the situation throughout a much larger area, such as the very coral snake-rich Brazilian state of São Paulo and throughout Brazil? Does the abundance ratio there also favor *Micrurus* mimicry?

Our natural history museum specimen collections cannot give a perfectly clear picture of the relative abundance of the different coral snake species, because specific genera are often preferentially collected by researchers. In both the Senckenberg Museum and the famed Butantan Institute, special emphasis has been placed on the venomous models (*i.e.*, the genus *Micrurus*). Nevertheless, the result of counting was surprising. Despite the collection preference for the genus *Micrurus*, it was found that in the snake collection of the Butantan Institute no more than 86 specimens of the two most common *Micrurus* species in the state of São Paulo, *Micrurus corallinus* and *M. frontalis* (55 *corallinus*, 31 *frontalis*) were present. Each of the three main *Micrurus* mimics in São Paulo was represented by about the same number of specimens: *Pseudoboa trigemina* (89), *Erythrolamprus aesculapii* (32) and *Simophis rhinostoma* (70). Thus, there are 86 models and 241 mimics, *i.e.*, no more than around 26% are models, whereas 74%, *i.e.*, almost three-quarters of the individuals, are mimics. All in all, therefore, in spite of the obvious preference for collecting *Micrurus*, we find completely the opposite relationship as we would have expected!

In order to exclude the source of error as far as possible, another count of all the snakes brought to the Butantan Institute was made. As is well-known, snakes are being collected for this institute throughout Brazil, indiscriminately with respect to whether they are venomous or non-venomous. The reptiles are transported alive to Butantan in freight-prepaid boxes specially provided by the Institute, where they are used for various purposes; for 4 snakes the submitter receives one ampoule of antivenom in return. The number of snakes sent in each year is surprisingly large: it now fluctuates between 14,000 and 26,000 specimens per year; among them, *Bothrops jararaca* is by far the most common. Coral snakes are rare: they may not account for more than 2-3% of the total number of individuals; for Panama, Dunn gives 5.2%. Since the collectors make no distinction between the different forms of the “cobras corales”, the source of error is minimized when comparing the percentages. The results for the state of São Paulo for the years 1950, 1951, 1952 and 1953 are highly instructive; all *Micrurus* species are considered, although again only the 3 most important aforementioned mimics are included. As before, the bi-colored species, *i.e.*, those with only a black-red coral snake pattern (see p. 4) are not included.

	1950	1951	1952	1953
<i>Micrurus corallinus</i> .....	33	19	38	29
<i>Micrurus frontalis</i> .....	23	17	18	23
<i>Micrurus lemniscatus</i> .....	3	5	2	3
<i>Micrurus decoratus</i> .....	—	—	—	1
<i>Micrurus</i> (combined) .....	59	41	58	56
<i>Simophis rhinostoma</i> .....	25	26	29	27
<i>Erythrolamprus aesculapii</i> .....	40	37	52	67
<i>Pseudoboia trigemina</i> .....	153	183	184	190
Mimics (combined).....	218	246	265	284
<i>Micrurus</i> (combined) .....	59	41	58	56
All snakes with a coral pattern (combined) ....	277	287	323	340

This list, converted into rounded percentages, gives the following picture:

	1950	1951	1952	1953
<i>Micrurus</i> .....	21.3%	14.2%	17.9%	16.5%
Mimics .....	78.7%	85.8%	82.1%	83.5%

Here we find a most unexpected result, which speaks even more strongly against the hypothesis of *Micrurus* mimicry than the counts of curated material in the Butantan Institute! Now one might argue that perhaps the frequency ratio for *Micrurus* is only so unfavorable in the state of São Paulo, but that the ratio of models to alleged mimics is different in other Brazilian states. But even if one extends the count to snakes sent in from the whole of southern and central Brazil, the values change little in favor of *Micrurus* and in fact are almost equal to the counts of the Butantan collection material from the state of São Paulo, as we can see from the following list:

	1950	1951	1952	1953
<i>Micrurus</i> .....	136	115	131	114
Mimics .....	275	266	320	334
All snakes with a coral pattern (combined) ....	411	381	451	448

In rounded percentages, that is:

	1950	1951	1952	1953
<i>Micrurus</i> .....	33.1%	30.0%	29.0%	25.4%
Mimics .....	66.9%	70.0%	71.0%	74.6%

Over 4 years, the following average values are obtained for the frequency of *Micrurus* compared to the “false” coral snakes: in São Paulo 17%, in Brazil 29%. Of course, “Brazil” is understood here with the limitation that far more snakes are sent in from São Paulo’s neighboring states than from the more remote ones.

It can thus be seen that these numbers in no way support our hypothesis of *Micrurus* mimicry, but on the contrary appear to undermine it. In the large states of central and southern Brazil, the elapid snakes of the genus *Micrurus* are too rare among the coral snakes (in the broad sense) to be recognized by the predators of these creatures as venomous animals and thus transfer these experiences to the harmless species. The relative abundance of *Micrurus* and mimics in Panama, where *Micrurus* seems to be the most abundant genus of coral-patterned snakes, cannot dispel the concerns raised by the results obtained in Brazil. The Panamanian numbers show only that the representatives of the genus *Micrurus* are more common in some parts of their vast range than others. We do not know the relative abundance in the southern United States; Hecht & Marien (1956) suspect that in Florida, *Micrurus* is more common than *Lampropeltis*, but numerical values are lacking. Finally, it may be recalled, as already mentioned on page 17, that in the southwestern United States there are areas inhabited by “false” coral snakes that are *Micrurus*-free. That, too, certainly does not speak in favor of *Micrurus* mimicry.

#### 6. Defensive abilities of models and mimics

Finally, Wallace presented the requirement that the imitators must be less capable of defending themselves than their models. This brings us to the issue, essential for the occurrence of mimicry, of the defensive abilities of all coral snakes. First, there is a group of small, feeble animals are likely to be defenseless in spite of their warning coloration: these include *Sibynophis*, *Cemophora*, *Sonora*, *Chionactis*, *Procinura*, *Tantilla*, *Pliocercus*, *Hydrops*, *Atractus*, *Lystrophis*, and *Dipsas*. Some may have an inclination to bite, but with their tiny and—with few exceptions—ungrooved teeth, they are certainly unable to damage their enemies in any significant way. It is otherwise with the remaining coral-patterned snakes that I have observed (mostly at Butantan).

It would be expected that *Micrurus corallinus* or *M. frontalis* would have the greatest disposition to bite, because they are models. What has been known for a long time, I found confirmed: the “true” coral snakes are very unwilling to bite. *Pseudoboa trigemina*, an opisthoglyphous snake, also shows little tendency to bite when caught. However, it is mildly toxic (although white mice are killed less by any lethal effect of the venom than by constriction); a *Chrysopelea ornata* died shortly after a *Pseudoboa* bite, according to Lankes. On the other hand, the large, lively, opisthoglyphous snake *Erythrolamprus aesculapii venustissimus* is very aggressive. When one is caught, it not only bites hard but also voids its intestinal tract and emits fragrant secretions from the anal glands. A bite from the related *E. a. bizona* to one finger produced a painful swelling of the arm to the elbow, which did not recede until 4 days later. *Simophis rhinostoma* is extremely aggressive and tireless in striking with partially open jaws, but only when freshly caught. *Lampropeltis doliata*, on the other hand, rarely seems to bite, although this snake will bite if handled roughly; the bite is commensurate to the size of the snake, very strong and unpleasant for the person, as it causes violently bleeding wounds. Thus, snakes with a coral pattern behave very differently according to their genus in terms of temperament, and all demeanors from defensive, biting animals to those that have lost the habit of biting as a defense are present. The coral snakes even behave differently with respect to their toxicity.

In this respect again a rather alarming difficulty arises for the adoption of *Micrurus* mimicry. That the members of the genus *Micrurus* are disinclined to bite was mentioned earlier. But when a “true” coral snake of moderate size is grasped, then the life of the attacker is usually over. The *Micrurus* species have such a potent toxin that there is hardly any way for the attacker—with the

exception of large mammals, including humans—to escape with its life. For the bite of a coral snake, a bird of prey or a smaller mammal probably must pay with its life; that there are animals that are immune to *Micrurus* venom is possible, but not yet known. Evidence of the strength of *Micrurus* venom comes from the fact that a mouse immediately falls dead after the bite of *Micrurus corallinus* or *M. fulvius*. Oddly enough, the venom of *Micrurus circinalis* and *M. frontalis* has less of an effect on other snakes (and lizards), as the bitten remain alive for several minutes; although de Grijns (1898) observed that wall lizards and *Chalcides* skinks died "almost instantaneously" after bites from *M. fulvius*. The bite of *Micrurus*, therefore, will not damage the enemy in a way from which it can recover; on the contrary, the enemy will usually have little opportunity to learn from experience, so it will not be able to utilize its bad experiences in future, similar encounters with *Micrurus* and other coral-patterned snakes.

All in all, it must be admitted—and the evidence of a *Micrurus* in the stomach of *Herpetotheres* communicated on page 13 confirms this—that there may also be special snake-eaters who have so much experience with coral snakes that they can safely overcome even the most venomous species; such species may, for instance, immediately smash the head of the snake or use similar techniques. The case of *Herpetotheres* also proves that the assumption of an instinctive aversion to coral snakes is at least unjustified for all snake enemies. An innate avoidance would be decidedly disadvantageous for the development of at least a Müllerian mimicry ring.

#### 7. The evolution of coral snake mimicry

So what do the findings presented here mean for the problem of *Micrurus* mimicry? Well, they suggest that the "true" coral snakes of the genus *Micrurus*, as models for the "false" coral snakes, may not have the great significance that has heretofore been attributed to them. This is not only because their abundance—as we have seen—represents a minority compared to that of their alleged imitators in many areas of their distribution, but also because these animals are too venomous to often give the enemy the opportunity to have repeat encounters, memorize their coral snake phenotype, and apply these unpleasant experiences to harmless coral-patterned snakes. Are we now justified, after these counterarguments, in regarding the mimicry doctrine of coral snakes as defeated? I think I cannot, because I believe that the only key to solving the problem of the exclusive occurrence of the many, sometimes distantly related snakes with coral snake phenotypes in the New World tropics lies with mimicry. It is now necessary to examine whether and how the aforementioned arguments against the assumption of coral snake mimicry can nevertheless be reconciled with this hypothesis.

If the snakes of the genus *Micrurus*, for the reasons discussed, cannot play a major role as models for other snakes, it seems reasonable to suppose that some of these other snake species should be considered as models: *e.g.*, species protected by their weakly venomous (opisthoglyphous) dentition such as *Erythrolamprus aesculapii* and *Pseudoboa trigemina* in South America, or those distinguished by their size and muscle strength such as North and Central American kingsnakes of the genus *Lampropeltis*. The enemies of these animals can accumulate sufficient negative experiences. Under these circumstances, one might think that the mimicry of coral snakes has evolved independently in several different areas of the New World; is of "polyphyletic" origin, so to speak. However, for the reasons already discussed, this assumption cannot be completely satisfactory: one would again be faced with the riddle of why coral snake mimicry evolved exclusively in the New World and why the many old-world snake genera do not also bear a coral snake-like phenotype.

There is no alternative but to assume a "monophyletic" origin—this term is to be understood as *cum grano salis* (with a grain of salt)—of coral snake mimicry. In fact, one must look at the whole problem from another, hitherto-ignored point of view: the historical one, which is generally common in morphology today. Just as, for example, the vertebrate skull is the result of a developmental process that has lasted for millions of years and can only be understood correctly if one has explored the individual stages of this development, snake mimicry, as well as any other ecological phenomenon, has naturally not emerged overnight but is a product of huge periods of evolutionary time. Even the elapid genus *Micrurus* did not suddenly become so venomous; rather, one may rightly assume that the ancestors of *Micrurus* were at first harmless and then weakly venomous creatures. As such, they may well have been very important models for other snakes in the past, while today they have lost their importance in this regard because of their high toxicity and low frequency in some areas. Of course, we cannot know today what the relative abundance of *Micrurus* species was in the past. But if we are to accept mimicry, then the relative abundance of the models must have at first been higher than that of their imitators. Mimics could not evolve all at once as species made up of many millions and billions of individuals, but at first only as isolated mutants, which certainly must have had very good prospects of passing on their genes and greatly increasing their numbers under the protection of mimicry.

Furthermore, we cannot know today what the color patterns of the ancestors of *Micrurus* were. However, the assumption that their pattern consisted of light and dark transverse bands or rings is at least not out of the question. This pattern is still a feature of the entire family Elapidae (which includes *Micrurus*) today; a ringed pattern occurs in juveniles of some species of Old World elapids that are completely solid in old age (*e.g.*, some species of *Naja*). The sea snakes (Hydrophiidae), which derive phylogenetically from the elapids, are usually ringed or transversely banded. Thus, it is quite reasonable to assume that this pattern is an ancient family trait, and that the ancestors of today's *Micrurus* species had at least a ringed pattern as a forerunner of the modern coral snake phenotype.

When the elapids appeared in the New World, we do not know. Because it is probably safe to assume that Elapidae is originally an Old World snake family, represented by many genera and species in Asia, Africa and especially in Australia (although absent from Europe), elapids must have migrated to the New World from the Old. One may assume that this took place over the North Pacific land bridge at the end of the Mesozoic or in the early Tertiary. From North America, the forerunners of today's "true" coral snakes advanced farther south and perhaps reached the South American continent in the middle Tertiary; in both Central and South America they seem to have found very favorable living conditions and diversified into a large number of species. K. P. Schmidt (1952:34), who is intimately familiar with the New World elapids, holds that the colonization of South America by *Micrurus* is even older, namely in the late Mesozoic or early Tertiary. In any case, if coral snake mimicry exists, it can barely be older than the beginning of the Tertiary Period; that is about 60 million years old.

The whole phenomenon of coral snake mimicry, today extremely complicated, can be made comprehensible when thought of as two successive steps. In the first, the ancestors of today's *Micrurus* species appeared as the first and only models. They were already living in South America but were only slightly venomous; their color pattern probably functioned as warning coloration. Thanks to this double selection value the same phenotype could also prevail where it appeared in some harmless snakes, such as the ancestors of today's *Erythrolamprus*, *Pseudoboa* and



*Lampropeltis*. Their relative abundance was probably initially low but increased steadily under the protection of mimicry. In the course of further evolutionary development of these models and their imitators, the former gradually became very toxic (proteroglyphs), some of the latter slightly toxic (opisthoglyphs); that this process is still ongoing is suggested by, for example, the genus *Erythrolamprus*, which includes both opisthoglyphous and aglyphous forms. This ushered in the second stage in the development of coral snake mimicry, which stands by and large before us today. This second stage is characterized by the fact that the former models in coral snake mimicry, the *Micrurus* species, no longer play such a significant role as models, and may not even be able to play such a role due to their low frequency in some places and their toxicity probably being too high. They have been partially replaced as models by their previous imitators, which now in turn act as important role models in appearance. They are either opisthoglyphous and slightly venomous (*Erythrolamprus*, *Pseudoboa*) or aglyphous (*Lampropeltis*) but protected by their muscle strength. Their relative abundance—as we have seen—is now very high almost everywhere, even so great that they are some of the most common snakes in some areas. These models are now being imitated today by a number of smaller, weaker snakes, such as *Simophis*, *Atractus* and *Lystrophis* in South America, *Pliocercus*, *Sibynophis* and others in Central America, and *Chionactis* and *Cemophora* in North America. Their number is consistently lower than that of the new models, all as required by the mimicry theory.

Thus, *Micrurus* does not seem to have as great an impact on mimicry today as it once did. Probably many of the species of this genus could be completely eliminated today without the coral snake mimicry ring suffering any malfunction. During the most recent Tertiary, species of the genus *Micrurus* were probably more widespread in North America than they are today, perhaps as much as their previous imitators in the genus *Lampropeltis*. As a result of Pleistocene cooling, the northern limit of the distribution of the tropical genus *Micrurus* shifted further south, *i.e.*, the “true” coral snakes died out in areas where the cold-tolerant forms of the genus *Lampropeltis* remained, perhaps to act at present models for coral snake mimics in North and Central America. In this, perhaps we can find an explanation for the somewhat absurd lack of models in fairly wide areas of the United States that are inhabited by non-toxic “false” coral snakes.

Such genetic aspects have hardly been considered in studies of the evolution of mimicry. Heikertinger (1954) barely mentions this theme and only in a negative sense. With his 3 “evaluations” of mimicry, he distinguishes morphological (description of basic appearance), ecological (description of the benefits of the appearance) and genetic (discussion of the mode of emergence of the appearance through positive natural selection). However, Heikertinger’s genetic approach is better described as evolutionary, while the term (phylo)genetic should be understood to mean the discussion of the “family tree” of the evolution of mimicry.

## V. CONCLUDING REMARKS

In conclusion, it must be noted that the basis for mimicry and mimetic events always lies in the ability of organisms to produce hereditary modifications. In coral snakes, the variation must have a tendency towards the formation of the coral snake phenotype, *i.e.*, towards the red color and the black and white ringing or transverse banding. It can be assumed that such variations are due to the action of one or only a few genes. For example, every snake connoisseur knows that the occurrence of red areas in snakes’ patterns is widespread; even within one species (*e.g.*, *Lampropeltis zonata*, *Leimadophis poecilogyrus*, *Rhinocheilus lecontei*) there may be races with and without large red spots. The development of transverse banding or ringing must be an

inherently simple process in terms of inheritance theory, because such patterns often occur as purely individual mutations: for example, in *Lampropeltis getula californiae* and *Grayia ornata* there are individuals with a pronounced longitudinal stripe, as well as those with a no-less-pronounced light-dark transverse banding; these variations are hereditary.

The coral snakes sometimes show an astonishing variability of their pattern, which also speaks in favor of mimicry. This variability can be individual or geographical, and these two forms of variation can also occur side by side. Individual variants of *Simophis rhinostoma* occasionally occur (Plate 14, Figs. 39, 40). *Pseudoboa trigemina*, which is very common in Brazil, is also very variable in its dorsal pattern (Plate 6, Fig. 4; Plate 13, Figs. 32, 34), whereas the ventral pattern has a tendency towards geographical variability (Plate 13, Figs. 33, 35). According to my findings *Atractus latifrons* and *Lystrophis semicinctus* also vary strongly. *Lampropeltis doliata* has likewise formed many races. Perhaps most astonishing in this respect, however, is *Erythrolamprus aesculapii* and its relatives, whose individual and geographical variability has been a fruitful subject of monographic investigation. Thus, within *E. aesculapii* there are individuals with simple, black rings (Plate 10, Fig. 20), whose left and right sides may sometimes be offset from one another to varying degrees, and those in which the rings are arranged in pairs (Plate 7, Fig. 5) or even in groups of four (Plate 14, Fig. 38). The most peculiar of these variants is that described as *ocellatus* (Plate 14, Fig. 37) (which also varies in the structure of the opisthoglyphous dentition): it no longer has any trace of ringing, but rather shows a long row of black spots with light centers against a sealing-wax red background.

The case of the anteroposterior development of the coral snake phenotype in the New World species of the genus *Sibynophis* is of considerable significance in terms of evolutionary importance. One species (*Sibynophis sumichrasti*<sup>17</sup>) has no hint of a coral snake pattern; that is, like the Old World species of *Sibynophis*, it has neither a red color nor a ringed pattern. Furthermore, there are species that have a double black-and-yellow band on only the neck (*Sibynophis carpincinctus*; Plate 9, Fig. 15), on only the neck and anterior dorsum (*Sibynophis annulatus*; Plate 9, Fig. 17), on the whole back but not on the tail (*Sibynophis nothus*), and finally on the whole upper side (*Sibynophis cyclurus*; Plate 9, Fig. 16). In all these species, shades of red make up the ground color. While these forms are reminiscent of *Erythrolamprus* or *Lampropeltis* in their black double banding, one species (*Sibynophis venustissimus*; Plate 9, Fig. 18) has solitary black bands, similar to those of *Erythrolamprus* and especially *Micrurus*. That the development of coral snake phenotype has taken place in the New World (and not Old World) forms of *Sibynophis* and of the subfamily Dipsadinae is very strong evidence in favor of mimicry, as was emphasized on page 11.<sup>18</sup>

Also theoretically important are those pattern variations in Old World snakes which approximate a coral snake phenotype. Of course, these are present mostly in close elapid relatives of the “true” coral snakes, but also in a very few cases in colubrids. Nevertheless, nowhere in the Old World, with its extremely formidable snake fauna, has there been the formation of a true coral snake phenotype—nowhere does one encounter such coral snake “uniforms” as those not uncommon among New World snakes. In our view and according to the present state of knowledge, the gradual evolution of mimicry through the work of natural selection offers the only reasonable explanation for the remarkable evolutionary similarity of the “true” and “false” New World coral snakes, not only in color and pattern, in body form and size, but to some extent also in behavior. It should be admitted, however, that the problem of coral snake mimicry still contains many open questions, and, perhaps, will appear in a different light as new findings emerge.

## VI. Summary

1. The “true” coral snake phenotype occurs in 18 mostly unrelated snake genera that live exclusively in warmer areas of the New World. Some unrelated species are surprisingly alike, and there are some parallelisms in behavior as well.
2. The very striking coral snake phenotype (“Korallentracht”) is by no means an example of cryptic protective coloration (“Verbergetracht”) but an aposematism. It has a positive selection value in two respects, primarily as a deterrent (“Schrecktracht”), secondarily as a distinguishing feature (“Warntracht”).
3. The assumption of opponents of mimicry that enemies of snakes must make a sharp distinction between the coral snake phenotype and other color patterns is not necessary. Rather, any hesitation of the enemy before grabbing is a significant advantage for snakes with a coral snake pattern.
4. Since many coral snakes can be active during the day, even in sunshine, the effectiveness of selection need not be questioned because of the supposedly very hidden or nocturnal way of life of the coral snakes. Likewise, there is no evidence against the assumption that many predatory birds are able to see the bright red of the coral snake phenotype.
5. The requirement of the mimicry theory that the relative abundance of the models must exceed that of their imitators (at least 51%) is met by the genus *Micrurus* (formerly *Elaps*), which has been viewed as the model in the “coral snake mimicry ring”, only in a small area (Panama), but not in Brazil. In the state of São Paulo only 16.5-17.9% of the individual snakes with a coral pattern belong to *Micrurus*, the others are the alleged imitators. Other counts show that in Brazil only about 25-30% of snakes with coral patterns are *Micrurus*.
6. Furthermore, the species of the genus *Micrurus* have such strong venom that an attacker (bird, small mammal) is usually killed and consequently cannot transfer its experience to future encounters with coral-patterned snakes, which is possibly contrary to the assumption that *Micrurus* is currently the model for other snakes with a coral pattern. However, it is possible that some snake enemies instinctively avoid snakes with a coral snake phenotype.
7. The appearance of coral snake mimicry is the result of a very long period of development (from about the beginning of the Tertiary, around which time *Micrurus* immigrated to America). The ancestors of today's members of the genus *Micrurus*, therefore, when they were only mildly venomous, could very well have been used as models by other snakes.
8. Their imitators at the time were probably the unprotected ancestors of the species today regarded as mimics, such as *Erythrolamprus aesculapii*, *Pseudoboa trigemina* and perhaps *Lampropeltis doliata*. These have evolved under the protection of mimicry and greatly increased their relative abundance; the former two species are today by far the most common snakes with a coral pattern in São Paulo.
9. As the *Micrurus* models have become very toxic proteroglyphs, their role as models in the mimicry ring has diminished. This has now been taken over by the snakes mentioned in the previous paragraph, some of which protected by a weakly venomous bite, others by muscular strength. They have now become models for many smaller and feebler snakes of the genera *Atractus*, *Simophis*, *Pliocercus*, *Sibynophis*, *Cemophora* etc. which are considered mimics.
10. The considerable variability of the pattern of many coral-patterned snakes is strong evidence for the mimicry theory. Of particular note are the New World forms of *Sibynophis* and the subfamily

Dipsadinae, which show no trace of a coral snake-like pattern in the Old World, but which in the New World have developed such patterns under the influence of models.

11. In most cases, coral snakes exhibit mimicry in the sense of Fritz Müller, but there are also examples of Batesian mimicry. A sharp boundary cannot be drawn between these two forms of mimicry in coral snakes.

12. The mimicry theory currently offers the only acceptable explanation for the exclusive occurrence of snakes with a coral snake phenotype in the New World. The problem as such, however, remains and can only be solved by large-scale experiments.

### BIBLIOGRAPHY

- Ahl, E. 1927. Zwei neue Korallenschlangen der Gattung *Elaps*. Zoologischer Anzeiger **70**:251-252.
- Allee, W. C., O. Park, A. E. Emerson, T. Park, and K. P. Schmidt. 1949. Principles of Animal Ecology. W.B. Saunders Co., Philadelphia and London.
- Bates, H. W. 1862. Contribution to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. Transactions of the Linnean Society of London **23**:495-566, Plates 55, 56 [incorrectly cited by Mertens as 1861].
- Brattstrom, B. H. 1955. The coral snake "mimic" problem and protective coloration. Evolution **9**:217-219.
- Carpenter, G. D. H. 1936. The facts of mimicry still require natural selection for their explanation. Proceedings of the Royal Society of London B: Biological Sciences **121**:65-67.
- Cope, E. D. 1860. Catalogue of the colubrid snakes in the Museum of the Academy of Natural Sciences in Philadelphia, with notes and descriptions of new species. Part 2. Proceedings of the Academy Natural Sciences of Philadelphia **12**:241-266.
- Cott, H. B. 1940. Adaptive Coloration in Animals. Oxford University Press, Oxford.
- Dunn, E. R. 1954. The coral snake "mimic" problem in Panama. Evolution **8**:97-102.
- Fassl, A. H. 1910. Ein eigenartiger Fall von Mimikry. Zeitschrift für wissenschaftliche Insektenbiologie **6**:310.
- Gadow, H. 1908. Through Southern Mexico. Witherby & Co., London.
- Gadow, H. 1911. Isotely and coral snakes. Zoologische Jahrbücher für Systematik, Ökologie und Geographie der Tiere **31**:1-24, 18 Figs., 1 Plate.
- Grijs, P. de 1898. Beobachtungen an Reptilien in der Gefangenschaft. Der Zoologische Garten **39**:265-280 [Mertens cited just the *Elaps fulvius* portion on pp. 276-279].
- Harnack, M. von 1953. Die Hautzeichnungen der Schlangen. Zeitschrift für Morphologie und Ökologie der Tiere **41**:513-573, 129 Figs.
- Hecht, M. K., and D. Marien. 1956. The coral snake mimic problem: a reinterpretation. Journal of Morphology **98**:335-365 [cited by Mertens as "in press"].
- Heikertinger, F. 1954. Der Rätsel der Mimikry und seine Lösung. Gustav Fischer, Jena.
- Ludwig, W. 1954. Die Selektionstheorie. Pages 662-712, 9 Figs. in G. Heberer, editor. Die Evolution der Organismen. Vol. II.
- Mertens, R. 1946. Die Warn- und Droh-Reaktionen der Reptilien. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft **47**:1-108.
- Mertens, R. 1956. Beobachtungen an Korallenschlangen im Terrarium. Die Aquarien- und Terrarienzeitschrift **9**:74-77, 103-106, 9 Figs.

- Mertens, R. 1957. Gibt es eine Mimikry bei Korallenschlangen? *Natur und Volk* **87**:56-66 [cited by Mertens as "in press"].
- Schmidt, K. P. 1952. The Surinam Coral Snake *Micrurus surinamensis*. *Fieldiana Zoology* **34**:25-34, 6 Figs.
- Schnee, P. 1900. Mimikry bei Schlangen? *Zoologische Garten* **41**:219-222.
- Sternfeld, R. 1913. Die Erscheinung der Mimikry bei den Schlangen. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* **1913**:98-117, Plates 10-13, 7 Figs.
- Wallace, A. R. 1867. Mimicry and other protective resemblances among animals. *Westminster Review* **88**:45-129.
- Werner, F. 1907. Das Ende der Mimikryhypothese? *Biologisches Zentralblatt* **27**:174-185.
- Werner, F. 1917. Mimikry bei Schlangen. *Blätter für Aquarien- und Terrarienkunde* **28**:186-188.
- Wied-Neuwied, M., Prinz zu. 1820. Über die Cobra Coral oder Cobra Coraës der Brasilianer. *Verhandlungen der Kaiserlich Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher* **2**:105-110, Plate 4 [cited by Mertens as Wied; not referenced in-text].

#### EXPLANATION OF THE PLATES

The names of the toxic (proteroglyphous and opisthoglyphous) species are designated by \* and † respectively. Plate 8, Fig. 9 is a photograph by H. Rosenberg, Hamburg; Plate 6, Figs. 1, 2, and Plate 7, Fig. 6, were taken by the author; the others were made by E. Haupt in the Senckenberg Museum.

##### PLATE 6

- Figure 1. *Micrurus lemniscatus*\*. Pitangueiras, São Paulo, Brazil.
- Figure 2. *Micrurus frontalis*\*. Municipio de Ponta Pora, Mato Grosso, Brazil.
- Figure 3. *Simophis rhinostoma*. Boituva, São Paulo, Brazil.
- Figure 4. *Pseudoboa trigemina*†. Itapetininga, São Paulo, Brazil.

##### PLATE 7

- Figure 5. *Erythrolamprus aesculapii venustissimus*†. Lima Duarte, Minas Gerais, Brazil.
- Figure 6. *Lampropeltis doliata oligozona*. Manacal, Chiapas, Mexico.
- Figure 7. *Lampropeltis doliata polyzona*. Finca Los Cedros near Santa Tecla, El Salvador.
- Figure 8. *Lampropeltis doliata oligozona*. Colombia.

##### PLATE 8

- Figure 9. *Rhinobothryum bovallii*†. Shipped to Hamburg with bananas.
- Figure 10. *Micrurus mipartitus semipartitus*\* (SMF.51821). Rancho Grande, Venezuela.
- Figure 11. *Scolecophis atrocinctus*† (SMF.43171). Hacienda El Triunfo, between Santa Tecla and La Libertad, El Salvador.
- Figure 12. *Boulengerina annulata*\*. Benito River, Gabon. From Boulenger 1900.
- Figure 13. *Oligodon albocinctus*. Arakan Hills, Burma. From Günther 1868.
- Figure 14. *Hydrops martii*. Chyavetas, upper Amazonas. From Günther 1868.

##### PLATE 9

- Figure 15. *Sibynophis carpocinctus*. Pietras Negras, Guatemala. From Taylor & Smith 1943.
- Figure 16. *Sibynophis cyclurus*. Cuautlapan, Veracruz, Mexico. From Taylor & Smith 1943.
- Figure 17. *Sibynophis a. annulatus*. Belize, British Honduras. From Taylor & Smith 1943.

Figure 18. *Sibynophis venustissimus*. Hacienda Rosa de Jerico, Matagalpa, Nicaragua. From Günther 1885/1902.

PLATE 10

Figure 19. *Micrurus corallinus*\* (SMF.37860). Hansa, Santa Catharina, Brazil.

Figure 20. *Erythrolamprus aesculapii venustissimus*† (SMF.51255). Mogy das Cruzes, São Paulo, Brazil.

Figure 21. *Micrurus clarkii*\*<sup>19</sup> (MCZ.245394). Panama.

Figures 22 and 23. *Erythrolamprus mimus micrurus*† (MCZ.18848, now SMF.51820). France Field, Canal Zone, Panama.

PLATE 11

Figure 24. *Micrurus nigrocinctus zunilensis*\* (SMF.51819). Santa Carlota, El Salvador.

Figure 25. The underside of the same snake.

Figure 26. *Pliocercus elapoides salvadorensis* (SMF.42998). Finca El Paraiso, El Salvador.

Figure 27. The underside of the same snake.

PLATE 12

Figure 28. *Lystrophis semicinctus* (SMF.51086). Bolivia.

Figure 29. The underside of the same snake.

Figure 30. *Lystrophis semicinctus* (SMF.46844). San Luis, Argentina.

Figure 31. The underside of the same snake.

PLATE 13

Figure 32. *Pseudoboa trigemina* (SMF.51241). Toriba, São Paulo, Brazil.

Figure 33. The underside of the same snake.

Figure 34. *Pseudoboa trigemina* (SMF.51247). Recife, Brazil.

Figure 35. The underside of the same snake.

Figure 36. *Atractus latifrons* (SMF.19348). Iquitos, upper Amazonas.

PLATE 14

Figure 37. *Erythrolamprus aesculapii* “*ocellatus*”† (Type ZMB.5059). South America.

Figure 38. *Erythrolamprus aesculapii tetrazona*† (SMF.20297). Sorata, Bolivia.

Figure 39. *Simophis rhinostoma* (SMF.51260). Jandyra, São Paulo, Brazil.

Figure 40. *Simophis rhinostoma* (SMF.51259). Ibaté, São Paulo, Brazil.

## TRANSLATOR'S NOTES

The idea to translate this article came from a conversation with Alison Davis Rabosky at the 2018 Joint Meetings of Ichthyologists and Herpetologists in Rochester, New York. She and her lab gave critical feedback on an earlier draft during a visit to Ann Arbor in April 2019.

General comments on translation decisions:

I added or spelled out genus names when they were abbreviated or otherwise unclear, but I did not update or change the spelling of any scientific names (though see the endnotes for cases where taxonomic revisions have significantly changed the importance of species to Mertens's argument). Readers are directed to The Reptile Database (Uetz et al., 2023) for synonymy.

I translated direct quotes that were in German and placed quotes English in italics. I did not translate titles of references in the reference list, but I did if they appeared only in the text (*e.g.*, "Brehms Tierleben" = "Brehm's Animal Life").

Internal references to pagination have been updated, references to figures remain the same (beginning with Plate 6, Fig. 1).

In the plate legend and in Part II, Section 1, the names of the proteroglyphous and opisthoglyphous species are spaced differently than the names of the aglyphous species (*e.g.*, "M i c r u r u s"). In the plate legend (but not in the text), I designated them using \* and † for proteroglyphous and opisthoglyphous species, respectively.

*Recommended citation:* Durso, A.M. 2023. A Translation of Mertens, R. 1956. Das Problem der Mimikry bei Korallenschlangen. Smithsonian Herpetological Information Service, 160:1-43.

*Acknowledgments:* First, I owe a debt of gratitude to my German teacher, Ellen Hascher, for inspiring me to become proficient in the German language and working through many thorny phrases together, and to Christel & Andreas Nöllert, with whom I practiced more spoken German than anyone else and who ushered me into the world of German herpetology. Hendrik Müller, Vanessa Schulz, and Wolfgang Wüster gave their opinions on various aspects of translation. Floriane Müller (University of Geneva), Isabell Clasen (Senckenberg), and Cathrin Korz (Elsevier Germany) helped clarify the rights situation, including granting permission to reproduce the plates. Robin Everly, Richard Greene, and Erin Rushing digitized the plates. Sebastian Lotzkat invited me behind the scenes at the Senckenberg Museum and showed me Mertens's office and some of his personal effects, including specimens he collected. Kraig Adler, Aaron Bauer, and Harry Greene helped verify that no previous translation had been published, encouraged me to complete the work, and advised on where to publish it. Aaron Bauer provided support with the bibliography. Harry Greene suggested that if I really want to make a mark with some further translation of Mertens, I should tackle his 1946 "Die Warn- und Droh-Reaktionen der Reptilien" which at 108 pages is more than three times as long as the present paper. Someday! I thank Alison Davis Rabosky for stimulating discussions about coral snake mimicry and for providing the initial push and scanned copy necessary to undertake this translation. Finally, I thank the patient and helpful editor of SHIS, George Zug, for his expertise and guidance shepherding this manuscript.

*Literature cited only in endnotes and translator's notes*

- Beebe, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. *Zoologica* **31**:11-52.
- Bernarde, P. S., L. C. B. Turci, A. D. Abegg, and F. L. Franco. 2018. A remarkable new species of coralsnake of the *Micrurus hemprichii* species group from the Brazilian Amazon. *Salamandra* **54**:249-258.
- Campbell, J. A., and W. W. Lamar. 2004. *The Venomous Reptiles of the Western Hemisphere* (2 Vol.). Cornell University Press, Ithaca, New York.
- Carr, A. F. 1940. A contribution to the herpetology of Florida. University of Florida Publication, Biological Science Series **3**:1-118.
- Carr, A. F. 1994. *A Naturalist in Florida: A Celebration of Eden*. Yale University Press, New Haven, Connecticut.
- Chandler, A. C. 1916. A study of the structure of feathers, with reference to their taxonomic significance. *University of California Publications in Zoology* **13**:243-446.
- Da Silva, C., H. Andrade, and E. J. R. Dias. 2017. *Micrurus ibiboboca* (Caatinga Coralsnake). Defensive behavior. *Herpetological Review* **48**:862-863.
- Da Silva, C., H. Andrade, and E. J. R. Dias. 2018. Erratum to “*Micrurus ibiboboca* (Caatinga Coralsnake). Defensive behavior”. *Herpetological Review* **49**:142.
- Guibé, J., and R. Roux-Estève. 1963. The generic status of the snake *Henicognathus sumichrasti* Bocourt 1886. *Herpetologica* **18**:268-269.
- Hartdegen, R. W., and B. Aucone. 2001. *Micrurus surinamensis surinamensis* (NCN). Arboreality. *Herpetological Review* **32**:264.
- Mostler, G. 1935. Beobachtungen zur Frage der Wespenmimikry. *Zeitschrift für Morphologie und Ökologie der Tiere* **29**:381-454.
- Mühlmann, H. 1934. Im modellversuch künstlich erzeugte Mimikry und ihre Bedeutung für den „Nachahmer“. *Zeitschrift für Morphologie und Ökologie der Tiere* **28**:259-296.
- Norberg-Schulz, C. 1980. *Genius Loci: Towards a Phenomenology of Architecture*. Rizzoli, New York.
- Sajdak, R. A. 2000. *Micrurus circinalis* (Trinidad northern coral snake). Arboreality. *Herpetological Review* **31**:105.
- Savage, J. M., and J. B. Slowinski. 1992. The colouration of the venomous coral snakes (family Elapidae) and their mimics (families Aniliidae and Colubridae). *Biological Journal of the Linnean Society* **45**:235-254.
- Schmidt, K. P., and H. M. Smith. 1943. Notes on coral snakes from Mexico. *Field Museum of Natural History Publication, Zoological Series* **29**:25-31.
- Shippey, T. 1982. *The Road to Middle Earth*. Allen & Unwin, London.
- Silva-Haad, J., and R. A. Rodriguez R. 1985. Las serpientes *Micrurus* de la Amazonia colombiana. *Amazonia* **85**:26-28.
- Uetz, P., J. Hallermann, and J. Hošek. 2023. *The Reptile Database*. <<http://www.reptile-database.org/>>



## Endnotes

1. Mertens used two different terms for mimics (“Nachahmer” and “Mimikrist(en)”) and differentiates them from a third term (“Mimetiker(n)”) that is never used again and has no obvious different translation in modern German but was evidently used at the time to refer to both mimics and models (“Modelle”) together (e.g., Mostler, 1935; Mühlmann, 1936), which I have translated here as “lookalikes”. This was the final puzzle solved during this translation; two German teachers described this as “eine harte Nuss” (“a hard nut [to crack]”). Mertens also uses two terms, “Mimikry” and “Mimikrylehre”, to refer to the phenomenon or theory of mimicry, although the second could also mean the study of mimicry.
2. I have translated “Korallenschlangen” as any snakes with this pattern (“coral-patterned snakes” or “false” coral snakes, depending on the context), and “Korallennattern” as “true” coral snakes (*Micrurus* & *Micruroides*). In German, “Natter” usually means a non-venomous snake but “Giftnatter” means an elapid snake, whereas “Schlange” means any snake.
3. Orthogenesis (“zielstrebigen Entwicklung”), also known as orthogenetic or progressive evolution or progressionism, is an obsolete hypothesis that organisms have an innate tendency to evolve in a particular direction towards some goal (here, the coral snake phenotype) due to some internal “driving force”. Gadow’s (1911) term “isotely” seems to have been used as a synonym for orthogenesis but could also be interpreted in a general sense as convergent evolution (e.g., “the attainment of the same end by different methods in different groups”; Chandler, 1916).
4. I adopted the widely-used terms monads, dyads, triads, tetrads, and pentads (Savage and Slowinski, 1992), most of which have direct analogues used by Mertens (“Zweiergruppen” = dyads, “Dreiergruppen” = triads, “Vierergruppen” = tetrads, “Fünfergruppen” = pentads).
5. Mertens meant *Micrurus stewarti* Barbour and Amaral, 1928 (Campbell and Lamar, 2004; p. 193).
6. The translator can offer an example of his own: while serving as section editor for snake natural history notes at the journal *Herpetological Review*, my co-editor and I handled a manuscript with photo claiming to show *Micrurus ibiboboca*, which after publication (Da Silva et al., 2017) was pointed out by Otavio A. V. Marques (Instituto Butantan) to really be *Erythrolamprus aesculapii* (Da Silva et al., 2018)!
7. One recently-described species, *Micrurus boicora*, is more boldly patterned on the venter than on the dorsum (Bernarde et al., 2018). There are many other examples of statements that are no longer true given the discoveries and taxonomic revisions of the past 67 years. I have pointed out only those that stood out to me as particularly egregious.
8. Mertens uses the terms “Korallentracht” (literally “coral costume” or “coral dress”) and “Farbkleid” (literally “color dress”) for the boldly banded red-black-white/yellow coloration and pattern of coral snakes and their mimics. I have translated these terms as “coral snake phenotype” or “coral snake pattern”, sometimes shortened to “coral pattern” when the full phrase would sound too repetitive (e.g., “snakes with a coral [snake] pattern”). I chose “warning coloration” for “Schrecktracht”, “Warltracht”, and sometimes “Verbergetracht” although the cumbersome phrase “warning coloration and pattern” is probably closer to the original meaning. Although Mertens uses “Verbergetracht” and “kryptische Schutzfärbung” as synonyms in the summary, these terms do not seem to be used interchangeably elsewhere. I used “cryptic protective coloration” for “kryptische Schutzfärbung” and, because the latter appears rarely and usually in passages that make heavy use of analogy, “costume” for “Verbergetracht”. The analogy of a garment is emphasized by Mertens’s consistent use of “Träger” (wearer) for snakes that have this pattern, though it can also mean “bearer” or “carrier”.

9. Not to be confused with *Micrurus ibiboboca* (Merrem, 1820).

10. “All species of *Erythrolamprus* bear a pronounced coral snake phenotype” is no longer the case, as this genus has undergone extensive taxonomic revision since the 1950s. There are several other such statements; I did not attempt to note them all, unless later taxonomic revision significantly changed the importance of the species to Mertens’s argument. Readers are directed to The Reptile Database (Uetz et al., 2023) for synonymy.

11. I used modern terminology to talk about evolutionary relationships here and elsewhere.

12. Neither Mertens nor Allee used the term “genetic drift”, but this is what seems to be implied.

13. “*Genius loci*” is a term that would be understood in modern times only by academics. Mertens seems to assume familiarity with “the famous idea” on the part of the reader, but no definition is given; the meaning becomes somewhat clear only from reading the text. In classical Roman religion, a “*genius loci*” was the protective spirit of a particular place, similar to numinous spirits of parts of Asia or Tolkien’s Tom Bombadil (Shippey, 1982). In a modern context, the term is sometimes used to describe the particular spirit or feel of a place, for example in architecture (Norberg-Schulz, 1980).

14. Mertens uses the first-person plural here (“our opinion”) and in the final paragraph before the summary (“in our view”), which I took to be a form of the “royal we”, expressing the opinion of supporters of the mimicry theory, including himself as the leader of this movement.

15. Amphibious species of *Micrurus* are not known” is now inaccurate. In fact, two of the three references cited by Campbell and Lamar (2004; p. 117) were published before 1956 but were apparently unknown to Mertens: “*Coralsnakes are frequently found in riparian habitats, and several species actively forage in water; Micrurus surinamensis and M. lemniscatus are semiaquatic (Silva-Haad and Rodriguez R., 1985). Seventeen of 35 M. lemniscatus taken in Guyana were captured in a marshy field (Beebe, 1946). Micrurus fulvius is sometimes seen in the water either swimming or in floating vegetation mats (Carr, 1940). We have collected M. alleni yatesi and M. lemniscatus helleri in swamps in Costa Rica and Peru, respectively.*”

16. “Arboreality is not found in *Micrurus*.” is another somewhat inaccurate statement. Summary from Campbell and Lamar (2004; p. 117): “*Most snakes of the genus Micrurus are terrestrial to subfossorial, but they occasionally climb into vegetation, apparently while foraging. Carr (1994) found a large M. fulvius eating a ratsnake (Elaphe obsoleta) about 7 m up in a cabbage palm, and Schmidt and Smith (1943) found a specimen of M. nigrocinctus in the limbs of bushes more than 3 m above the ground. We found the shed skin of a M. nigrocinctus 2 m above the ground in a tree, and we encountered a specimen of M. tschudii foraging by day in a mesquite tree (Prosopis). Sajdak (2000) observed a M. circinalis in Trinidad just after midnight 2.75 m above the ground climbing a vertical tree trunk that was covered with vines and roots. A juvenile M. surinamensis from Peru was discovered coiled on a vine 1.35 m above the ground (Hartdegen and Aucone, 2001). The latter species is primarily aquatic and unlikely to forage above the ground.*”

17. At first I assumed this was *Thamnophis sumichrasti* (Cope, 1866) but that seemed unlikely because that species was never classified in *Sibynophis* and some individuals have a coral-snake-like pattern. Mertens was in fact referring to the Asian species *Sibynophis chinensis* (Günther, 1889), which at the time was erroneously thought to have been collected in Mexico; this was corrected by Guibé and Roux-Estève (1963).

18. The *Sibynophis* and Dipsadinae examples are now almost completely invalid in the details though still conceptually valid, and could be applied e.g., to *Erythrolamprus* and *Sibynophiinae*.

19. Misspelling of *Micrurus clarki* Schmidt, 1936.

PLATE 6

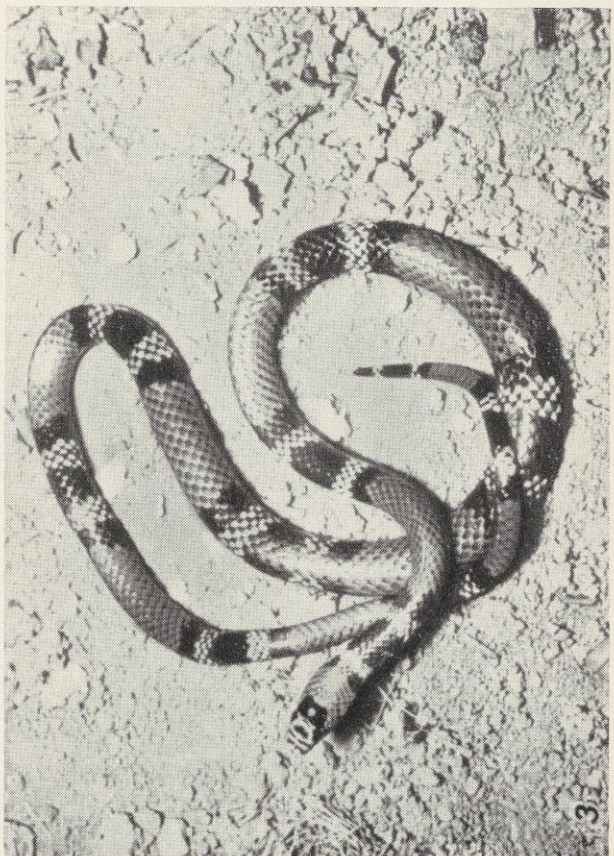
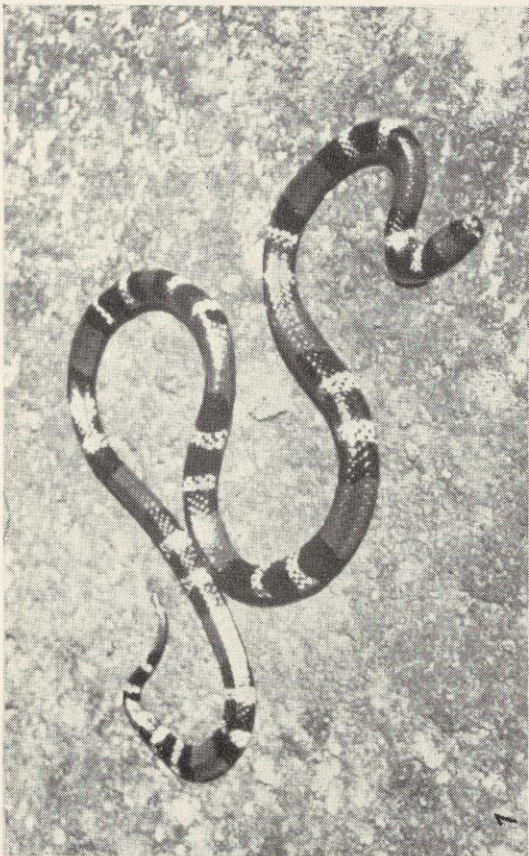
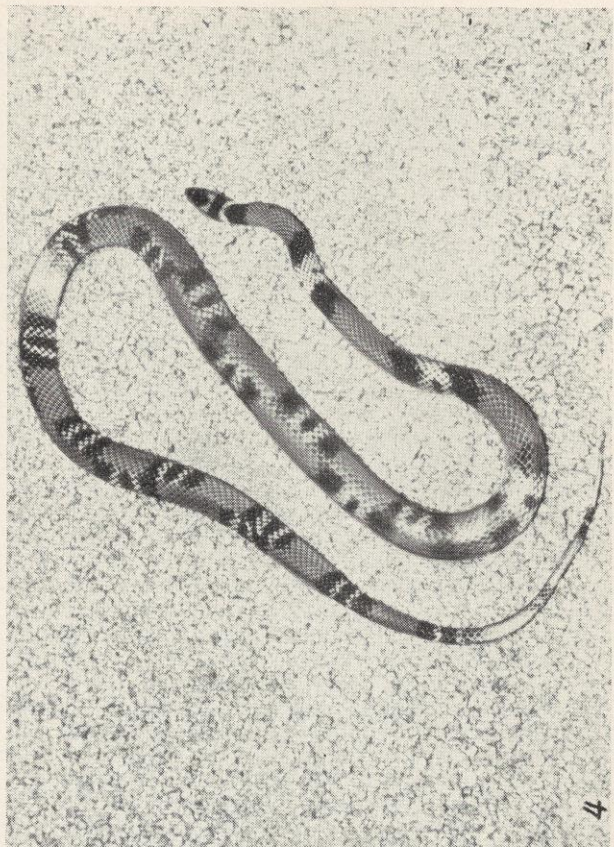
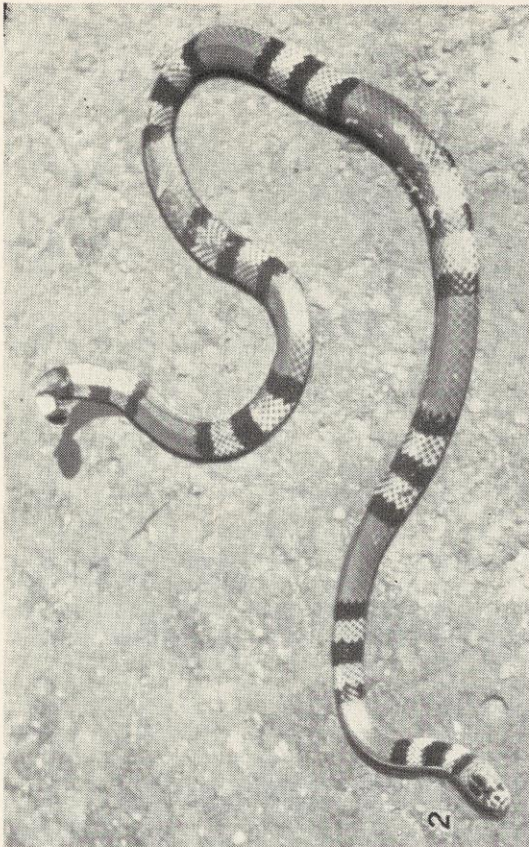


PLATE 7

