Coral Snake Mimicry: Does It Occur?

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Batesian and Müllerian mimicry, studied extensively in arthropods, are rare phenomena among vertebrates (1-4). The possibility that brightly colored, venomous and nonvenomous New World coral snakes comprise a mimicry system has been widely debated for almost a century (3, 5, 6) and is mentioned dogmatically in textbooks and other general works (7). Unfortunately, the primary literature on this topic is highly speculative, often relies on erroneous assumptions, and usually addresses only the first of two questions: (i) Are color patterns of venomous species aposematic? (ii) Do similar color patterns provide an advantage to harmless and mildly venomous colubrid snakes? Several harmless or mildly venomous colubrid snakes are indeed mimics of highly venomous elapids.

Summary. Field observations and experimental evidence refute previous objections to the coral snake mimicry hypothesis. Concordant color pattern variation spanning hundreds of miles and several presumed venomous models strongly suggests that several harmless or mildly venomous colubrid snakes are indeed mimics of highly venomous elapids.

Coral Snake Pattern as a Warning Signal

The New World coral snakes—about 50 species of Micruroides and Micrurus, of the cosmopolitan family Elapidae—usually have a single, enlarged, calciculate tooth on each maxillary bone. The venoms of these animals, referred to here as front-fanged coral snakes, include strong neurotoxins capable of killing large mammals, including humans (9-11). Thus, an early and persistent objection to the hypothesis that coral snake patterns are aposematic has been that a small predator will not survive to profit from the experience of being bitten (3). Five ways in which this “deadly model” problem could be circumvented have been suggested (7):

1) Very small individuals of front-fanged species, incapable of delivering a deadly quantity of venom, may be the models. Likewise, small coral snakes probably can be dispatched more easily than larger snakes by a predator (12), and they may be less likely to deliver venom.

2) Small predators may become ill, but not die, because of the supposedly ineffective venom delivery system of front-fanged coral snakes. The outcome of encounters with adult Micrurus and Micruroides varies greatly, including successful predation on the snakes (11, 13), painful or debilitating nonfatal effects (14), and death of the predator (9, 11, 15, 16).

3) Many colubrid snakes, including most presumed coral snake mimics, have enlarged rear fangs on the maxillary bones that conduct toxic secretions from paired Duvernoy’s glands, which are located in the head (17, 18). Possibly, these mildly venomous, rear-fanged snakes are Batesian or Müllerian models, and the front-fanged coral snakes are actually Batesian (19) or Müllerian mimics. This is unlikely to apply in areas where only front-fanged coral snakes and truly harmless colubrid mimics exist (for example, Micrurus and Lampropeltis, in western Mexico).

4) Individual predators may learn the consequences of attacking coral snakes by observing the fate of conspecifics that are bitten (20, 21). However, such “empathic” or social learning could operate only in species in which young or adults forage together. Even in situations where empathetic learning can occur, conventional learning (if the bitten predator survived) or selection for innate avoidance (if the bitten predator died) also may operate (7).

5) A simple but, until recently, underemphasized mechanism is innate avoidance (22): an individually variable, genetically based response of potential predators to brightly ringed snakes and a subsequent reduction in fitness in those with the greatest tendency to attack venomous coral snakes. This hypothesis is supported by the responses of inexperienced predatory mammals (23) and birds (24) to coral snake color patterns. Smith’s studies (24) are particularly convincing because (i) motmots and kiskadees feed on small reptiles in tropical forests, (ii) naïve birds were tested, and (iii) she treated bright colors and a ringed pattern independently in her experiments.

Another persistent and inappropriate objection to the mimicry hypothesis is that front-fanged coral snakes are nocturnal and, therefore, not subject to attack by diurnal predators with color vision (3, 5, 25-27). Observations on various North (28), Central (11, 26, 29), and South American (30-32) species show that these snakes often are active during daylight. Moreover, those hidden during the day are subject to discovery by predators that search in surface litter (23).

Mimicry and Coral Snakes

The mimicry hypothesis postulates increased survival of coral snake phenotypes among a spectrum of available patterns, and implies that this survival results from the exposure of predator populations to a dangerous coral snake model. A series of successive approximations to a coral snake pattern exists among living snake species, and even within and among populations of a single species (33). The presumed models and mimics are sometimes diurnal (11, 25, 28–32, 34–37) and are attacked by birds (34, 38) and mammals (16, 39). However, the unlikelihood of observing the crucial interactions in the field (differential survival of mimics as a result of predator avoidance) and the problems of conducting appropriate experiments make direct proof for the coral snake mimicry system difficult to obtain.

Studies of mimicry in other organisms almost always have relied on indirect evidence (3, 40), including:

1) Coincidence of model and mimic in one region and a lack of mimics in areas lacking models. This criterion has been used to argue both for (5, 41) and against (25, 27) coral snake mimicry. The ambiguity is caused by the likelihood of multiple functions for brightly ringed patterns, including background matching, protein effects, and prey location (25, 42, 43); the possibility that migratory predators are involved (44); and the possibility that allopatrium among some possible models and mimics is a comparatively recent phenomenon (5, 45).

2) Coincidence of size of model and mimic. In the uplands of the Costa Rica–Panama border, juvenile kingsnakes (Lampropeltis triangulum) have a pattern of bright red, yellow, and black rings but change ontogenetically until the adults are uniformly black. It was suggested that this situation supports a mimicry hypothesis because adult king snakes are supposedly too large to effectively mimic local venomous coral snakes (3, 5, 6). However, this example is not compelling evidence for mimicry as presented, because it is restricted geographically, because black color in the adults might have a thermoregulatory function (46), and because a sympatric front-fanged coral snake (Micrurus alleni) actually undergoes similar ontogenetic color pattern shifts (47).

3) Differential abundance of model and mimic. A classic criterion for mimicry has been that models must exceed mimics in abundance in order for predators to profitably avoid a particular prey phenotype. Analyses of two large samples (N = 1175 and 1227) show that venomous coral snakes do exceed their non-venomous counterparts in collections from Panama and Brazil, respectively (3, 6, 26). However, the relevance of these studies is uncertain because of possible collection biases and because the necessary ratio of models to mimics is dependent on the relative noxiousness of each (48, 49).

Geographic Concordance in Color Patterns

Avian predators can precisely distinguish among alternative color patterns (45, 49–51), and increased resemblance of a model can result in an increased advantage for a mimic during predator encounters (3, 48–52). For these reasons, geographic concordance in color pattern between presumed models and mimics has been viewed as strong circumstantial evidence for mimicry in other snakes (52) and in insects (3). The argument for coral snake mimicry would be greatly strengthened if it were shown that widespread, presumed mimics consistently have concordant color pattern shifts as presumed models with different color patterns drop in and out of sympathy (45, 49, 53). Here we summarize four such examples of geographic concordance:

1) Lampropeltis triangulum (a non-venomous colubrid) differs from most North and Central American Micrurus in that the yellow or white rings are separated from the red rings by black rings, rather than lying between the red and black rings. However, within the United States, these snakes resemble Micrurus more closely in areas of sympathy (54). In western Mexico, L. triangulum shows color pattern shifts in concordance with changes in the width of red bands and presence or absence of black spots in the red bands of sympatric Micrurus (53). Other examples of color pattern concordance in this widely distributed species include black encroachment onto the red bands in Oaxaca, Mexico (55), where M. epiphris is similarly patterned; breakup of the crossbanded pattern to yield spotted or unicolored red snakes at some localities on the Yucatan Peninsula (55), where M. diastema exhibits the same effect (56–57); a tendency to form secondary black rings in extreme southern Mexico (58), where M. elegans has such a pattern (Fig. 1E); and the presence of a pattern of red-orange and black rings in Honduras (39), resembling sympatric M. nigrocinctus (60).

2) Micrurus euryxanthus, a small, front-fanged coral snake, inhabits the Sonoran Desert of the southwestern United States and northwestern Mexico. This species has relatively wider red bands and narrower yellow bands in Sinaloa, Mexico, where its distribution overlaps that of Micrurus distans, a larger front-fanged species with unusually wide red and narrow yellow bands (8, 54).

3) Rear-fanged colubrid snakes of the genus Erythrolamprus occur in tropical forests of Central and South America, and their bites can produce painful symptoms in man (61–63). The most striking among several color pattern shifts apparently associated with mimicry (64–67) occurs in the Amazonian region of southeastern Ecuador and adjacent Peru. In this area, Micrurus langsfordii and M. steindachneri have black and red bands of about equal widths (three to four dorsal scales) separated by light yellow or white bands about one scale wide. In this same region, Erythrolamprus guentheri has the same pattern. Micrurus margaritiferus occurs in the lower reaches of the Rios Cenepa and Santiago in northern Peru, and has a pattern of speckled white bands on the black background. Of four E. guentheri from the Rio Cenepa locality, two have the typical tricolored pattern described for eastern Ecuador and two are essentially identical to the sympatric, bizarrely colored M. margaritiferus (Fig. 2). This pattern of white speckled bands on a black background apparently occurs only in these sympatric populations in both genera (68). A similar black and white patterned Atractus elaps, a non-venomous colubrid, recently was found sympatric with M. margaritiferus along the Rio Santiago (69).

4) Colubrid snakes of the genus Pliocercus are small (<80 centimeters total length), brightly marked, rear-fanged inhabitants of tropical forest litter (70) and provide a particularly good test (71). Although several species have been described from Latin America, apparently at most two, and perhaps only one, species should be recognized (72). Color pattern is of three basic types and generally consistent within populations. Geographic differences correlate very closely with the patterns of sympatric front-fanged coral snakes (73) (Fig. 1). The resemblance extends to general habitus, except that Pliocercus has an extremely long tail (74).

Throughout most of Mexico and northern Central America, Pliocercus and Micrurus have red bands alternating with yellow-bordered black bands (Fig. 1, A and C). The red bands of Micrurus are relatively wide in southeastern Mexico and parts of Guatemala (M. diastema, M. latifasciata) and northern Yucatan (M. diastema); the black and yellow
bands are narrow in *M. diastema* from southeastern Mexico and Guatemala, and wider in *M. latifasciata* (Guatemala) and *M. diastema* (Yucatan). Elsewhere in southern Mexico (*M. browni, M. diastema, M. nigrocinclus*) the red bands are narrower. Variation in relative band widths of *Pliocercus* among these areas parallels that in the sympatric *Micrurus*.

Within the range of *Pliocercus*, only in *M. elegans* do secondary black rings border the yellow rings, and the red rings are very narrow (Fig. 1E). Only within the range of *M. elegans* (parts of southern Mexico and adjacent Guatemala) are the secondary black rings of *Pliocercus* well developed. The red rings of *Pliocercus* in this region are relatively wide, suggesting that here it has combined elements of the color pattern of two sympatric models (*M. diastema* and *M. elegans*).

In lower Central America and northwestern South America, *M. mipartitus* and *M. stewarti* are bicolored; broad black bands alternate with red, pink, or white rings of equivalent or lesser width (Fig. 1D). *Pliocercus* has a bicolored pattern with such relatively broad black bands only where sympatric with these species.

Color pattern concordance also extends to at least four unusual localized variants of *Micrurus* and *Pliocercus*. In Hidalgo and Puebla, Mexico, *M. bernadi* is red with a dorsal pattern of narrow

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**Fig. 1.** Geographic color pattern variation in rear-fanged colubrid snakes of the genus *Pliocercus* in relation to sympatric front-fanged snakes of the genus *Micrurus*. The presumed dangerous models, on the left in each set, are (A) *M. fulvius*, (B) *M. limbatus*, (C) *M. diastema*, (D) *M. mipartitus*, (E) *M. diastema*, and (F) *M. diastema*. In (E), the center snake is *Pliocercus*, and the right snake is *M. elegans*. For further details see (82).
cross bars or spots instead of rings; *Pliocercus* from this area is similarly patterned. *Micrurus limbatus*, endemic to the Sierra de Tuxtlas, Veracruz, Mexico, is bicolored with numerous black and red rings at the type locality (Volcán San Martín). A few kilometers away on the eastern shore of Lago Catemaco, it is red with a black nape band and a few large, irregular, black dorsal spots and bands (Fig. 1B). Two *Pliocercus* from this locality are red with black nape bands, and have either a single dorsal black spot or a few spots and broken bands; of two offspring from one of these snakes, one was patterned exactly like the female (a single black spot), and the other was banded red and black. *Micrurus diastema* from Guatemala and *M. nigrocinctus* from Honduras have numerous red bands separated by black bands (elsewhere both are tricolored); *Pliocercus* from these areas have the same color pattern (Fig. 1F). Finally, a *Pliocercus* from the Pacific slope of the Sierra Madre, Oaxaca, Mexico, has the red bands replaced by black middorsally (75). It thus closely resembles the adults of an endemic and unusually patterned Oaxacan coral snake, *M. ephippifer*.

A competing explanation for these similarities is that venomous and non-venomous coral snakes have similar color patterns in sympatry by chance or as convergent responses to some nonmetric environmental factor (23, 76, 77). We find this highly unlikely for several reasons: (i) the presumed models and mimics sometimes occupy different microhabitats in a single area (78); (ii) the pattern shifts in presumed mimics are repeated and precisely concordant with the presumed models over a large geographic area, sometimes involving seven or eight model patterns; (iii) in one instance (*Pliocercus* in southern Mexico) the presumed mimic compromises the patterns of two sympatric models (*M. diastema* and *M. elegans*); and (iv) in several instances the resemblances include bizarre color patterns not found elsewhere in either genus (for example, spotted *Micrurus* and *Pliocercus*; black *Micrurus*, *Erythrolamprus*, and *Atractus* with white-speckled bands).

**Alternative Concepts and Terms**

Classically, mimicry has been divided into two general types: Batesian and Müllerian. Batesian mimicry involves resemblance between two species, one of which (the model) is distasteful or has some other unpleasant characteristic, and the other (the mimic) is edible or harmless. The mimic, through its resemblance to the model, deceives a third species (a predator) and thereby suffers less predation. The deception most often involves bright warning coloration which the predator recognizes as unpleasant and avoids. In Müllerian mimicry, two or more species also resemble each other. Here, however, both species are distasteful or unpleasant, and both are recognized and avoided by predators. In Müllerian mimicry, each species acts as a model and mimic.

Wickler (3, 19) popularized the concept of a mildly venomous model, a deadly mimic, and a harmless mimic—a situation he termed Mertensian mimicry. Smith’s studies (24) made it clear that any of the venomous coral snakes (rear- or front-fanged) may be models, but the precise direction of predator deception remains unknown. In any case, all possible combinations involving coral snakes can be accommodated within the concepts of a Batesian-Müllerian dichotomy or continuum (49, 79), and we agree with Vane-Wright (80) that Mertensian mimicry is an unnecessary term.

Grobman (27) mentioned several objections to aposematism in venomous coral snakes (81), and proposed that resemblance to these animals by other snakes be known as pseudomimicry. We agree that two species might resemble each other as a result of some factor or factors other than predator deception (25, 42, 43). However, such factors need not be exclusive of aposematism or mimicry; even if they are, such interspecific similarity has long been termed convergence.

**Conclusions**

The coral snake mimicry hypothesis states that the bright color patterns of venomous species serve as warning signals to predators and that these predators also avoid harmless or other venomous species with similar patterns. Most arguments against mimicry object to the contention that the venomous species possess aposematic color patterns; these objections were based on incorrect assumptions. Ample evidence of diurnal activity in these snakes now exists, and recent experiments demonstrate that at least two species of relevant predators innately avoid coral snake patterns.

Most previous support for the mimicry hypothesis was based on indirect arguments that are plausibly subject to alternative explanations. However, concordant geographic pattern variation strong-
Micruroides, Micrurus, and Pliocercus are involved in mimicry systems. The Atrac-

terms Mertensian mimicry and pseudo-

mimicry are not useful. Batesian and Müllerian mimicry, and the

12, E. R. Dunn, ibid. 25.


18, R. H. MacArthur (personal communication in

19, J. D. Groves (personal communication) experi-

20, R. M. Blaney and P. K. Blaney, in The Snakes of the New World. 834 (1978); J. D. Goodman and J. M. Groves (personal communication) on


22, J. A. Peters (76) suggested that an ontogenic color pattern shift occurs in E. guacharos, but specimens of a typical black phase were never seen in Costa Rica (47); Venezuela [J. A. Roze (62); Ecuador [W. E. Duellman (33)]; Western Ecuador, Peru, Brazil, and Paraguay (R. W. McDermid unpublished).


24, J. A. Peters (67) suggested that an ontogenic color pattern shift occurs in E. guacharos, but specimens of a typical black and white morph from the River Cenepa population are not known (or even collected, respectively). Perhaps polychromatism exists, as in certain other mimicry systems (3), but resolution of the situation in Erythrolamrus may not enhance the evolution of a more efficient venom delivery system.

25, J. H. Mertens, A. do Amaral, and J. D. Groves (personal communication) point out that Placobasistus resembles Micrurus in size because it has an exceptionally long tail;
Present in all eukaryotic cells, the Golgi apparatus is generally agreed to be of fundamental importance in the processing and sorting of newly synthesized proteins. However, the underlying principles that must somehow relate the Golgi's striking stacklike structure to its exact functions have been elusive. The possibility that the Golgi may carry out a previously unsuspected form of sorting, the sorting of endoplasmic reticulum proteins in multiple stages, is explored in this article, and may provide the needed connection between structure and function.

Many different proteins that must ultimately reside in such diverse cellular compartments as the surface membrane, secretion granules, and lysosomes are synthesized or initially found in the same compartment, the endoplasmic reticulum (ER). Herein lies a sorting problem of considerable proportions (1). The newly synthesized membrane proteins destined for export from the ER are subjected to a series of purification steps interposed between the ER and the final destinations. To help clarify the relation between Golgi structure and function, we must understand (i) why the mixture of proteins exported from the ER needs to pass through the Golgi before reaching their final destinations, (ii) why all of the necessary purification cannot be completed at the level of the ER, without the involvement of a Golgi apparatus, and (iii) how this vital task of purification can be accomplished.

The Golgi apparatus is strategically located in the midst of this sorting process, interpreted as a series of intermediate stages and final destinations. The Golgi apparatus consists of distinct cis and trans compartments that may act sequentially to refine the protein export of the endoplasmic reticulum by removing escaped endoplasmic reticulum proteins. Refinement may be a multistage process akin to fractional distillation; the stack of cisternae comprising the cis Golgi may be the plates in this distillation tower. The trans Golgi, consisting of the last one or two cisternae, may be the receiver that collects from the cis Golgi only its most refined fraction for later distribution to specific locations throughout the cell.