

## 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 pri-

clude 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):

**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.

mary 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 species and to other venomous species during predator encounters? In this article we discuss some widely held misconceptions and summarize new evidence bearing on these issues.

### Coral Snake Pattern as a Warning Signal

The New World coral snakes—about 50 species of *Micruroides* and *Micrurus*, of the cosmopolitan family Elapidae (8)—usually have a single, enlarged, canaliculate tooth on each maxillary bone. The venoms of these animals, referred to here as front-fanged coral snakes, in-

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 empathic 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).

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## 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, 26, 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, protean effects, and prey location (25, 42, 43); the possibility that migratory predators are involved (44); and the possibility that allopatry 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 kingsnakes 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 aleni*) 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 ven-

omous 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 to 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 sympatry (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 sympatry (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. ephippifer* 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 (59), resembling sympatric *M. nigrocinctus* (60).

- 2) *Micruroides 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, 53).

- 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 langsdorffii* 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 Ríos Cenepa and Santiago in northern Peru, and has a pattern of speckled white bands on a black background. Of four *E. guentheri* from the Río 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 Río 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. nigrocinctus*) 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

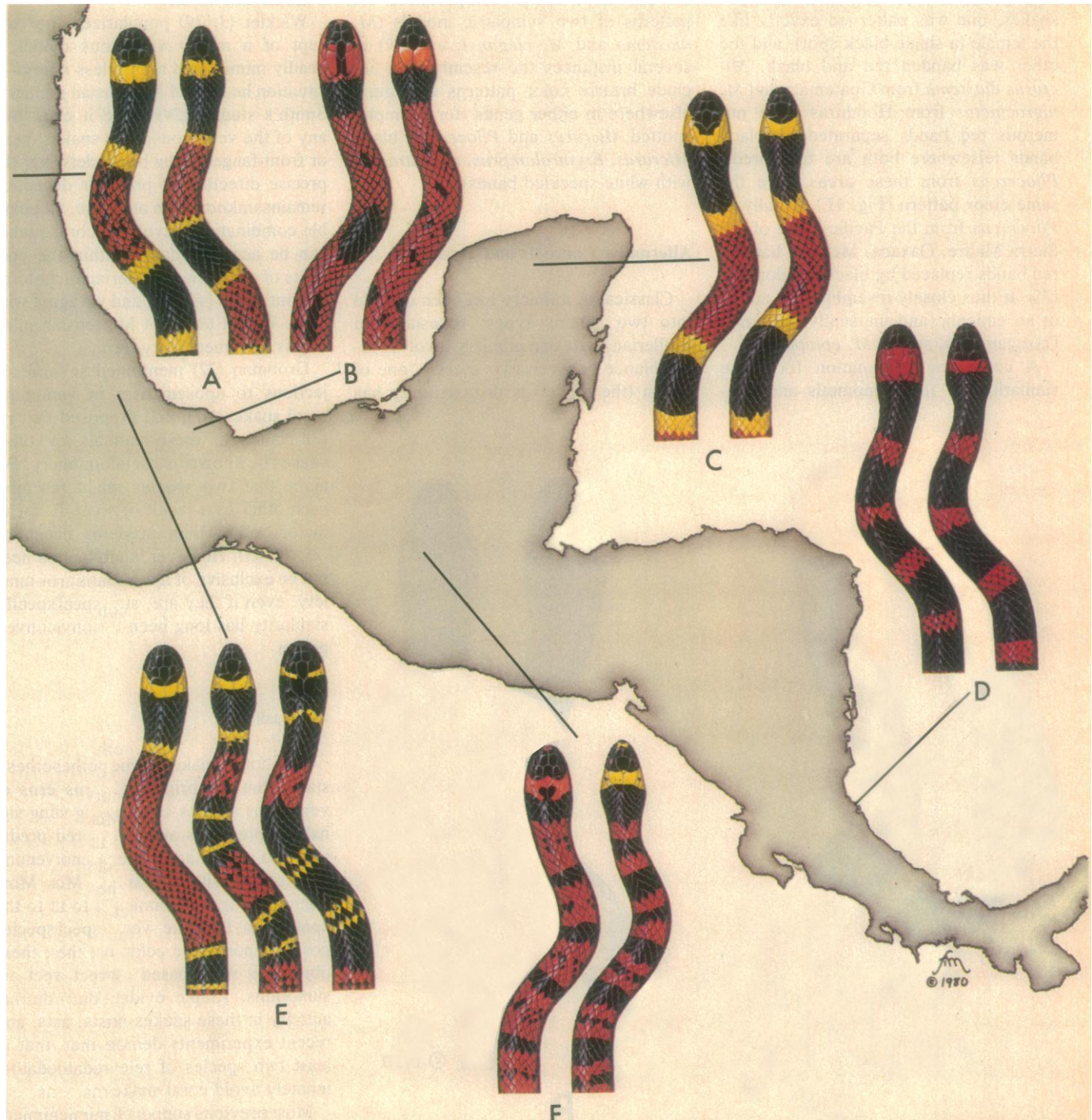


Fig. 1. Geographic color pattern variation in rear-fanged colubrid snakes of the genus *Pliocercus* in relation to sympatric front-fanged snakes of the genus *Micrurus*. The presumed dangerous models, on the left in each set, are (A) *M. fulvius*, (B) *M. limbatus*, (C) *M. diastema*, (D) *M. mipartitus*, (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 nonmimetic 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-

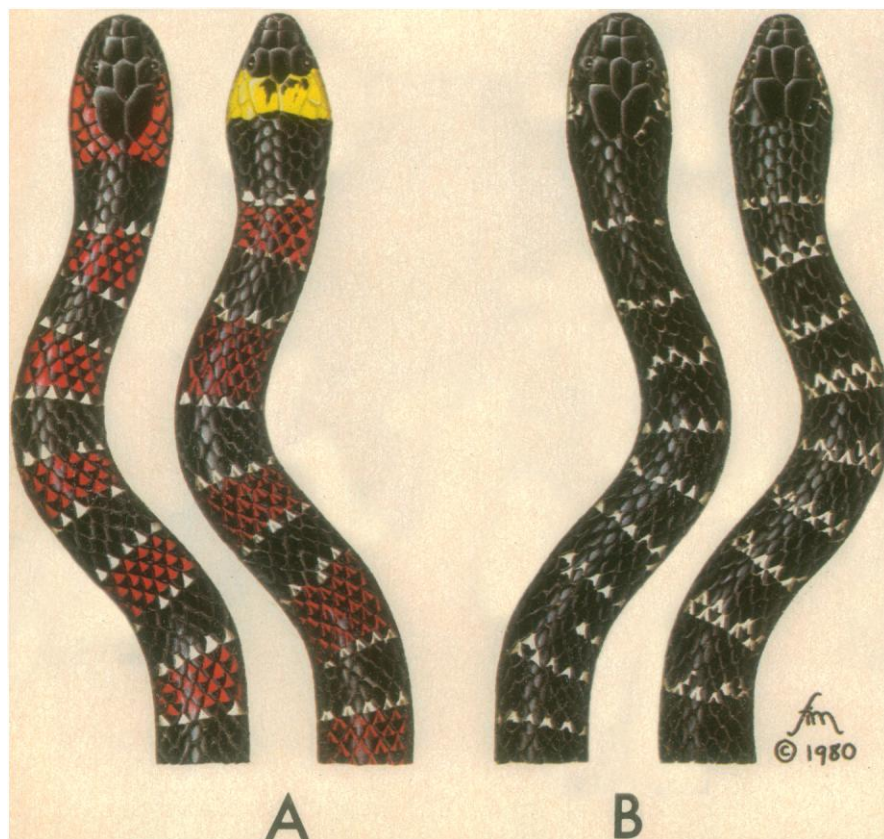


Fig. 2. Geographic color pattern variation in the rear-fanged colubrid snake *Erythrolamprus guentheri* in relation to sympatric front-fanged coral snakes of the genus *Micrurus*. The presumed dangerous models, on the left in each pair, are (A) *M. langsdorffi* and (B) *M. margaritiferus*. For further details see (82).

ly suggests that some species of *Atractus*, *Erythrolamprus*, *Lampropeltis*, *Micruroides*, *Micrurus*, and *Pliocercus* are involved in mimicry systems. The dynamics of these relations remain uncertain because most of the snakes involved are venomous; it seems likely that, in at least some situations, the *Micrurus* are dangerous Batesian models. These interactions can be accommodated within the classical concept of Batesian and Müllerian mimicry, and the terms Mertensian mimicry and pseudo-mimicry are not useful.

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17. For a survey of Duvernoy's gland in colubrid snakes, see A. M. Taub [Bull. Am. Mus. Nat. Hist. 138, 1 (1967)]; D. M. McKinstry [Toxicon 16, 523 (1978)] reviewed toxicity of venoms of rear-fanged colubrids.
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64. Our information on *Erythrolamprus* and coral snake mimicry is based on (3, 5, 6, 26, 40, 47), and R. W. McDiarmid (unpublished).
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66. Throughout their range, species of *Erythrolamprus* are diurnal, occur with one to seven species of *Micrurus*, and resemble different species of the venomous models at different sites: Trinidad (40); Costa Rica (47); Venezuela [J. A. Roze (62)]; Ecuador [W. E. Duellman (31)]; Western Ecuador, Peru, Brazil, and Paraguay (R. W. McDiarmid, unpublished).
67. The Linnaean type series of *Erythrolamprus aesculapii* includes a *Micrurus* [J. A. Peters, *Am. Mus. Novit.* No. 1851, 1 (1957)].
68. J. A. Peters (67) suggested that an ontogenetic color pattern shift occurs in *E. guentheri*, but specimens of a typical morph and a black and white morph from the Rio Cenepa population are of nearly equal total lengths (58 and 59 cm, respectively). Perhaps polychromatism exists, as in certain insect mimicry systems (3), but resolution of the situation in *Erythrolamprus* must await additional material.
69. *Atractus elaps* is a relatively small snake occurring from low to intermediate elevations in eastern Colombia, Ecuador, and Peru eastward into the Amazon Basin of Brazil. In their review of geographic variation and color pattern polymorphism, J. R. Dixon, R. A. Thomas, and H. W. Greene [*Herpetologica* 32, 221 (1976)] recognized four pattern types. They found no consistent geographic trends and reported several patterns from single localities in Peru; several species of *Micrurus* also occur at these localities [Dixon and Soini (32)]. Hecht and Marien (5) argued that *Atractus elaps* and its relatives are Batesian mimics and listed several sympatric species of *Micrurus* as possible models. The color plate in Duellman (31) and our experience with the species in the field also convince us that it is a Batesian mimic. R. W. McDiarmid recently collected an essentially black and white morph of *Atractus elaps* among eight more typically patterned individuals along the Rio Santiago in northern Peru. This snake is black with 29 complete, narrow white rings and 11 partial white rings. A single partial ring immediately posterior to the anus is the only red color dorsally. Other than this ring and traces of red on the chin, ventral 14, and subcaudals 15-16 and 20-21, the entire ventral surface is black and white. The previously unrecorded pattern of *A. elaps* is similar to sympatric *Micrurus margaritiferus*, parallels the situation described for *Erythrolamprus*, and strengthens the argument for mimicry.
70. *Pliocercus* has a Duvernoy's gland and enlarged, ungrooved rear fangs; it is closely related to other colubrids known to possess toxic saliva [C. W. Myers (18)]. R. L. Seib [*Toxicon* 18, 399 (1980)] reported severe local effects from the bite of a very small *Pliocercus*.
71. The close resemblance of *Pliocercus* to *Micrurus* at three localities was mentioned by Hecht and Marien (5) and C. M. Bogart [cited as personal communication in K. P. Schmidt, *Feldiana Zool.* 39, 201 (1958)].
72. Color pattern variation in *Pliocercus* is based on J. M. Savage and J. L. Vial (47); A. K. Smith, Jr., thesis, Baylor University (1969); L. D. Wilson and D. D. Dugas, *Bull. South. Calif. Acad. Sci.* 71, 159 (1972); H. W. Greene, *J. Herpetol.* 3, 27 (1969); \_\_\_\_\_, unpublished. J. A. Peters and B. Orejas-Miranda (65) recognized seven allopatric species apparently distinguished only by difference in color pattern. Variation within and between populations suggests that no more than two species can be recognized: *elapoides* in Mexico and northern Central America (including *andrewsi*, *bicolor*, and *euryzonus aequalis*); and *euryzonus* in Central America and northern South America [including *annulatus*, *arubricus*, and *dimidiatus* (47)].
73. Color pattern variation in *Micrurus* is based on (5, 8, 47, 57); L. D. Wilson and J. R. Meyer (60); K. P. Schmidt (71); E. R. Dunn, *Proc. Acad. Nat. Sci. Philadelphia* 92, 105 (1940); H. W. Greene, unpublished.
74. A. H. Savitzky (personal communication) pointed out that *Pliocercus* resembles *Micrurus* in size because it has an exceptionally long tail;

- front-fanged coral snakes have exceptionally short tails and elongate bodies.
75. H. M. Smith and D. A. Langebartel, *J. Wash. Acad. Sci.* 39, 409 (1950).
  76. F. R. Gehlbach (23, p. 319) concluded that "color resemblance alone does not confer special protection on colubrid snakes, hence may simply represent concealing (disruptive) coloration." However, javelinas (*Tayassu*) and coatis (*Nasua*) responded significantly more often to his coral snake model with "fright" and to the normal snake model with "predation" [Fisher Exact Test,  $P < .05$ , for data in table 1 of (23)].
  77. Gehlbach (23) also found similar frequencies of a banded morph in populations of a colubrid snake, *Sonora episcopa*, where they occur allopatrically or sympatrically to *Micrurus fulvius*. He concluded (23, p. 318) that "no mimetic advantage is apparent." We agree, but suggest that no such advantage is to be expected because even the banded morph of *S. episcopa* bears no special resemblance to a local coral snake; the banded *S. episcopa* morph is bicolored, brown or reddish brown with narrow dark crossbars—see color illustrations of it and *M. fulvius* in R. Conant, *A Field Guide to Reptiles and Amphibians of Eastern and Central North America* (Houghton Mifflin, Boston, 1975).
  78. In the Gómez Farías region of Tamaulipas, Mexico, *Pliocercus* occurs only in cloud forest, and *M. fulvius* is found in tropical deciduous and semievergreen forests [P. S. Martin, *Misc. Publ. Mus. Zool. Univ. Mich.* 101, 1 (1958)]. Note that mimicry requires only that model and mimic exist within the foraging range of relevant predators, not actual syntopy (5).
  79. P. M. Sheppard and J. R. G. Turner, *Evolution* 31, 452 (1977).
  80. R. I. Vane-Wright, *Biol. J. Linn. Soc.* 8, 25 (1976).
  81. Grobman (27) concluded that little or no predation occurs on coral snakes because no records exist in the U.S. Fish and Wildlife Service files, and, therefore, that the banded color patterns of coral snakes are not adaptive. We suspect that few records of predation exist for most snakes, and that this does not necessarily reflect actual predation rates. Grobman also cited brightly patterned bellies in other burrowing snakes as evidence that this feature is not adaptive, but did not mention that some such species (for example, *Farancia abacura*, *Diadophis punctatus*) have defensive displays that suddenly expose the bright colors [H. W. Greene, *J. Herpetol.* 7, 143 (1973)]. Grobman [table 1 in (27)] examined the distributions of 28 taxa said to resemble coral snakes, and concluded (p. 7) that "the frequency of races of nonvenomous snakes 'mimicking' the coral snake is independent of the presence of a model." However, we can reach exactly the opposite conclusion on the basis of figures, maps, and color pattern descriptions in Conant (77) and R. C. Stebbins [*A Field Guide to Western Reptiles and Amphibians* (Houghton Mifflin, Boston, 1966)]. *Chionactis palarostris* and eastern populations of *C. occipitalis annulatus* closely resemble the sympatric *Micruroides euryxanthus*. *Chilomeniscus cinctus*, three subspecies of *Chionactis occipitalis*, *Lampropeltis triangulum multistrata*, and *L. t. snyderi* are largely or entirely allopatric to and do not particularly resemble front-fanged coral snakes. We must point out that *Ficimia quadrangularis* is sympatric with *Micruroides*, but in the northern part of its range it does not especially resemble a coral snake. However, the intensity of red in the color pattern increases to the south where it is sympatric with *Micrurus distans* and *Micruroides euryxanthus* (R. W. McDiarmid, unpublished). We agree that four subspecies of *L. triangulum*, one subspecies of *L. pyromelana*, five subspecies of *L. zonata*, and two subspecies of *Rhinocheilus lecontei* are largely or completely allopatric to venomous coral snake models and that they do bear some resemblance to the latter. However, none of them resembles *Micrurus* as much as do the subspecies of *L. triangulum* (*amaura*, *annulata*, *elapsoides*) that are sympatric with *M. fulvius* (54). *Rhinocheilus lecontei antoni* has much brighter and more contrasting red, yellow, and black markings in northwestern Mexico where it occurs sympatrically with *M. distans* and *Micruroides euryxanthus neglectus* (R. W. McDiarmid, unpublished).
  82. Color patterns in the figures are based on preserved museum specimens. Museum numbers and specific localities are on file with the authors.
  83. We thank the many herpetologists who permitted us to study specimens, loaned color slides, or assisted in other ways. Versions of the manuscript were criticized by W. Altman, G. M. Burghardt, J. E. Cadle, J. A. Campbell, A. C. Echternacht, M. S. Foster, J. D. Groves, F. H. Pough, W. F. Pyburn, J. A. Roze, A. H. Savitzky, R. L. Seib, W. W. Tolbert, and D. B. Wake. F. J. Irish prepared the excellent illustrations. Greene was supported by the University of Texas at Arlington, Foundation for Environmental Education, Field Museum of Natural History (Karl P. Schmidt Fund), Center for Latin American Studies (UCB), Smithsonian Tropical Research Institute (Noble Fund), and Museum of Vertebrate Zoology (Alexander Fund); McDiarmid was supported by the University of South Florida, Organization for Tropical Studies, U.S. Fish and Wildlife Service, and National Science Foundation (grant to O. B. Berlin, UCB).

## The Golgi Apparatus: Two Organelles in Tandem

James E. Rothman

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

**Summary.** 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.

present in only trace amounts at any given moment. Yet, within minutes of synthesis, these proteins are removed from the ER and delivered to their separate destinations, virtually free of any

contamination by the vast excess of characteristic ER membrane proteins that are left behind. The question then arises as to how this vital task of purification can be accomplished.

The Golgi apparatus is strategically located in the midst of this sorting process, 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 ER needs to pass through the Golgi before sorting can be completed, and (ii) why all of the necessary purification cannot be completed at the level of the ER, without the involvement of a Golgi apparatus.

Clues to these central problems have now emerged from several independent lines of investigation. After a brief re-

view of the biochemistry and morphology of the Golgi apparatus, I point out how these recent developments suggest a novel but speculative view of this organelle. Specifically, I propose that the

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