Isotely[1]) and Coralsnakes.

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With Plate 1 and 18 figures in the text.

In every part of tropical Mexico are known "Coralillas", little corals, i. e. Coralsnakes, and thus the belief has grown that *Elaps fulvius* is a very common species, and further, that every Coralilla, every beautiful snake with red, black and yellow or white bands, is poisonous. A practical proof indeed of the effectiveness of warning colours — so far as the White man is concerned. The Indians discriminate between them to a certain extent. In some parts of the country the Coralillas are considered quite harmless, in others as deadly, or again it is held that you can never tell except in so far as that those, which live in the bush, are bad, whilst those which establish themselves in the huts, do no harm whatever, "because they are already tame", and therefore do not bite the "Cristiano", i. e. Man.

In certain villages of the hotlands of Guerrero, for instance at San Luis Allende, such a snake is supposed to live beneath the watertub of every house. The explanation of the puzzling information about the Coralsnakes is twofold. First, the uncertain behaviour of *Elaps*. A specimen may be caught and handled with impunity; it hardly struggles, does neither hiss nor bite; but the same snake

1) Isotely, the attaining of the same end through similar successive stages. Isotely is ectopic if the respective cases occur in different parts of the world; entopic if they occur at the same place, and these may eventually lead to mimicry.

may suddenly turn and bite, not with a quick blow of the widely opened mouth of a viper or rattle, and then let go, but it fastens onto, and deliberately chews the stricken spot with its small-gaped mouth, so as to make sure that the poison shall get in, always with bad, sometimes with fatal effect. Second. There are in Mexico, Central and South America a surprising number of harmless snakes, many of which resemble in their colouration the poisonous *Elaps* to a wonderful extent, so much indeed that it requires an expert to appreciate the differences. The harmless Brazilian *Erythrolamprus venustissimus* has been actually described by WAGLER, and figured by SPIX, as a species of *Elaps*.

Most species of the poisonous *Elaps* wearing such a conspicuous dress, as the combination of black, red and yellow rings or bands, are naturally instanced as first rate examples of warning colours, whilst the harmless snakes, on the strength of the same striking garb, and occuring in the same countries, are considered as equally good cases of mimicry. Both views seem so obvious as to beyond challenge, and yet they lose much of their strength when considered critically and in detail.

There is no prettier and more conspicuously coloured object than a live Coralsnake when examined as a specimen. Unfortunately the red colour is extracted by alcohol, and it fades in the light to a sickly white, so that Museum specimens give but a poor idea of their original beauty. In their natural surroundings, on the ground, amongst vegetation, they are just as conspicuous at a close distance, the red catching our eye at once, but at a distance, say beyond five yards, they seem to vanish, at least parts of them according to the pattern. It may not appeal to the closet-zoologist, but it is nevertheless a most instructive experiment to have some flexible tubes painted with the various patterns and colours of these snakes and to study the effect of these toys when thrown at random into an herbaceous border, upon the grass, into shrubs in bright sunshine or on a dull day. In most cases the effacive effect is surprising, whilst a similar toy painted monochrome, draws attention at once.

Other conditions prevail at dusk, to be studied of course at close distances. Black, alternating with red produces an effacive blurr; black and yellow in equal proportions enhance each other.

All Coralsnakes, and nearly all their supposed imitators lead a decidedly hidden life; always on the ground underneath dense vegetation where there is no direct light, under rotting trees, moss and

ferns, in termite hills etc.; they hunt in the dusk and during the night, although they have round pupils. Their food consists chiefly of other snakes which lead a similar life. These they follow by scent, digging into the loose humus, or they catch the lizards sleeping in their holes, and those snakes which live as tolerated lodgers in the burrows of termites and ants are actually known as "hormigueras", ant-catchers.

Which are in turn the enemies of *Elaps*? The professional snake-eating birds of prey scarcely deserve consideration since they are strictly diurnal and hunt mostly on the wing. But there are the Turkeys, natives of some parts of Mexico, which like Peafowl eat any snake they can master. Where Turkeys are kept in numbers they practically clear the vicinity of snakes. More effective foes are the Peccaries with their wide distribution and up-rooting habits. Neither against these pigs nor against turkeys are warning colours of any avail. Then there are the fierce Iguanas, *Ctenosura*, which are great diggers and deal lashing blows with their tails.

Now as to Mimicry. No fault can be found with this principle if it means only that occasional resemblance may convey immunity, but most advocates of mimicry go further, asserting that natural selection has not only fixed but has produced such cases. They know well, that to be effective, the resemblance must be of an appreciable degree, and they are reluctant to assume that effective resemblances can turn up without many previous intermediate stages. They may therefore be delighted to learn that and how first class cases can be evolved easily out of indifferent stages, but — and this they will not relish — without any selection.

However, the whole question of the effects of mimicry can be turned round. Supposing the 'enemy' has learned that the 'humbugs' are harmless after all, and that, no longer frightened, he boldly attacks also the original bearer of the warning colours? There would result accidents regretted by both parties, a condition of things which in the long run must be harmful to the original warner. In America such a state of anarchy actually does reign, there being in all *Elaps*-countries so many humbugs that the trick has ceased to be effective.

To appreciate this condition the following facts have to be considered.

1. There are, country for country, more mimickers than species of *Elaps*, or rather of badly poisonous individuals, what alone is of

importance. There are large districts of unquestionable *Elaps*-terrain, where the harmless species and individuals form the great majority.

2. The range of harmless species in the typical dress of *Elaps* often extends far beyond that of the nearest species of *Elaps*, and it would be ridiculous to suppose that the harmless snakes have spread the fame of *Elaps* and still reap the benefit of their bad reputation. The only reasonable conclusion is that they have developed the identical coloration without any reference to *Elaps*, and since they are harmless their's cannot be warning colours. This conclusion is subversive to the usually accepted theory which presumes the noxious sample to be copied. In the case of North Mexico and the United States it would be almost more reasonable to assume that the sly *Elaps* is the copy and now parades the loud dress so much affected by harmless snakes.

3. The majority of the harmless kinds are 'constrictors', like *Coronella*, which eat not only other indifferently coloured snakes, but each other, so that at least amongst these humbugs themselves the warning principle is not effective.

4. Although there are well ascertained instances of *Elaps* and its copies having been collected in the same district (in most cases the only information available is the name of the nearest town) I have not yet come across a single instance of what may be called occurrence side by side, and my own not inconsiderable collecting experience has hitherto yielded the same negative result. Perhaps *Elaps* is shunned, or it clears the others out, or it is killed by *Coronella micropholis*, and none of these concealed snakes travel far or have a large beat. Some of the North American Coronellas are called Kingsnakes, because they attack and master Rattlesnakes and Moccasins.

5. The variations of pattern in *Elaps* are manifold, and every one of these most diverse patterns and combinations of colours occurs also in one or more of the socalled copying genera, but rarely in the same district.

6. Certain striking patterns, very common in harmless genera, do not occur in *Elaps*. These harmless snakes have therefore a greater range of pattern than the genus *Elaps* which they are supposed to copy.

7. A very great amount of variation exists not only in snakes of the same species but also in members of the same brood, and

even in the same individual in the successive regions of the body and tail.

The above propositions, and others, will be discussed in the following pages, after a description of the evolution of some of the more important colour-patterns which might be considered to be warning colours and therefore worth imitating. It is as well to mention that most of the respective genera, *Elaps* as well as the others, comprise some species which have a plain brownish or dark dress, without any conspicuous colouration.

There are two types of pattern and colouration, or rather modes of procedure, in each of which the variations can be so arrangend as to represent an apparently evolutionary series. That they are not fundamentally different is shown by the occurence of both, or either in the same species.

DM. The Melanistic series with Double black rings.[1]) In the typical condition the pattern consists of broad red bands which are separated by a triad of two black rings divided by a yellow ring. A further diagnostic feature is that the red and black are always neighbours, but never red and yellow.

This series begins with a longitudinal row of darker dorsal patches upon an indifferent xanthic (yellowish-fuscous-olive) ground colour. The races of some of the North American *Coronella doliata*, sometimes also the individual changes from youth to age, show how a pattern of repeated darker and paler rings is produced by the distension of the original patches. The dark patches follow the principle of growing ocelli. They alone contain, or receive melanine which in the widening, growing ocellus assumes a peripheral position and then concentrates into narrow black curves, which are ultimately transformed into regular transverse rings, by the time that the ocellus has either 'burst', or reached the ventral side. The

1) It is remarkable that this typical pattern, two black rings divided by a yellow ring, is not known to occur in any *Elaps* and yet it is the pattern, or stage, out of which the complicated combination DM. 5, cf. also Table I, 7, seems to have been evolved. On the other hand it is difficult to account by it for the pattern of *Elaps decoratus*, *E. elegans* and *E. filiformis*, cf. Table I, 8, in which the three black rings together with the two yellow rings are often so narrow that the five rings together are less broad than one red band. However the length of the "segments" varies much, witness the proportions of black and yellow in the various tails figured.

area of the distending ocellus becomes lighter and within it appears a pigment which may vary from warm brown to bright red; the areas of the ocelli become the red bands and all that remains of the xanthic ground colour appears now in the shape of the yellow, or white, interstitial rings, bordered by black in front and behind.

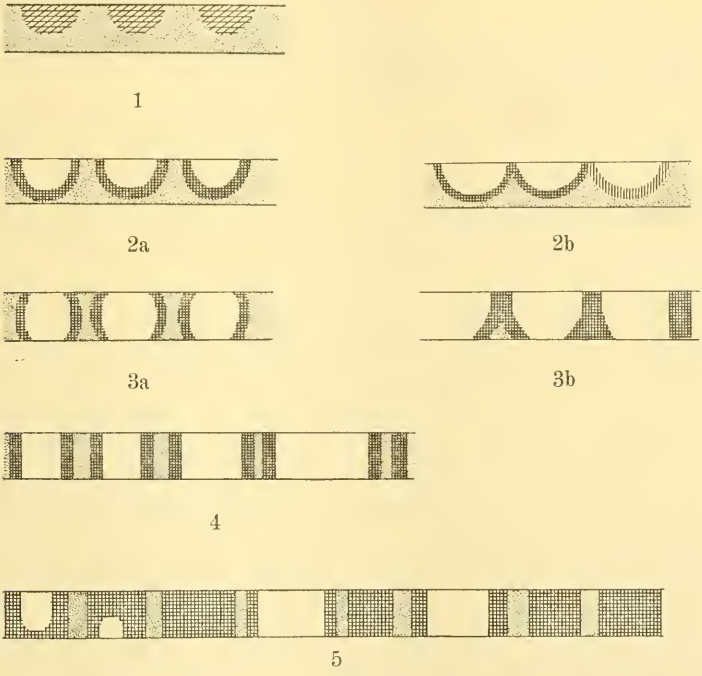
It is important to note that in this series a unit is composed of one red band, one anterior and one posterior black ring (the remnants of the black rim of the original ocellus. A complete segment containing all the three colours is in this DM. series composed of Black + Red + Black — Yellow (or in the reverse order), whilst in the SE. series the sequence is Red — Yellow + Black + Yellow (or in the reverse order).

Further changes. In the DM. series the Yellow or light ground-colour holds its own; it may often be purified into bright yellow, occasionally into white in correlation with mineral deposits, but it is not invaded by melanine. There are however two black rings to every red one in each unit, and black pigment strongly tends to become the dominant colour within its morphological unit. When this happens, increase of the black results in the encroachment upon the red until this is reduced to small patches or even vanishes completely; cf. DM. 5. The respective segment is then composed of one long black band and one narrow yellow ring.

If this conversion of the red fields or bands happens to every segment the whole snake will be black, with narrow yellow rings, eg. *Coronella micropholis* var. F. in BOULENGER's Cat. Snakes Brit. Mus., the tail of *Elaps euryxanthus*, and often of *E. fulvius*. But most specimens retain some of the red bands intact, sometimes alternating so that two red bands are separated by five other rings and bands, namely two yellow and three black of which the middle one is the broadest. The most interesting stages are of course those in which the conversion of the red bands is arrested, so to speak in a lopsided manner, as if there were some constitutional obstacle; cf. the specimen of *Coronella micropholis* collected by myself at Carrizal, West of the lower Balsas river in Michoacan, and the specimen of *Elaps fulvius* found by myself at the Jorullo Volcano. This regularly alternating suppression and preservation of the red bands is exactly repeated by *Elaps surinamensis* (see JAN, pt. 42, tab. 6), or in specimens of *E. margravi*.

An interesting but simple departure from any of the above stages is the change of yellow into red rings, so that the paired

black rings are divided by narrow red; or the whole snake is black with narrow red rings. The frequent occurrence in *Tropidodipsas dumerili* and *T. fasciata* of red enclaves or vestiges within now black broad bands which are separated by red narrow rings, shows clearly what has taken place. The change from red, through orange into red is so common an event in animals and plants that it needs no further comment.



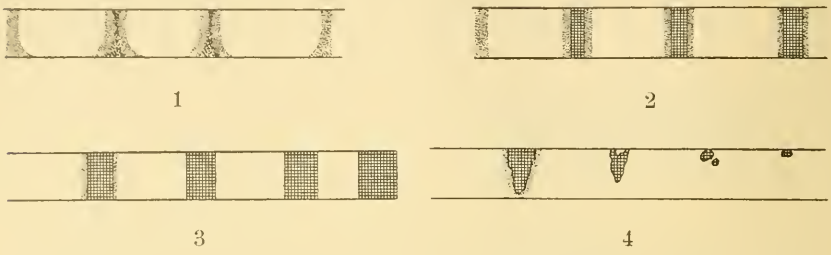
Diagrams No. I.

Evolution of the melanistic series with mostly double black rings.

Fig. 1, 2a and 2b are represented by *Coronella doliata*, cf. p. 5 and 20.
Fig. 2b and 3b, cf. p. 8. An example of 3b is figured by Guenther, in: Biolog. Centr. Americ., *Coronella micropholis*, Tehuantepec, var. C.
Fig. 4. The typical condition; for examples see Fig. 5 of the table on page 15.
Fig. 5. Various results and stages of the conversion of red into black bands; see p. 6, and Figs. 6—9 of the table on page 15; also Plate I.

An important side-departure takes place when the original ocellar patches are so large as to become confluent, the peripheral black curves touching each other first on the back, producing a black inverted X, the shanks of which alone enclose the yellow

colour. The ultimate result are single black rings separating the red bands. See DM. 2b and 3b. This is interesting since the result resembles the frequent stage 3 of the SE. series although it is brought about in a different way.



Diagrams No. II.

Evolution of the erythristic series with single black rings.

For examples see Figs. 1—4 of the table on table on page 15; also Plate 1.

SE. The erythristic series with single black rings. When yellow, or white, is present, it always separates the red from the black, and the black rings are always undivided, single, from the beginning. We assume that from the first the reddish patch-colour has prevailed over the xanthic ground colour and that the black pigment has made its appearance later, in the centres of the pale interstices. Therefrom result single black rings with narrow white or yellow margins. It is a well ascertained fact that black pigment appears with increasing tendency within a pale or pigmentless stripe when the latter widens, either with the individuals's growth or when surpassing its proper dimensions. Boulenger has recently described (On the Ophidian Genus *Grayia* [African *Tropidonotus*] in: Proc. zool. Soc. London, 1909, p. 944—952) some most interesting cases which illustrate this principle. In the species of *Grayia* black pigment first appears in the centre of the white interstitial bars and by increase converts them into black bars during the growth of the individual. In the same paper he illustrates cases of the equally important principle of alternative colour compensation: a pattern of black fields, with pale interstices changes with advancing age into a pattern of pale fields with black interstices.

In the way described above arises directly the striking colour-pattern which is the usual dress of *Elaps fulvius*, namely long red fields or bands alternating with narrow black rings, the black and

red being separated by narrow yellow or whitish margins, the last remnants of the original xanthic ground colour.

This handsome dress, seemingly very complicated, is in reality easily evolved and therefore very common. It is the usual dress of *Elaps fulvius* in Mexico, of *E. corallinus* and *E. buckleyi* in South America. Exactly the same is worn by the aglyphodont *Polyodontophis venustissimus* of Central America, and by some specimens of the opisthoglyph *Erythrolamprus aesculapii* in Ecuador; also by the opisthoglyph *Scolecophis aemulus* of Batopilas.

Further changes. The pale yellow or white margins between the black and red are encroached upon by the black. Result an essentially red snake with sharply marked black rings, e. g. *Elaps fulvius* SE. 3; compare also with DM. 3b.

Or, the whole interstitial black pigment shrinks, is encroached upon by the dominant red which next suppresses the yellow margins, until the whole body is red with irregularly shaped, paired or unpaired black spots, the last vestiges of the recessive coloration; e. g. specimens of *E. fulvius var. affinis*; specimens of the usually banded *Geophis semidoliatus* and of *G. fasciatus*.

The whole process is beautifully demonstrated by the individual variations of a family young *Streptophorus atratus* which I was lucky enough to find near Orizaba. They all have the usual jet black head and broad collar, divided by a yellow band of variable width. Specimen I was dull red owing to every red scale being slightly tipped with brown. Specimen II was bright brick red with one single deep black spot on the left side of the neck, covering one scale and a half. Specimen III brick red with many small black spots on the back, but so irregular that it is not possible to arrange them either in two long series or in transverse pairs. Specimen IV brick red with many rather large black spots, some irregular, others alternating, others almost meeting in pairs, and some forming complete crossbars; moreover most of the larger spots, and all the bars are margined in front and behind with pale yellow. — The same conditions prevailed among the immature specimens of another family which I found at La Raya, on the confines of the States of Vera Cruz and Oaxaca.

Streptophorus atratus, a small snake which scarcely reaches 400 mm in length, ranges from South Eastern Mexico to Ecuador and Venezuela. It is known to vary much. Boulenger, Cat. Snakes . . . sums up the main variations as follows. 1. Dark brown,

with or without yellow collar. 2. Brown with a black bar across the nape, and with black spots or bars on the back. 3. Head and nape black, separated by a yellow collar; body red or redbrown, uniform or spotted, or banded, with black.

It is interesting to note that in South Eastern Mexico occurs also the closely allied species *St. diadematus*, which is uniform dark brown or black above, with the exception of the yellow band across the head. I found such black specimens within a few hundred yards of *St. atratus*, both under stones, but on perhaps under more rocky and open ground. It is further suggestive that near Orizaba, and thence to the Isthmus of Tehuantepec occurs also *Homalocranium rubrum*, the usual colour of which is quite red and spotless like specimen I of *St. atratus*.

The monochrome red dress represents the terminal, not the incipient stage of the whole series.

Comparison of the two series, and general conclusions: In the DM. series the pale xanthic groundcolour is encroached upon by the red and black patch-colours, and the black may ultimately dominate the red, producing an almost monochrome black snake.

In the SE. series the ground colour is encroached upon by the red patch-colour, and by the black which grows within the pale interstitial bands; and then this black is eventually driven out by the red patch-colour. The ultimate possibility is the production of an almost monochrome red snake.

In both series therefore those colours will dominate which originated in the patches, probably because these patches represent growing points, directing centres of metabolic activity. Originally these centres were most likely quite segmental, but this metamerism has been lost long ago through confluence of neighbouring spots into larger, more effective units, and in the majority of our snakes they arrange themselves in transverse bars. The type of procedure characteristic of Lizards: longitudinal stripes breaking up into spots, rearrangement into crossbars, and eventually ultimate monochromes — does not apply to these snakes. With them erythrism means suppression of the black, and melanism means the suppression of the red pigment, in both cases by concentric invasion. The yellow is a more stabile lipochrome than orange or red. Since the latter is so easily destroyed by light, we may assume that this red owes its existence to a deficiency of certain environmental light; a condition which

is moreover often unfavourable to the formation of melanine in the skin. The question is further complicated by the frequent deposition of white mineral deposits (carbonates of lime, urates, guanine etc.) in the skin, in the white and in the yellow scales, while melanine and these deposits are mutually exclusive; and melanine can encroach upon such deposits only where these are being removed by some subtle metabolic process.

There is however another kind of melanistic tendency which may be termed secondary or universal melanism. Brown to black pigment appears in tiny specks almost all over the body, upon every scale, either giving the red scales a dusty appearance or darkening their apices, and this darkening proceeds towards their bases. The result is that the otherwise red bands of *Coronella micropholis*, *Streptophorus*, *Erythrolamprus*, *Elaps* etc. lose much of their conspicuous colour, and that the whole snake assumes an eminently effacive coloration so that any possible warning effect is correspondingly destroyed. In the snakes mentioned above this is of frequent occurrence. Whether these generally darkened individuals lead a more open life than those which are conspicuously beautiful, still remains to be found out.

What are then the conclusions to be drawn from all these variations of pattern and colours? First, that they do not follow promiscuously, but upon predetermined lines, or rather in stages the succession of which is fixed so clearly that they can be predicted. They are not cases of lawless variation, but represent orthogenetic variation since they can, without effort, be strung together so reasonably as to represent all those stages which a species must have passed through when changing for instance from a tricoloured many-ringed to a monochrome dress. In but few cases can such great changes be accomplished within the life of the individual.[1]) In the vast majority it is the aggregate number of the individuals of the "species" which reveal the drift of its evolution. Some retain most of the older features; others get along a fair way and then stand still; a few reach the goal, and some precocious specimens are born in a very advanced stage, or even in the perfect stage.

1) Our knowledge of the changes of colouration during the individual life of snakes is still very limited. In a variety of *Coluber porphyraceus* at Canton the young are alternately ringed black and red, whilst the adult are almost completely red with narrow black cross lines.

not however in the sense of a beau ideal set by Natural Selection, but in the sense of an attainable terminus, for instance a completely red, or black dress. There is no further change possible beyond these, except bleaching into a sickly white by loss of pigment, or, for arguments sake, in the case of monochrome red, a dusting or smothering with new melanine. Only a monochrome is at comparative rest; the more complicated a pattern, the less stabile it is, and the changes are by no means always improvements.

Since the same changes, even the most perplexing combinations, proceed alike in *Elaps* and in a great many other genera of diverse groups, these changes are of supreme significance.[1]) They are not

1) Certain patterns are very complex and have a long history, for instance that where alternate red bands have been turned into black. The chances for this identical pattern to turn up in two different localities are small for the same species, much smaller than that it should happen in the same place which is inhabited by several different genera. And yet this very pattern occurs in many species and in many places. Concerning its usefulness it may be urged that the detail does not matter, but only the general impression of the three colours. Some evolutionists favour the assumption that everything is the picked out residue of originally endless variations, or as some prefer to say, radiation in every conceivable direction. The apparently endless variations of our snakes seem to support their view, and it might even be urged, that it would be good for *Coronella* to vary in every direction, so as to have a better chance of hitting off any *Elaps* dress which they might come across. No doubt if the kaleidoscopic game of all the possible combinations and permutations is played long enough, the same pattern is bound to crop up repeatedly but the chances would be very small. And yet this is of much more frequent occurrence, because Nature plays with loaded dice. Only superficial acquaintance with the material can doubt this. The variations are not endless, they are bound to rules. Even the oddest are not brand new, but have a long history and are but stages of an ascertainable series of events. The sudden appearance of an ocellus with a pale centre, black ring and white outer rim, is really the outcome of quite a complex evolution; and if now an individual is born with a complete ocellus it is because its previous stages have been condensed, on the strength of cumulative inheritance. We deceive ourselves, forgetting that the individual has a history beyond that little ontogenetic spell which to the embryographer is his all in all. In the repetition of a triad of colours there must be anterio-posterior symmetry, eg. r e d - black-yellow-black - r e d, but not red-black-yellow and then again red-black-yellow. These snakes produce rings easily, but they cannot form longitudinal stripes because in their early history they had developed dorsal blotches. The disposition of mineral matter has a far reaching effect upon that of the other pigments. The above instances of correlation are sufficient to indicate Orthogenesis.

specific features, nor are they family characters, considering that but few members of a large group undergo these Elapoid changes. Nor are they always local, since at a given place *Elaps* may exhibit pattern A and *Coronella* pattern B, and in another district the reverse, and yet certain possibilities occur only in certain countries. If it were a question of mere individual freaks, why are there no red snakes in African forests?

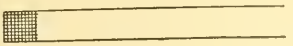
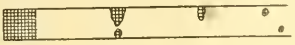
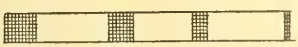
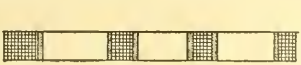
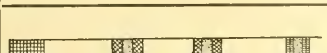
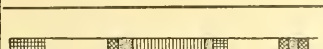
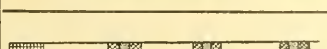
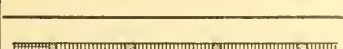
We may have to distinguish between variations which are within the domain of reasonable, normal development and others which find no place in the plan of a normal organism. The latter are "freaks", and they may also be inherited but they are sure to be eliminated, perhaps after generations, as surely as a foreign substance will be expelled. We cannot start a lasting race of stump-tails by amputation, or a four-toed beast by pairing off the inner toes, nor has nature proceeded in this violent way. But by throwing more weight upon the other toes and thereby relieving the inner, the former are stimulated to further growth, at the expense of the inner which therefore becomes dwarfed. Then may be born future generations of precocious individuals in which that inner toe exists no longer and this defect by an "apparent" leap is likely to continue since it fits into a perfectly conceivable new line of development, with new possibilities.

The Ultra-Selectionists, by referring everything to selection, action by elimination, have hypnotised themselves so far as to have eliminated from this speculations the positive side of Nature's action. Verily, their's is "der Geist, der stets verneint". Nature, whatever is meant by it, does not stand opposed to the organic world. An organism is not merely a corpus vile or "Versuchstier", it is itself a factor; it does not merely and meekly submit to being put through the selection sieve, but it remonstrates, is stimulated by being sieved to make new efforts, to invent; and thence result some variations. If not traced, or not traceable through their stages, they may appear to us as leaps, as ready-made mutations à la DE VRIES; a gratuitous explanation like that which derived our terrestrial life from some meteoric flora. Neither DE VRIES' saltos mortales nor the properly conceived mutations of WAAGEN are freaks but the reasonable outcome of prevailing conditions, and an organism, be it in evolution or in devolution, tends to work reasonably, barring accidents, and in the long run so well as to seem to have a purpose. Because since the beginning of life every "attempt" upon a new line leading to unreasonable ends has come to grief sooner or later, now only the reasonable lines are left. The organism has learned to nip the silly variations in the bud before they can do harm since the omission has, in the long run, invariably implied the death of the individual. In this sense selection is not only destructor but also instructor, not however constructor of her pupils, and if they had not Mneme, a subtle substitution for capability to inherit acquired characters, that class would make no progress.

Consequently the causes of these changes and their orthogenesis must be both environmental and constitutional; and the cases of isotely, eventually of mimicry, are the effect of the same environmental agencies upon a similar organic substratum. There is a cause for the increased production of melanine, and another for red pigment; say, deficiency of certain light which disfavours black and enhances red, and if this condition continues, erythrism will in the long run assert itself, and ultimately there will be descendants born red without a trace of black. And where the first patch of red shall appear first, is a constitutional question, just as is the peculiar mode of growth of an ocellus; and the deposition of mineral salts is also constitutional. The same applies to the concentration of black into rings. Although possibly influenced by the affinity of the respective pigment the cells will congregate and increase where the surrounding tissues makes it easiest for them. Further, in such eminently bilateral creatures as snakes, symmetry is a powerful factor, and since they are also very elongated, repetition asserts itself. It is not accidental that on depressed bodies longitudinal striation gives way to transverse pattern, and that this itself is easiest to accomplish on narrow and long bodies, witness the tail. Of course there are many lizards and snakes with striped tails, but then their bodies are also striped in the same way; but a survey of longtailed creatures shows the frequency of a banded tail whilst the body is still striped, or still ocellated, or still patchy. The Jaguar's body and tail are marked by the same principle of rosettes, but whilst these remain separate on the body they are fused into confluent rings on the tail. The vertebrate tail is not a mere appendage, it has in many respects a longer history than the body.

Concerning the pattern of the tail of our elapoid-coloured snakes, it is safe to state that in the overwhelming majority the tail is sharply and completely ringed, and bicoloured, black and yellow or black and white, whilst the body is still in the tricoloured phase and in process of variation, the drift of which is obvious. Perhaps these conditions may underlie EIMER's law of hystero-protero undulation, a principle by no means universal, but at least suggestively frequent.

Although all the elapoid-coloured snakes show an unmistakable drift towards either melanism or erythrism, we have no right to expect that they will all end in either black or red species. Being so plastic, in such a flux, and so easily reacting upon external

		Elaps	Opisthoglyph	Aglyph
1			*Homalocranium rubrum*	*Streptophorus atratus*
2		*fulvius var. affinis Callophis*	*Erythrolamprus aesculapii var. venustissima* L.	*Streptophorus atratus* *Coronella micropholis* E.
3		*fulvius Callophis macclellandi*		*Coronella micropholis* *Geophis semidoliata* *Urotheca elapoides* *Rhinochilus*
4		*fulvius typic.* *corallinus* *buckleyi* *euryxanthus* *Callophis*	*Erythrolamprus aesculapii* *Scolecophis aemula*	*Streptophorus atratus* *Polyodontophis venustissimus*
5			*Homalocranium michoacanum* *Erythrolamprus aesculapii*	*Coronella doliata* *Coronella micropholis* *Atractus latifrons* *Cemophora coccinea* *Urotheca elapoides*
6				*Coronella doliata* *Coronella microphol.* *C. pyromelanus s. zonat.* *Urotheca*
7		*fulvius* *surinamensis* *marcgravi* *lemniscatus*		*Urotheca elapoides*
8		*decoratus* *elegans* *filiformis*		
9		Tail of: *E. fulvius* *E. euryxanthus* *E. corallinus*	*Erthrolamprus aesculapii, var.* 0	*Tropidodipsas* *Coronella microphol.* Tail of: *C. microphol.* and *C. zonatus*

Diagrams No. III.

Table showing instances of Isotely in Pattern and Colours between Elaps and other „Coral-Snakes".

Black is indicated by crossed lines; in Fig. 6—9 also by vertical lines to emphasize the change of originally red into black fields. Red is left white. Yellow is indicated by stippling.

The black at the left end of each diagram represents the first black ring on the neck immediately behind the bright yellow bar across the black head; a pattern almost universal in these snakes.

Patterns 1—4 belong to the Erythristic series with single black rings: E. S. cf. page 8.

Patterns 5—9 belong to the Melanistic series with double black rings: M. D. cf. page 5.

Pattern 3 indicates that the black rings may vary much in width.

Pattern 4 is the commonest pattern of *Elaps fulvius* in Mexico, and the sole dress of this species in Northern Mexico and in the United States. — This pattern does not occur in *Coronella*!

Pattern 5. This very common pattern does not occur in any *Elaps*! In some specimens of *Coronella micropholis* the narrow rings between the black rings are red instead of yellow.

Pattern 6—9. Conversion of originally red bands into black. If the white or yellow interstitial rings are changed into red, the ultimate result is the individual tail-pattern of *Coronella* as figured on Plate 1.

influences, they are sifting themselves into new varieties in kaleidoscopic fashion. By accident of isolation in particularly favoured localities an identical variation may become dominant for a time, as a local race, being, in such a case instances of „discontinuous distribution", in reality due to „parallel evolution". Parallel, not convergent, since they have reached the identical condition through corresponding stages. Shifting of the habitat, an unavoidable result of their spreading (and they must spread if they multiply) will put an end to their epistasis, or apparent permanence of that local race.

Orthogenesis is not necessarily a good thing; its momentum, to a great extent due to cumulative inheritance, often leads to deplorable results, and it remains to be shown whether monochrome red snakes are better off than their more oldfashioned banded relations.

It is most likely that Natural Selection considers these variations as going too far, and calls a halt, but this is not what is meant by Epistasis. By ruthlessly cutting down every tree before it has reached its attainable height we cannot prevent the rest from growing. Mehely's statement that Epistasis is caused by the „Ungunst der Verhältnisse" is therefore not happily conceived, and is liable to be misunderstood. Unless it is merely a commonplace, it can mean only — to take a concrete example, that the fixing of a tricoloured race with lopsided pattern, is an unfortunate inhibition. For all we know to the contrary such a dress may be more advantageous in certain localities than the more advanced stage with regularly arranged rings, provided always that these variations do matter at all. The Stag with eight points has a more dangerous weapon than the one with sixteen and if the latter goes back to ten (owing to unfavourable conditions, as food, age etc.) it conceivably retrieves its apparent loss.

A List of Snakes with Elapoid coloration.

I. ***Elapinae***; proteroglyphous and very poisonous.

Elaps, most of the two dozen or more species, for instance:
E. fulvius, from Venezuela to South Eastern U. S. A.
E. euryxanthus, Arizona and Sonora.
E. corallinus, Tropical South America and Lesser Antilles.
E. marcgravi, Tropical South America.
E. surinamensis, Tropical South America.
E. elegans, Guatemala to Vera Cruz.
Callophis macclellandi and *C. bibroni*, Assam to Southern China.

Doliophis bivirgata, Malayan. Head and neck and undersurface red, rest black with a white lateral stripe.
Pseudechis porphyraceus, The Black snake of Australia; with red bases of the outer row of scales.
Furina, a few species in Australia, of which *F. occipitalis* with black and white rings.
Homorelaps and *Aspidelaps*, with a few species in South Africa.
H. lacteus, yellowish white with black bars or rings.
A. lubricus, orange or red with black rings.

II. **Opisthoglyphous** ***Colubrinae***; the poisonfangs stand so far back in the maxillary series that they are effective only during deglutition.

Homalocranium, More than 20 species, from tropical South America into Southern United States.
H. rubrum, Orizaba to Tehuantepec.
H. bocourti, Guanajuato, pale red without black spots.
H. annulatum, Nicaragua.
Scolecophis, Mexico and Central America.
S. atrocinctus, Central America.
S. michoacanensis, Michoacan to Zacatecas.
S. aemula, Batopilas between Sonora and Chihuahua.
Erythrolamprus, about 9 species, Tropical America to Texas.
E. aesculapii (= *Elaps venustissimus* WAGL.). With endless variations in tropical South America.

III. **Aglyphous** ***Colubrinae.*** Not venemous.

Coronella (*Ophibolus* s. *Osceola* of American authors), e. g. *syspila* COPE; *gentilis* B. et G.: *elapsoidea* HOLBROOK; *coccinea* SCHLEGEL; *annulata* KENNICOT; most of them treated by BOULENGER as varieties of *C. doliata* L., United States.
C. micropholis s. *polyzona*; Mexico to Para.
C. pyrrhomelas, Arizona etc.
Cemophora coccinea, Carolina, Florida to Mississippi.
Rhinochilus lecontei, California to Texas.
R. antonii, Mazatlan, Sinaloa.
Urotheca = *Elapochrous*, Tropical Mexico to Guiana.
U. elapoides = *E. aequalis*, Mexico to Guatemala.
U. bicincta, Guiana.
Geophis, many species in Central and South America.
G. semidoliata Orizaba district.
Tropidodipsas, Central America.
T. dumerili and *T. fasciata*.
Atractus South America.
A. latifrons, Brazil; red with black and yellow rings.
A. elaps, Ecuador; black with white rings, or reddish with double black rings.

Streptophorus, Southern Mexico to N.W. South America.
S. atratus, Vera Cruz to Ecuador and Venezuela.
Polyodontophis (*Enicognathus* pt.) Central America.
P. venustissimus, Nicaragua.
P. annulatus, Guatemala.
Coluber conspicillatus, Japan; red ground with black spots with yellowish margins.
C. porphyraceus, Indo-China. Sometimes red with narrow black cross bars.

Coluber, cosmopolitan genus with more than 40 species, of which scarcely any approach elapoid coloration.
C. dichrous, Brazil to Peru; uniform olive black brown, young black with narrow yellowish crossbands.
C. novae-hispaniae = *Spilotes salvini* GUENTHER, Mexico and Central America; black and yellow, the yellow forming regular cross bands on the posterior body and on the tail.

IV. ***Ilysiidae.*** Only about 5 species. Harmless.

Ilysia scytale, Guyana etc. Coral red with numerous black rings. Often called Coralsnake.
Cylindrophis rufus, Indo-Malayan. Black, often with many white narrow, irregular rings; red neck-ring and red under parts of the tail.

V. ***Uropeltidae.*** About 40 species. „Burrowing snakes of small size, restricted to Ceylon and the mountains of Peninsular India, or to heavy forests at the immmediate foot of the mountains, as far North as 19°." BOULENGER, Cat. Snakes, Vol. 1.
Many of them are beautifully coloured black with vivid red and yellow; e. g. *Rhinophis*.

A numerical census like the above is not satisfactory. The genera and species are not equivalent, many of them being based upon unimportant characters. It is also impossible to define the limits of "elapoid" coloration, especially since not a few individual variations of *Elaps* look far less Elapoid than many harmless sharply ringed snakes which common sense excludes form such a list.

However there are about 6 Elapine against 15 harmless genera, but whilst two thirds of the total species of *Elaps* have mostly "warning colours", only a few each of the almost equally large genus *Homalocranium* are thus conspicuously coloured, and the same applies to *Geophis* and *Coronella*. In fact what is the rule in the Elapine genera, is the exception in most of the others, but mere comparison of the respective numbers of species does not bring out the really

important fact that Elapoid dress occurs in about two dozen poisonous species against as many harmless species; or 20 against 25 if we reject the less conspicuous. To make these statistics yield any useful results we have to restrict them to the various geographical units.

In Africa we have one or two cases amongst the Elapines and none amongst the harmless snakes.

In Australia, which is swarming with Elapines, which there actually form the majority of snakes, we have only *Furina occipitalis* (*Pseudechis* is a still weaker case) and no harmless kinds with such colours.

In Indian and Malay countries are the Elapine *Callophis* and *Doliophis* against *Cylindrophis* and *Rhinophis*, all of them conspicuously coloured. Some specimens of *Callophis macclellandi* assume exactly the typical dress of *Elaps fulvius*, but *Callophis* ranges from Nepal (where it is sombre) and Assam to China, and nowhere does it approach the range of the Uropeltids; but *Cylindrophis rufus* and *Doliophis* may meet, and this would be the only instance of Elapine mimicry in the Old World.

A very different aspect prevails in America. From Maryland and California to Argentina scarcely a state is without some snake which does not show the striking dress of Coralsnakes. First there is *Elaps* itself, a typical and characteristic American genus with almost the same enormous range. Secondly there are 4 opisthoglyphous and 8 aglyphous genera, about 20 species of which greatly resemble one or more of the 18—20 conspicuously coloured species of *Elaps*. If put in this way, with the addition that two of the commonest species, *Elaps fulvius* and *Coronella micropholis*, both range from the Southern United States into South America, that they often appear in the identical complicated dress, and lastly that where these species give way, others, e. g. *Elaps corallinus* and *Erythrolamprus aesculapii*, take up the resemblance — the case for mimicry would seem to be well established. And yet it would be based upon an insiduously misleading mode of stating the case.

It is a true generalisation that in every country where the conspicuous dress is worn by some *Elaps*, it also occurs in some other snakes; but the reverse is not true.

Let us now examine Mexico. It possesses only the widely spread *Elaps fulvius* with its abundant varieties in dress, and where this species gives way in the North West it is represented by *E. euryxanthus*, called thus because the yellow between the red and

black appears in rather broad rings. Against these 2 species stand 3 opisthoglyphous and 6 aglyphous genera with about 10 species, and it is at least my own personal experience in Mexico, born out by the numbers of specimens in good American and European Museums, that the harmless kinds in Elapoid dress are much more common than *Elaps*. The supposed advantage of its dress with reference to other creatures must thereby be seriously impaired, but it would be fully justified when referred to physiological, constitutional, and environmental, physico-chemical agencies.

The resemblances between *Elaps* and some other snake are often surprisingly close, almost to minute detail in pattern and colours. Sometimes these close resemblances occur in the same district, more often not. The pattern which the otherwise most versatile *Coronella* cannot produce is the very kind which is the socalled typical dress of *Elaps fulvius*, and in which this likewise most versatile snake appears invariably in Northern Mexico and in the United States! *Coronella* has hit off the wrong combination! This being so, the cases of close resemblance in the same districts are reduced to mere lucky coincidences, the luck supposed to be on the side of *Coronella*.

Within the United States great resemblances to *Elaps* are reduced to the genus *Coronella*, and from Florida to Lousiana with the addition of the monotype *Cemophora coccinea* which is a *Coronella* modified for digging. The genus *Coronella* (*Ophibolus* and *Osceola* of American authors) flourishes much in North America, where it has produced a great number of varieties, the synonymy of which is in confusion. It suffices for our purpose that they show the tendency of changing from North to South from a pattern more or less brown with dark blotches or saddles, into one which is sharply ringed, red with double black rings divided by yellow, typical instances of series DM. This gradual progressive change is best illustrated by the species which are commonest in the states East of the Mississippi.

Three of these Kingsnakes, called thus because they occasionally eat poisonous kinds, for instance *Elaps* itself, are beautifully figured in Ditmars, Reptile-Book, New York, 1907, tab. 105.

Ophibolus doliatus triangulus, New York State. Shades of olive-brown; blotches complete, reaching but a moderate distance down the sides; interstices pale.

O. doliatus clericus, Maryland. Blotches complete, but reaching

nearly to the abdomen; the areas of the patches are dull red; interstices white.

D. doliatus coccineus. Florida. The blotches have burst so as to form scarlet and black rings with yellow interstitial rings.

Nearly a dozen varieties have been described. The only reasonable way is to group them into a few variable species, and these show the unmistakable tendency to become more brilliantly and sharply ringed from North to South. For instance the typical *O. doliatus*, from Maryland into Texas, is dull red, likewise as *var. gentilis* in Arkansas; as *var. annulata* it is bright red in Southern Texas whence it ranges into Nuevo Leon and further South, but in the rest of Mexico, and thence into South America, it continues as *Ophibolus s. Coronella micropholis*.

The most brilliant Coronellas occur in the hot and moist regions from Florida into Texas, as *C. coccinea*, *C. elapsoidea* and *Cemophora*. But the *C. coccinea* has been found also at Fort Union in New Mexico; and *C. doliata var. syspila* ranges from Indiana to Apache in Arizona.

Peculiar distribution prevails in the Sonoran region. From Fort Whipple, near Prescott in Arizona, have been returned: *Elaps euryxanthus*, *Coronella pyromelanus* s. *zonata* (California to Arizona); *Rhinochilus lecontei* (from Kansas to Mazatlan). At Fort Union in New Mexico occur *Coronella coccinea*, *C. pyromelanus* and almost certainly *R. lecontei*, but not *Elaps*.

The most significant fact is that specimens of *Coronella* with fully developed tricoloured ringed dress occur so far North as Maryland, Indiana, Kansas, even Nebraska, in some instances at least 400 miles beyond the nearest possible station of *Elaps*. The latter is alleged to have been found as far north as Ohio, and it has been suggested that this snake has made its way up up the valley of the Mississippi. Even if true, this would not affect the following consideration. It cannot be seriously thought of that Coronellas, having acquired their beautiful garb in the South and having there found it useful as humbugs, have then spread northwards, carrying their fame with them. Even the more serious alternative cannot be entertained, that *Elaps* may have withdrawn from an originally more northern range, but leaving its fame behind. We do not know the geological age of *Elaps*, but it is certainly an arrival, not only in North- but also in Central America, after the separation of the Antilles in postmiocene times. It entered the New World neither by the proverbial route of Behring's Strait, nor from Africa,

but more probaby from the South, its nearest relations living now in Australia. Exactly the reverse applies to *Coronella*, which genus, in the wider sense, comprises about six species in Europe, North and West Africa, one in the old Deccan, and the rest, about ten species with endless varieties in North America, whence only a few have extended into Mexico, and *C. micropholis* alone to the Equator. So far as America is concerned, *Coronella* is a Nearctic, *Elaps* a Neotropical genus, each having sent a few species into Mexico, that interesting meeting ground of the faunas and floras of the Northern and of the Southern World.

But why, it will be asked, is America full of this Elapoid coloration, which is so rare in Indo-Malaya, and practically absent elsewhere? Because the America environment favours the production of red in snakes. There would be plenty of harmless Coralsnakes although *Elaps* had never found its way into the New World, and the many sorts of *Elaps* would be just as pretty as they are now, if there were none to copy them.

Tropical American forests are inhabited by a surprising number of animals with prehensile tails, Marsupials, Edentates, Rodents, Insectivores, Carnivores and Monkeys. In the equally luxuriant tropical forests of the Old World this effective principle is unknown amongst mammals. Why? Or why not? A Mexican Indian's answer would be „no es costumbre", it is not the fashion; the Scientist appeals to environment and natural selection, and means, but does not like to say: Genius loci.

November 2nd 1910.

Explanation of plate.

Plate 1.

A few Samples of „Coralsnakes".

Fig. 1. *Streptophorus atratus.* Half-grown specimen from near Orizaba, cf. page 9.

Fig. 2. *Elaps fulvius.* San Juan Evangelista, State of Vera Cruz. Beyond the black neck-ring, there are on the trunk 15 narrow black rings. Only a few yellow scales above and below the black rings. Every scale of the red bands has black pigment near the apex; total result rather dark. Tail with 8 black and 8 yellow-rings; end of tail black.

Fig. 3. *E. fulvius.* Near the Mouth of the Balsas River, Michoacan. Typical, or most frequent pattern of *E. fulvius.* Sole pattern in N. Mexico and in U. S. A. In this specimen the neck-ring covers 4 longitudinal scales. Then follow, on the trunk 14 narrower black rings, bordered above and below by one row of pure yellow scales.

Each scale of the red bands slightly tipped with dark brown pigment.

Tail with 6 broad black bands, divided by 5 yellow rings; end of tail white.

Fig. 4. *E. fulvius.* Volcan del Jorullo, Michoacan; cf. page 6. On the trunk with only 7 red bands, slightly stippled with dark pigment; separated by 6 quintets of 3 black and 2 yellow rings.

Tail with 3 black and 3 yellow bands and rings; end of tail black.

Fig. 5. *E. surinamensis.* Copied from Jan, pt 42, 1.

Fig. 6. *Coronella micropholis*. Carrizal, South Michoacan.

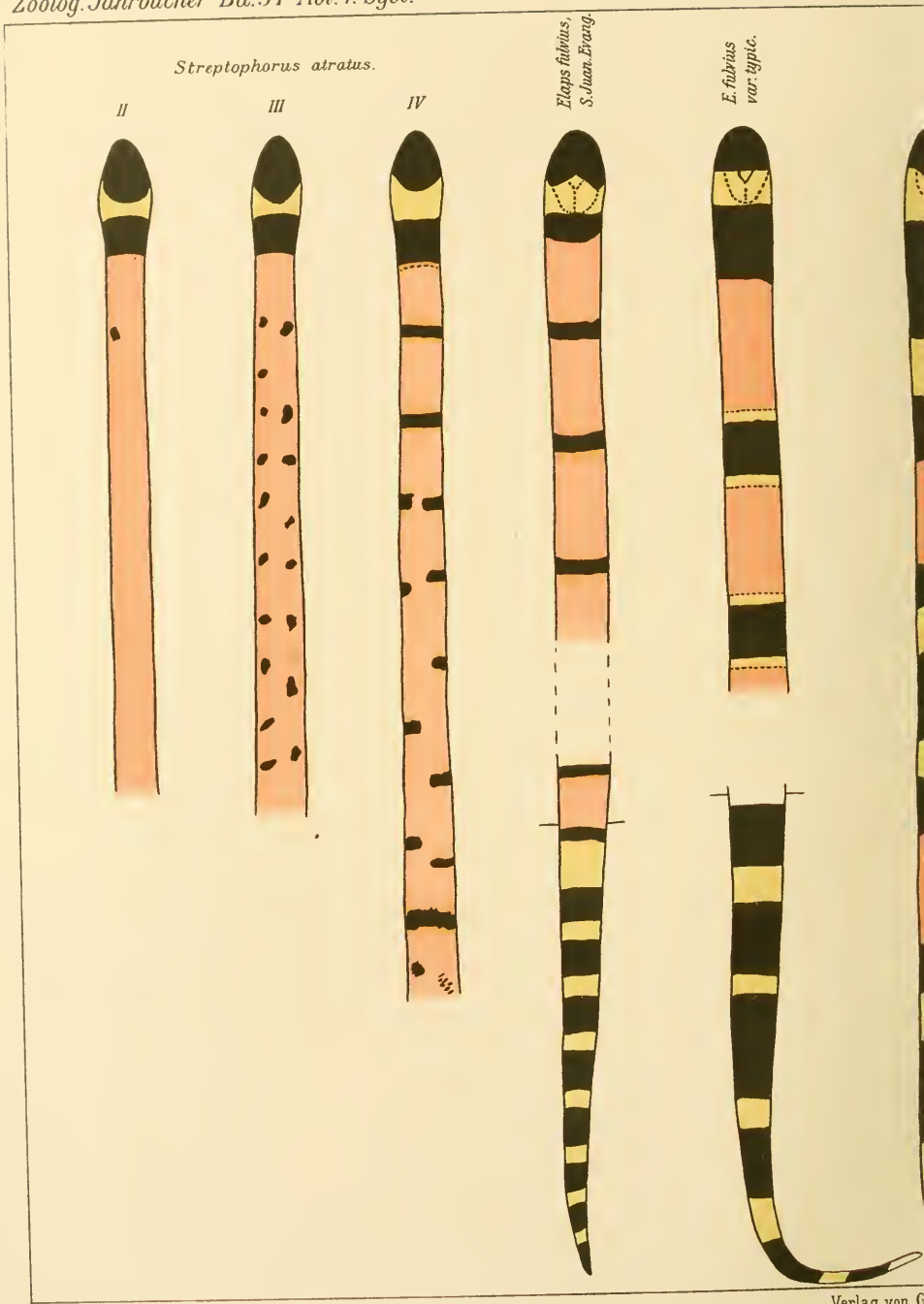
15 red bands on the trunk, each scale with a tiny dusky speck at the apex.

15 yellow bands on the trunk. The 2nd, 5th and 14th red fields are encroached upon by the black of the distorted neighbouring rings.

Tail with 3 red bands and 3 pairs of black rings, the first pair of which immediately behind the vent.

Fig. 7. *C. micropholis*. Chilpancingo, Guerrero. The usual pattern of this species in South Mexico.

In this specimen are 14 pairs of black rings on the trunk, enclosing a red instead of a yellow, narrow, ring.



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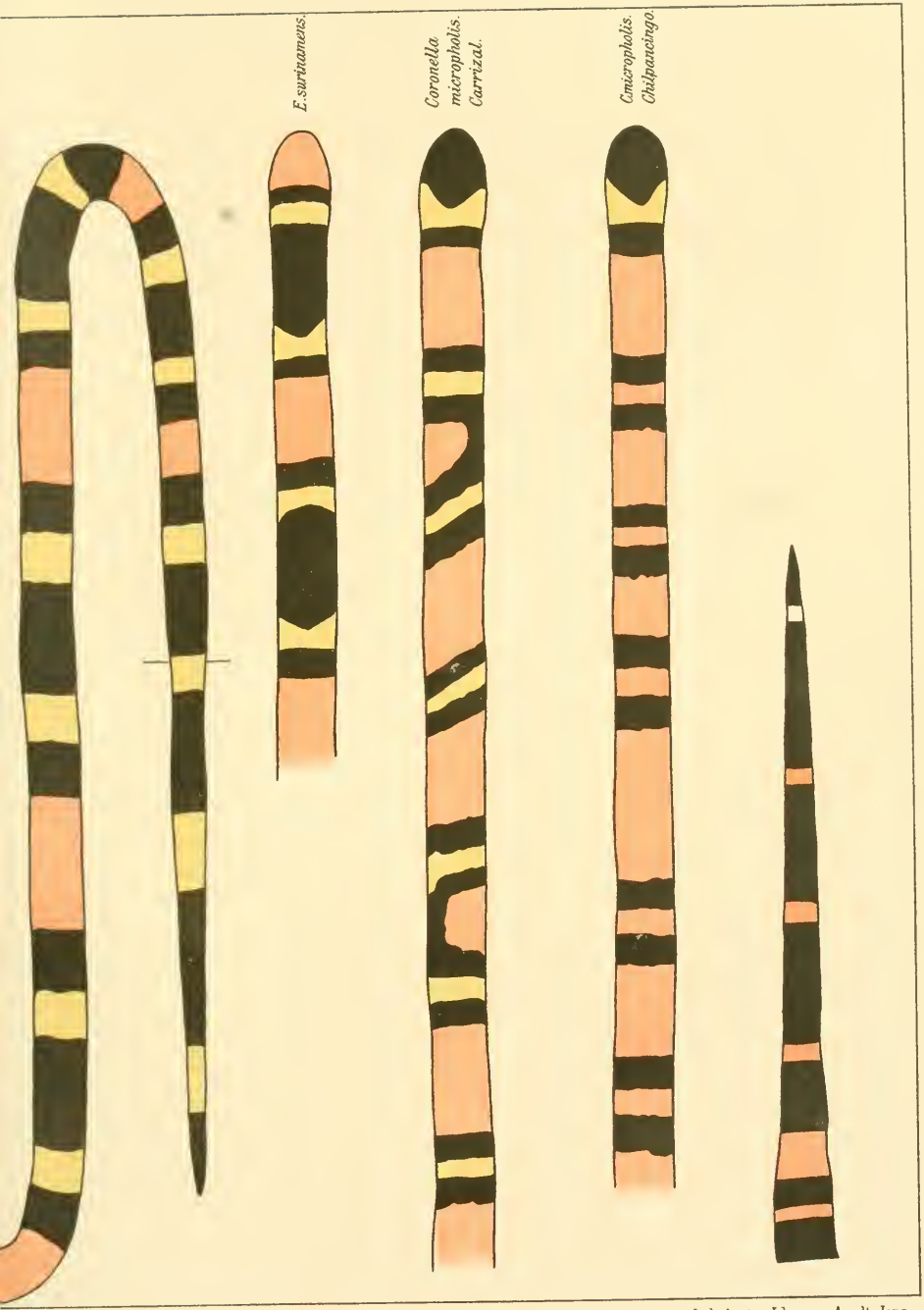

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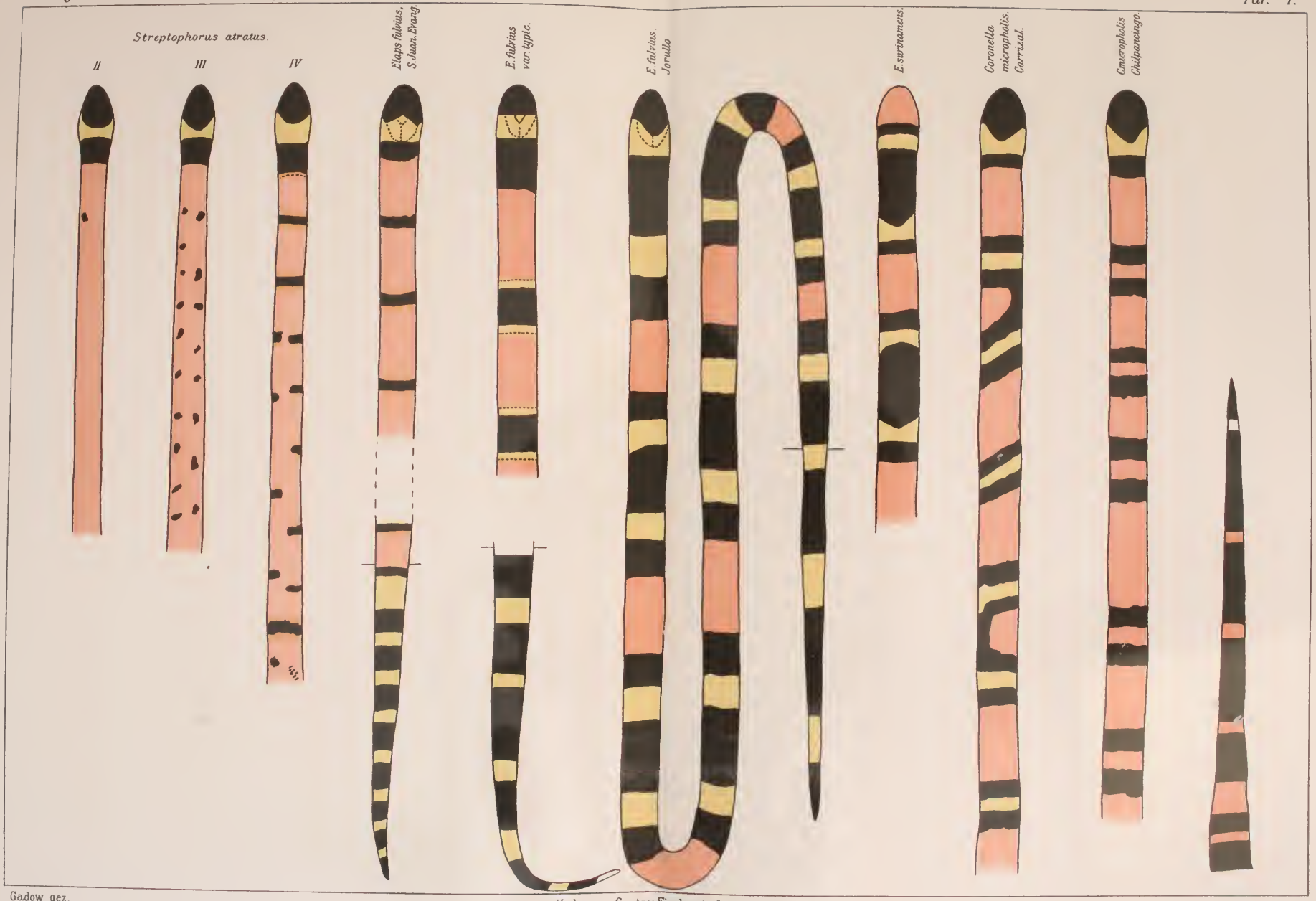

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