XXXII. *Contributions to an Insect Fauna of the Amazon Valley.* LEPIDOPTERA: HELICONIDÆ. *By* HENRY WALTER BATES, *Esq.* (Communicated by the Secretary.) *

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"Die wissenschaftliche Untersuchung der Natur strebt in den Einzelheiten das Allgemeine zu erkennen, um endlich dem Grunde aller Dinge näher zu kommen. Für diese Art Untersuchungen, die immer das Ziel der Naturforschung sein sollte, bietet wohl keine Thierclasse so reichen Stoff als die Insecten."—*Karl Ernst von Baer*, Address on the Opening of the Russian Entomological Society, St. Petersburg, May 1860.

THE family *Heliconidæ* was established by Mr. E. Doubleday in 1847, in Doubleday and Hewitson's 'Genera of Diurnal Lepidoptera.' It was founded on a number of Butterflies, remarkable for the elongated shape of their wings, and peculiar (with the exception of one genus, *Hamadryas*, which the author placed provisionally in the family, *op. cit.* p. 98) to the intertropical and subtropical zones of America. Many of them had been described by the older authors under *Heliconia*, *Mechanitis*, and several other ill-defined genera. They had been previously (in 1836) united in a tribe, *Heliconides*, by Dr. Boisduval in his 'Spécies Général des Lépidoptères;' but this comprehended also the group *Acræidæ*, which Doubleday excluded from the family. Linnæus treated them as a section of the genus *Papilio*, under the name of *Heliconii*. The nearest allies of the *Heliconidæ* are the *Acræidæ* just mentioned and the *Danaidæ*: all are distinguished from the true *Nymphalidæ* by the discoidal cell of the hind wings being always closed by perfect tubular nervules. Mr. Doubleday, placing more reliance on the shape of the antennæ and the abdominal border of the hind wings than on the far more important character above named, was led to exclude the genus *Eueides* from the family: this rendered the definition of the two groups very difficult, if not impossible, *Eueides* having the wing-cells closed in the same way as the *Heliconidæ*. Excepting that I re-admit *Eueides*, and exclude *Hamadryas*, which does not enter into the series of the American *Heliconidæ*, the family will be treated of in the present memoir as defined in the work above quoted.

The position of the *Heliconidæ* in the order Lepidoptera may be understood when I state that in a natural system the group would stand at the head of the whole series of families of which the order is composed. At least, this should be its place according to the view now taken of the order by many systematists, who arrange the families of *Rhopalocera*, or Butterflies, according to their degree of dissimilarity to the *Heterocera*, or Moths—in other words, according as their structure shows a lower or a higher stage in an ascending scale of organization. For, as the lower families of Moths are allied to other orders of insects, the further a group recedes from them in structure, the higher is the grade of perfection of the Lepidopterous type which it exhibits. The families show their degree of affinity to Moths by many characters, the principal of which is the

* The materials on which this memoir is founded were collected by the author during eleven years' research on the banks of the Amazons.

structure of the anterior legs in the adult state of the insects. The *Heterocera* have always six perfect legs: most of the families of *Rhopalocera* have the anterior pair in a more or less rudimentary condition; and as the atrophy seems to have reached its furthest stage in the *Heliconidæ*, this group must be considered as occupying the highest rank in the order. Other characters accompany the one derived from the structure of the legs, which it is unnecessary here to enumerate. It will be seen from these remarks that the order Lepidoptera is one of those groups in the Animal Kingdom which show, beyond the many collateral branches of development that always exist, a clear linear advancement of organization.

The *Heliconidæ*, *Danaidæ*, and *Acræidæ* are related to each other in a different way from that which appears in the received classifications. A few remarks on their mutual affinities are necessary, in order to exhibit the true relations of the *Heliconidæ* to the allied groups of the Old World tropics. It has escaped the notice of all authors, that the *Heliconidæ* are composed of two groups, which differ very considerably in important points of structure; in fact, the majority of the genera of which the family is composed ought to be withdrawn from it, and placed with the *Danaidæ*. The very great superficial resemblance between the two sets of genera has led to their being united by all authors, and prevented inquiry into their real relationship. To avoid innovation, I will retain the family as it stands, and call the group which is allied to the *Danaidæ*, DANAOID HELICONIDÆ, and the other, which approximates somewhat to the *Acræidæ*, ACRÆOID HELICONIDÆ. The Acræoid group comprehends the genera *Heliconius* and *Eueides*; the Danaoid, the whole of the remaining *Heliconidæ*. The following are the distinguishing characters of the two groups:—

Acræoid Heliconidæ. The hind wing-cell is very small, and the nervures are so arranged that the upper and lower radials* (discoidal nervures of Doubleday) appear to be branch and sub-branch of the subcostal nervure, the discocellulars being short and continuous with them; the costal nervure is prolonged to the apex of the wing. The larvæ are similar to those of *Acræa* and *Argynnis* (*Nymphalidæ*), being beset with hispid spines†. The head is broad, the palpi thick.

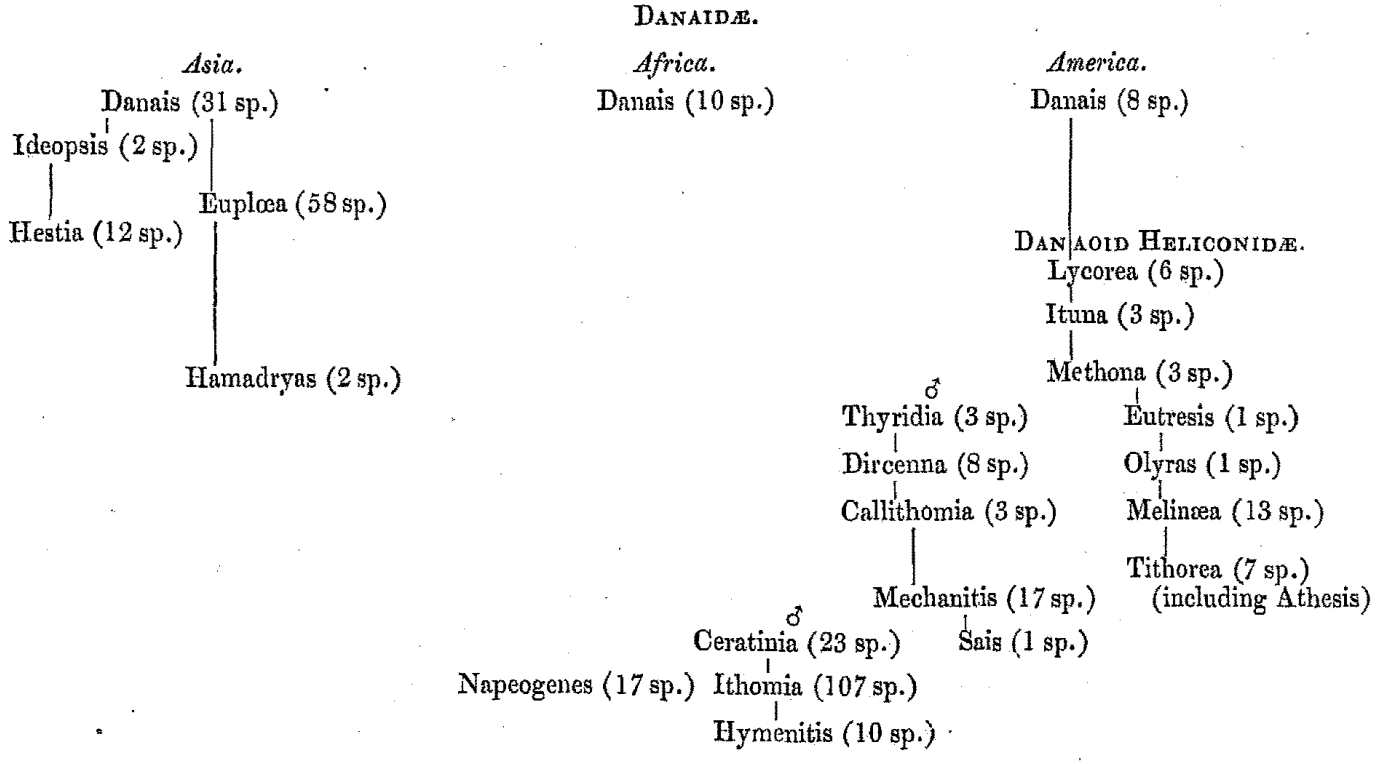
Danaoid Heliconidæ. The hind wing-cell is very large, and irregular in shape; the two radials never appear as branches of the subcostal, but are very uncertain in position, owing to the very vacillating length and direction of the discocellulars: the costal nervure is short, and terminates on the costa, not reaching the apex of the wing. The larvæ (only one species is known) are smooth, like those of the *Danaidæ*, but are furnished with tubercles, instead of long fleshy threads. Head small, orbicular; palpi slender‡.

* I have adopted the terminology of Doubleday (Doubl., Hewits., and Westwood's Genera of Diurnal Lepidoptera) with regard to the neuration or veining of the wings, excepting that I call the "nervules" of the subcostal and median nervures "branches," and the "discoidal nervures" "radials," these alterations appearing necessary to prevent the verbal confusion of nervule with nervure, and discoidal with discocellular.

† The early states of these insects were not known to Doubleday. I reared, myself, *Heliconius Erato* (and *Doris*) and *Eueides Lybia*. We are acquainted, through other sources, with the larvæ of *H. Melpomene*, *H. Ricini*, and *Mechanitis Polymnia*.

‡ Since the above memoir was read, Dr. C. Felder of Vienna, in an article entitled, "Specimen Faunæ Lepidopterologicæ riparum Negro superioris in Brasilia septentrionali," 'Wiener Entomologische Monatschrift,' March 1862,

This view of the affinities of the family will make a great difference in the conception of the group as regards the affiliation of the forms. Instead of being a group isolated in its structure, and peculiar to the tropical parts of America, it results that the bulk of the genera have a very close relationship to the *Danaidæ*, which are found in all hot countries of both hemispheres: the *Acræoid Heliconidæ* alone are an isolated set of forms. The American productions, however, show a great superiority in structure and in the diversity of the forms over those of the Old World. In Africa only one genus occurs, namely, *Danais*. In the tropical parts of Asia four genera are found, besides *Danais*; these are *Ideopsis*, *Hestia*, *Euplœa*, and *Hamadryas*, which contain together 74 species. In the hot parts of America 16 genera (of *Danaoid Heliconidæ*) have been discovered, comprising 233 described species. Besides this greater diversity of generic and specific forms, the American productions show a much greater advance in organization than those of the Old World; in other words, they recede further from what may be considered as the common type, namely, *Danais*. This is clear from the great and progressive modification in the position of the radial nervures and discocellulars of the hind wings, and the advanced stage of atrophy of the male fore legs reached by most of the genera. In all the Asiatic genera the fore legs are in the same condition as in *Danais* and the *Nymphalidæ*. The following Table will show the relative value of the productions of the two hemispheres in a clearer manner. I have placed the genera in accordance with what seem to be their mutual affinities. The relative length of the lines between them is a rough expression of the degree of relationship. The collateral lines of connexion are also attempted to be expressed.



has ventured to withdraw the whole of the genera composing the group *Danaoid Heliconidæ*, placing them with the *Danaidæ*, and restricting the family *Heliconidæ* to the two genera *Heliconius* and *Eueides*. He has discovered an excellent and constant character for the *Danaidæ* (in which the *Danaoid Heliconidæ* participate), in addition to those already known, namely, the existence of a small nervule at the base of the fore-wing median nervure which ana-

There is a very wide dissimilarity in minor points and in general appearance between the Asiatic set of forms and the American: the only Old World genus which at all approaches the New World group is *Hamadryas*; but the shape, colours, and neuration of the wings show that it has no close affinity with them. The two sets of forms seem to agree, however, in habits, and apparently occupy the same sphere in the economy of nature in their respective countries. Mr. Wallace, who has had the good fortune to observe both in their native abodes, says, the habits of the South Asian *Euplœæ* (the most numerous genus) are precisely those of the *Heliconidæ*. The Asiatic *Danaidæ* are mostly above the middle size, and include some of the largest Butterflies known; their American equivalents are in general below the middle size. Both are extremely prolific or abundant in individuals, and are amongst the most characteristic productions of their respective countries. Each set, also, are the objects of numerous mimetic resemblances on the part of other Lepidopterous insects of their own region belonging to different families,—the Asiatic mimickers being modelled after the Asiatic *Danaidæ*, and the American after the American members of the same family. The entire dissimilarity of the two sets of forms would seem to teach us that there can have been no land communication east and west between the tropical parts of Asia and America since they first came into existence, and therefore that the great continents must have remained separate in those quarters from a very remote epoch to allow for such an extensive independent development of forms. They are both strictly confined to the hottest parts of their respective hemispheres. In America they are not found beyond the northern tropic, nor much further south than 30° S. lat. They are not known to occur so far from the equator as either tropic in the Old World, but are limited to the south-eastern parts of Asia and the islands of the New Guinea group. The genus *Danais*, with which we have seen both groups are connected, ranges as far north as 41° in Europe, and 45° in North America. It is interesting thus to find that the only genus which is common to the three tropical regions is the sole one of the family that occurs in high latitudes. The only means of communication between the intertropical lands of America and Asia seems to have been a circuitous route by the north (or south); and the essentially tropical forms do not appear to have passed along it. The fact of the peculiar equatorial Asiatic *Danaidæ* not reaching Africa is explicable on the same grounds as their entire distinctness from the American ones, namely, the non-existence of an equatorial connexion of land of a nature suitable for their transit between the two continents since the remote date when the first forms of the group came into being.

The habits of the *Heliconidæ* have been described by various travellers,—Lacordaire having given a complete account of the Cayenne species, and Dyson and Gosse some interesting notes on those of Venezuela and Jamaica. The total number of species described is 284, namely, 233 belonging to the Danaoid, and 51 to the Acræoid group. They are peculiarly creatures of the forests, and, like the Platyrrhine Monkeys, the arboreal

stomoses with the median a short distance from its origin. In the systematic part of the present memoir I shall follow Dr. Felder in this altered classification. The two groups which composed the family *Heliconidæ* are, it must be repeated, completely and widely distinct. Yet the analogical resemblance between them is so great, that some species of the one might easily be confounded (if not closely examined) with species of the other.

Gallinacea (*Penelopidæ* and *Cracidæ*), and other groups of the same region, point to the gradual adaptation of the fauna, during an immense lapse of time, to a forest-clad country.

I found on the banks of the Amazons 94 species (besides many local varieties, considered by some authors as species) of the two groups (67 Danaoid and 27 Acræoid), representing all the genera of the family but three. They are most numerous in those parts of the country where the forests are most extensive and the climate most sultry and humid. I found the number of species to increase in travelling from east to west, from the Lower Amazons towards the eastern slopes of the Andes. They were rare in the somewhat drier tract of country which borders the Lower Amazons about the middle of its course. I found in this large district only 26 species, namely, 10 belonging to the Danaoid and 16 to the Acræoid group. Within an area of about the same dimensions, in the moist region of the Upper Amazons, I collected 64 species, of which 42 were Danaoid and 22 Acræoid *Heliconidæ*. I should judge, from the collections received in England from those parts, that the hot Andean valleys near Bogota, or in Ecuador, contain a still larger number of species than the plains of the Upper Amazons. In the dry forests which clothe a great part of the banks of the Tapajos I found exceedingly few: at one locality, where I collected four months, and which was rich in other families of Lepidoptera, I saw only one species of the Danaoid and four of the Acræoid group. According to Dyson, many species (*Ithomiæ*) of the lowlands in Venezuela have a vertical range of 2000 feet, and some genera (*Hymenitis* [*H. Dercetis*], *Olyras*, *Eutresis*), which do not inhabit the Amazon region, occur at an elevation of 8000 feet. The species are exceedingly abundant in individuals wherever they occur: they show every sign of flourishing existence, although of slow flight, feeble structure, unfurnished with apparent means of defence, and living in places which are incessantly haunted by swarms of insectivorous birds. The pathways in the forest near towns are quite enlivened by the multitudes which fly about amongst the lower trees, in their bright dresses of orange, blue, and yellow, and red and black.

The mode of flight of the members of the two groups is somewhat different. The *Heliconii* and *Eueides* move along in a sailing manner, often circling round for a considerable time, with their wings horizontally extended. The species of the Danaoid group, for the most part, keep near the ground, and have a very slow irregular flight, settling frequently. They are all of social or gregarious habits. Not only do individuals of the same species congregate in masses, but the set of closely allied species which people a district keep together in one or more compact flocks. I noticed in four districts rich in Danaoid *Heliconidæ*, where I collected, that about half the species of *Ithomia* flew together in one circumscribed area of the forest, and the other half in a second similar locality, the rest of the tolerably uniform wooded country, in each case, being nearly untenanted by them. The larger species (*Heliconii*, *Lycoreæ*) frequent flowers, probing the nectaries with their proboscides; but the smaller kinds (*Ithomiæ*), and the members of the Danaoid group generally, are very rarely found thus occupied: I noticed them sometimes imbibing drops of moisture from leaves and twigs. The fine showy *Heliconii* often assemble in small parties, or by twos and threes, apparently to sport together or

perform a kind of dance. I believe the parties are composed chiefly of males. The sport begins generally between a single pair: they advance, retire, glide right and left in face of each other, wheel round to a considerable distance, again approach, and so on: a third joins in, then a fourth, or more. They never touch: when too many are congregated, a general flutter takes place, and they all fly off, to fall in again by pairs shortly afterwards. The species which I have seen most frequently employed in this way is the *Heliconius Rhea*, a glossy blue-black species, with bright yellow belts across its wings.

The larvæ of the two or three species whose transformations I observed feed together in clusters on the leaves of trees of moderate elevation, near the places where the adult insects are found.

The majority of the species have very limited ranges. I was surprised, when travelling on the Upper Amazons from east to west, to find the greater part of the species of *Ithomiæ* changed from one locality to another, not further removed than 100 to 200 miles. For instance, there were 11 of these *Ithomiæ* at a place called Fonte Boa, and 9 at St. Paulo, 180 miles distant; but only two of the total number (20) were found in both localities. This is remarkable when we consider that the whole of the country of the Upper Amazons is a nearly level plain, uniformly covered with forest, and offering no perceptible difference in soil or other physical conditions. Five only out of the 20 species have been met with in any other part of South America. The areas of distribution of most of the remaining 15 must be, in each case, a very limited tract of country. The species which inhabit other parts of Tropical America must have similarly contracted ranges, if we may judge from the collections received in England from different districts.

Now, many of these local species have the appearance of being geographical varieties; I could not help suspecting them to be such when I met with them in nature, the differences between the forms of one and those of another locality relating in many cases simply to the colours and colour-patterns of the wings. The marks of distinction, however, are in the majority so well defined, so ordinarily common to all the individuals concerned, and there is so generally an absence of connecting links, that they are held on all hands to be good and true species. Moreover, in those cases already mentioned, where a number of very closely allied species fly together, they keep themselves perfectly distinct; there are no hybrid forms (I am speaking of the *Ithomiæ* and allied genera), and on observing individuals *in copula*, I almost always * found the pair to be precisely the same in colours and markings. In the multiplicity, apparent distinctness, and restricted ranges of the species, this group much resembles the family of Humming-birds of the same regions.

I believe, nevertheless, that the suspicion of many of the species being nothing more than local modifications of other forms has proved to be well founded. Amongst the great number of perfectly distinct and well-marked species, a few occurred which showed great variability: these, I think, afford a key to the explanation of the origin of the rest. The details of variation will be given under the head of each species:

* The exception was in the case of *Mechanitis Polymnia*, which, as will be seen, on referring to the account of it in its place, is a polymorphic species, whose local varieties are in an imperfect state of segregation.

those which supply the most decisive results are *Mechanitis Polymnia*, *Ithomia Orolina* and *Illinissa*, *Ceratinia Ninonia*, and the *Lycoreæ*. The varieties of these present all the different grades between simple individual differences and well-marked local varieties or races, which latter cannot be distinguished from true species, when two or more of them are found coexisting in the same locality without intercrossing, as takes place in *Ithomia Illinissa* and its allies, and probably in *Mechanitis Nesæa* and *Lysimnia*. A striking case of the production of a local variety now spread over a wide area, and undistinguishable from a true species, is afforded in *Heliconius Thelxiope*, to the details of which, given in the systematic part of this memoir, I must refer the reader.

These species, when carefully studied, seem to me conclusively to show that many of the now distinct species of *Heliconidæ* have arisen from local varieties, segregated from the variations of preexisting widely disseminated species; for these distinct forms or species do not essentially differ from the undoubted varieties of the species cited. The genera show different degrees of susceptibility of change under altered local conditions. Thus, many species of *Heliconius* (*H. Rhea*, *Clytia*, *Ricini*, *Vesta*, *Thelxiope*, *Antiocha*, &c.) are unchanged over the whole of the wide country which includes the areas of several successive local races of many *Ithomiæ* and *Napeogenes* *.

The process of the creation of a new species I believe to be accelerated in the *Ithomiæ* and allied genera by the strong tendency of the insects, when pairing, to select none but their exact counterparts: this also enables a number of very closely allied ones to exist together, or the representative forms to live side by side on the confines of their areas, without amalgamating.

The course followed by Nature in the formation of these numerous local species, I think, is clearly exhibited in *Mechanitis Polymnia*, to the details of which, given in its place, I must beg the reader to refer. We see here the manufacture, as it were, in process. The species is widely disseminated and variable. The external conditions in certain localities are more favourable to one or more of the varieties there existing than to the others; those favoured ones, therefore, prevail over the others. We find, in this most instructive case, all the stages of the process, from the commencement of the formation of a local variety (var. *Egaënsis*) to the perfect segregation of one (var. *Lysimnia*, considered by all authors as a true species). In this species, most of the local varieties are connected with their parent form by individuals exhibiting all the shades of variation; and it is on this account only that we know them to be varieties. In the species allied to *Ithomia Flora*, the forms are in a complete state of segregation (with the exception of *I. Illinissa*, which throws light on the rest), and therefore they are considered as species; they are, in fact, perfectly good species, like all other forms considered as such in natural history. It is only by the study of variable species that we can obtain a clue to the explanation of the rest. But such species must be studied in nature, and with

* These are *Ithomia Flora*, an inhabitant of the whole Lower Amazon region (from the Atlantic to the Rio Negro), which is represented by *I. Hippodamia* in Cayenne, and *I. Onega*, *Illinissa*, *Gunilla*, *Priscilla*, *Ilerdina*, in different areas on the Upper Amazon; *Napeogenes Cyrianassa*, which becomes *N. adelphe* on the banks of the Cupari (Tapajos), and *N. Tunantina* on the north bank of the Upper Amazons; *N. Inachia*, which is changed to *N. sulphurina* at Bahia, and to *N. Ercilla*, *N. Corena* and *N. Pharo* in different areas on the Upper Amazon. Other species might be added in confirmation. Most of the species of *Heliconius* quoted are found unchanged over the collective areas of all these forms of *Ithomia* and *Napeogenes*.

strict reference to the *geographical relations* of their varieties. Many closet naturalists, who receive disconnectedly the different varieties in any group, treat them all as independent species: by such a proceeding, it is no wonder that they have faith in the absolute distinctness and immutability of species.

The sexes in the *Heliconidæ* very rarely differ in colours. Secondary sexual characters of another description occur, however, very generally in the Danaoid group. The males, in all the genera but two (*Lycorea* and *Ituna*) of this section, are furnished with a pencil or fringe of long hairs near the costal edge of the hind wings on the upper surface. It sometimes arises from the bottom of a shallow horny cup situated between the costal and subcostal nervures; the hairs are long, soft, and adpressed. I was unable to discover any use in this structure; it seemed not to be under the control of the insect. There is no movement in flight, or position in repose, peculiar to the male sex, which might require an instrument to hold the wings together—a function which the position of the hairs, in the place where the fore wing overlaps the hind wing, suggests to the mind. I believe the appendage must be considered as an outgrowth of the male organization, which is not in this case applied to any especial purpose: it may be taken to be of the same nature as the pencil of hairs on the breast of the male Turkey. Growths of one kind or other, on the surface of the wings, peculiar to the male sex, are frequent in Butterflies: in *Danais* the males have a small horny excrescence on the disk of the hind wings, which, considering the near relationship proved to exist between the two groups, I take to be homologically the same as the pencil of hairs in the *Danaoid Heliconidæ*. In the genus *Pavonia*, belonging to the family *Brassolidæ*, the males in some species have a fringe of hairs near the abdominal border; in others, a long pencil of the same on the disk; and, again, in others, instead of these appendages, a thickened plate on the inner margin of the hind wings.

The most interesting part of the natural history of the *Heliconidæ* is the mimetic analogies of which a great many of the species are the objects. Mimetic analogies, it is scarcely necessary to observe, are resemblances in external appearance, shape, and colours between members of widely distinct families: an idea of what is meant may be formed by supposing a Pigeon to exist with the general figure and plumage of a Hawk. Most modern authors who have written on the group have mentioned the striking instances of this kind of resemblances exhibited with reference to the *Heliconidæ*; but no attempt has been made to describe them fully, nor to explain them. I will give a short account of the leading facts, and then mention some circumstances which seem to throw light on their true nature and origin.

A large number of the species are accompanied in the districts they inhabit by other species which counterfeit them in the way described. The imitators belong to the following groups:—*Papilio*, *Pieris*, *Euterpe*, and *Leptalis* (fam. *Papilionidæ*), *Protogonius* (*Nymphalidæ*), *Ithomeis* (*Erycinidæ*), *Castnia* (*Castniadæ*), *Dioptis*, *Pericopis*, *Hyelosia*, and other genera (*Bombycidæ* Moths)*. I conclude that the *Heliconidæ* are the *objects imitated*, because they all have the same family facies, whilst the analogous species are dissimilar to their nearest allies—perverted, as it were, to produce the resemblance, from

* The accompanying Table, in which a number of the most striking of these are arranged in parallel columns, will give some idea of the extent to which this system of imitation prevails.

SPECIFIC MIMETIC ANALOGIES IN THE LEPIDOPTERA OF TROPICAL AMERICA, ESPECIALLY BETWEEN THE DOMINANT FAMILY HELICONIDÆ AND DIFFERENT OTHER FAMILIES.

Danaoid Heliconidæ.	Acræoid Heliconidæ.	Acræidæ.	Papilioninæ.	Pierinæ.	Erycinidæ.	Castniadæ.	Bombycidæ.
Lycorea Atergatis			Papilio Zagreus*	Euterpe Eurytele*			Pericopis angulata.
Methona Psidii { Ituna Phenarete* / I. Ilione*				Leptalis Orise*		Castnia Linus*	P. *sp.*
Dircenna Epidero							Hyelosia Tiresia.
Tithorea Bonplandii	Heliconius Hecuba.*						
Melinæa Egina	H. Sylvana.						
M. Pardalis	H. Pardalinus*.						
M. Lucifer	H. Aurora.						
M. Messatis	H. Ismenius.						
M. (?) Hezia	H. Zuleika.						
M. Mnasias*—Ceratinia Ninonia.							
M. Mneme	H. Numata.						
Mechanitis Egaënsis	H. Eucoma, var.			L. Egaëna*.			
M. Nesæa—Napeogenes Xanthone*.	H. Ethra			L. Astyoche*.			
M. Lysimnia	H. Eucrate.						
Callithomia Alexirhoë* — Ceratinia Ninonia.							
Ithomia Flora { I. Cymo / Napeogenes Ithra*				L. Theonoë*	Ithomeis satellites*		Dioptis Cyma.
I. Phono							D. diaphana.
I. Illinissa and allies } Napeogenes Ereilla*				L. Lysinoë, *var.**	I. aurantiaca*		D. Æliana.
I. Chrysodonia and allies } N. Corena*				L. Erythroë* *var.* of Theonoë.	I. mimica*		D. *sp.**
I. Ilerdina				L. Leuconoë* *var.* of Theonoë.			Dioptis Ilerdina* } Pericopis, *sp.**
Ceratina Fluonia							Dioptis, *sp.**
Ithomia Onega				L. Melanoë* *var.* of Theonoë.	I. Heliconina*		Dioptis Onega.
I. Virginia				L. Argochloë*. *var.* of Theonoë.			
I. Primula—Napeogenes Pharo.							
I. Euritæa—N. sulphurina.							
I. Eurimedia				L. Eumelia.			
I. Celemia—Napeogenes Tolosa.							
Ceratinia villula—N. Apulia				L. Siloë*.			
	Eueides Lampeto*				Stalachtis Calliope		Pericopis, *sp.**
	Heliconius Thelxiope						P. Isse*.
	H. Clytia		P. Pausanias*.				
	H. Vesta { Eueides Eanes*. / E. Thales.						
		Acræa Thalia.		L. Acreoides*		C. Acreoides*.	
			P. Zacynthus ♀	Euterpe Tereas.			
			P. Æneas and allies ♀				Pericopis turbida*.
			P. Bolivar ♀			C. *sp.**	
				Leptalis Lysinoë* *var.* of Theonoë	Ithomeis stalachtina* } Stalachtis Duvalii.		

* Those species marked * have been ascertained beyond all doubt to be very much fewer in individuals than the species which they mimic.

the normal facies of the genus or family to which they severally belong*. The resemblance is so close, that it is only after long practice that the true can be distinguished from the counterfeit, when on the wing in their native forests. I was never able to distinguish the *Leptalides* from the species they imitated, although they belong to a family totally different in structure and metamorphosis from the *Heliconidæ*, without examining them closely after capture. They fly in the same parts of the forest, and generally in company with the species they mimic.

I have already given an account of the local modifications to which the *Heliconidæ* are subject. It is a most curious circumstance, that corresponding races or species of counterfeiting groups accompany these local forms. In some cases I found proof that such species are modified from place to place to suit the peculiar forms of *Heliconidæ* there stationed. As this is an important point, and one which throws light on the origin of mimetic species, I must ask the reader's careful attention to the details, referring to the plates.

Plate LV. fig. 1 *a* (*Ithomia Flora*) and fig. 1 (*Leptalis Theonöe*) represent a Heliconide and its imitator, both of which inhabit the banks of the Cuparí, a river belonging to the Amazon system, in 55° W. long. Neither of these is found on the Upper Amazons (60° to 70° W. long.), where I made the remaining part of my observations on these insects. At Ega, on this upper river, in 65° W. long., two species of *Ithomia* occurred, which I consider to be local varieties or races of *I. Flora*, namely, *I. Onega* (Pl. LV. fig. 2 *a*) and *I. Illinissa* (Pl. LV. fig. 6 *a*). It is immaterial to the question in hand whether these be considered absolutely distinct species or races; the *Leptalis* which was found in their company was the form called *L. Lysinoë* (Pl. LV. fig. 3), with its admitted varieties (figs. 4, 5, 6, and 8). Only one of these varieties of *Leptalis* mimics an *Ithomia*; this is our fig. 6, which evidently counterfeits *Ithomia Illinissa* (fig. 6 *a*). The prevailing form of *Leptalis*, the *L. Lysinoë* (fig. 3), has no resemblance to any *Ithomia* of Ega, but is, when flying, a wonderful imitation of the *Stalachtis Duvalii* (Pl. LV. fig. 3 *a*), a common insect belonging to a genus (family *Erycinidæ*) equally flourishing and abundant in individuals with the members of the family *Heliconidæ*. I think there will be no doubt in the mind of any one that the Ega *Leptalides* are local varieties of the Cuparí *L. Theonoë* (fig. 1), when all the connecting links between them are studied in the figures given on our two plates. It is highly probable, therefore, that this species has been by some means modified with especial reference to the changed *Ithomiæ*, or other insects, of the locality. The varieties, figs. 4, 5, and 8, were excessively rare: they have the appearance of *sports*, and show how variable the species has been in this district.

The same takes place at St. Paulo, in 69° W. long. Here we find the *Ithomiæ* again changed. Neither the *I. Flora* of the Cuparí and Lower Amazons nor the *I. Illinissa* of Ega occurs; but the second Ega species, *I. Onega*, inhabits the district, and several other species not found in other places, amongst them *I. Ilerdina* (Pl. LVI. fig. 4 *a*), *I. Chrysodonia* (Pl. LVI. fig. 3 *a*), and *I. Virginia* (Pl. LVI. fig. 6 *a*). The prevailing species of

* This may be seen from the figures given of *Leptalis*,—fig. 5, Pl. LVI. being *L. Nehemia*, a species exhibiting the usual form of the family *Pieridæ*, to which the genus *Leptalis* belongs; whilst all the other *Leptalides* figured are mimetic species, totally unlike, as far as facies is concerned, this normal form.

Ithomia of the locality being thus changed, how stands it with the *Leptalides*? They are changed also, and again with close reference to the *Ithomiæ*. I found a number of different varieties, which I could not doubt were local forms of the same species as that found on the Cuparí and at Ega. Thus, there was one (Pl. LV. fig. 2) closely resembling *L. Theonoë* (fig. 1), but modified to produce a nearer imitation of the *Ithomia Onega* (Pl. LV. fig. 2 *a*), which I believe to be a local form of *I. Flora*. Another (Pl. LVI. fig. 3) resembled *Ithomia Chrysodonia* (Pl. LVI. fig. 3 *a*); but the imitation is not fixed or exact in all the specimens taken, as may be seen by comparing figs. 1, 2, 3, of the same Plate. We here detect nature, as it were, *striving* after a correct imitation: the explanation of this will be attempted further on. A third form of *Leptalis* found at St. Paulo is the one figured Pl. LVI. fig. 6, which mimics the *Ithomia Virginia* (Pl. LVI. fig. 6 *a*). Besides these, a few varieties occurred which did not closely counterfeit any *Ithomia*; they were very much rarer than the others. I figure two of these (Pl. LV. figs. 7, 9), to show how they connect the other more strongly modified varieties with the Ega forms.

The *Ithomiæ* concerned in these imitations have the character of true species, being distinct and constant, with the exception of *I. Chrysodonia*, whose varieties are detailed under the head of the species, which is variable, and throws light on the origin of the rest. They are all excessively numerous in individuals, swarms of each kind being found in the localities they inhabit. The *Leptalides* are exceedingly rare; they cannot be more than as 1 to 1000 with regard to the *Ithomiæ*. It may be asked, how can we know they are all varieties (using the term as meaning forms descended from others) of one species? I must refer to the figures given, which, although they do not include all the connecting varieties that were collected, show how nearly all the forms are linked together. The most distinct amongst them are those figured Pl. LVI. figs. 4 and 6. The feature which distinguishes fig. 4 is the white colour of the disk of the hind wings, and the veins which traverse it. This character is shown to be due to variation, from the facts that *Ithomia Oncidia*, an undoubted variety of *I. Chrysodonia* (or *Orolina*), exhibits a commencement of this milky shade of the wings, and that many individuals of *I. Ilerdina* (Pl. LVI. fig. 4 *a*) display steps of modification in the colours of the veins. The variety figured Pl. LVI. fig. 6, appears distinct, from the single pale spot near the tips of the wings; an approximation to this is seen in the variety figured Pl. LV. fig. 9, which is an undoubted modification of *L. Lysinoë* (Pl. LV. fig. 3). The remarkable variety figured Pl. LV. fig. 4 has been described by the only author who has treated on these insects (Mr. Hewitson) as a variety of *L. Lysinoë*. In a polymorphic form, like this *Leptalis*, none of the varieties can be taken from the rest and denominated species, (using the term as meaning forms which cannot have descended from other closely allied ones), without exercising the art of species-making in the most arbitrary manner. For if we allow so great a latitude to variation as that from figs. 3 to 4, 5, 6, 7, 8, and 9, Pl. LV., how can we venture to say that natural modification, having gone so far, was incompetent to go further, so as to produce figs. 4 and 6, Pl. LVI., and that those forms must have arisen by some unknown agency? It is true, they have not arisen by simple variation, or *sports*, in one generation, but, as we shall presently see, by an external agency accumulating the modifications of many generations in two diverging directions. As

the connecting links have not all been found, they may be called species: the word is of little importance. The habits of all are the same. When I had collected only two or three of the most distinct, I considered them separate species; but intermediate forms successively occurred, every capture tending to link the whole more closely together. The explanation that the whole are the result of hybridization from a few originally distinct species cannot at all apply in this case, because the distinct forms whose intercrossing would be required to produce the hybrids are confined to districts situated many hundred miles apart.

None of these *Leptalides* have been found in any other district or country than those inhabited by the *Ithomiæ* which they counterfeit. A species very closely allied to *L. Lysinoë*, var. *Argochloë* (Pl. LVI. fig. 6), has been received from Mexico (*L. Antherize*); but an *Ithomia*, of nearly the same colours (*I. Nero*) also inhabits Mexico. Many other species of *Leptalis*, of much larger size than the one here discussed, also mimic *Heliconidæ*, the objects of imitation not being *Ithomiæ*, but other genera of the family. Two of these are figured on Pl. LVI. *L. Orise* (Pl. LVI. fig. 8) is a remarkably exact counterfeit of *Methona Psidii* (fig. 8 *a*), the resemblance being carried to minutiæ, such as the colour of the antennæ and the spotting of the abdomen. *L. Amphione*, var. *Egaëna* (Pl. LVI. fig. 7), is very curious, as being a satellite of *Mechanitis Polymnia*, var. *Egaënsis* (fig. 7 *a*), both peculiar to the district of Ega,—the typical *L. Amphione* being found at Surinam, in company with the typical *M. Polymnia*, which it resembles—local varieties or sister species of *Leptalis Amphione* accompanying local varieties of *Mechanitis Polymnia* in other parts of tropical America.

Several species of *Dioptis*, a genus of Moths, and *Ithomeis*, a genus of *Erycinidæ*, also accompany these species or distinct local forms of *Ithomia*. A few of the Moths are figured on Pl. LV. figs. 10, 11, 12, 13. The imitations may not appear very exact from the figures; but when the insects are seen on the wing in their native woods, they deceive the most experienced eye.

A similar series of mimetic analogies occurs in the Old World, between the Asiatic and African *Danaidæ*, or representatives of the *Heliconidæ*, and species of other families of Butterflies and Moths. No instance is known in these families of a tropical species of one hemisphere counterfeiting a form belonging to the other. A most remarkable case of mimicry has been recorded by Mr. Trimen* in a *Papilio* of Southern Africa, *P. Cenea*, whose male wears to deception the livery of one species of *Danais*, namely, *D. Echeria*, whilst the female resembles a quite different one, *D. Chrysippus*,—both African. Mimetic analogies, however, are not confined to the Lepidoptera; most orders of insects supply them; but they are displayed only by certain families. Many instances are known where parasitic Bees and two-winged Flies mimic in dress various industrious or nest-building Bees, at whose expense they live in the manner of the Cuckoo. I found on the banks of the Amazons many of these Cuckoo Bees and Flies, which all wore the livery of working Bees peculiar to the country.

The instances of this kind of analogy most familiar to European entomologists are those of the European species of *Trochilium* (a genus of Moths), which strangely mimic various

* 'Rhopalocera Africæ Australis,' p. 21. Cape Town.

Bees, Wasps, and other Hymenopterous and Dipterous insects. The parallelism between these several forms and their geographical relations have not yet, I believe, been investigated. The resemblances seem to be more closely specific in tropical countries than in Europe; and I think it likely that the counterfeits in high latitudes may not always be found in company with their models. It is possible the geographical relations between the species concerned may have been disturbed by the great climatal and geological changes which have occurred in this part of the world since the date when they first came into existence.

Not only, however, are *Heliconidæ* the objects selected for imitation; some of them are themselves the imitators; in other words, they counterfeit each other, and this to a considerable extent. Species belonging to distinct genera have been confounded, owing to their being almost identical in colours and markings; in fact, many of them can scarcely be distinguished except by their generic characters. It is a most strange circumstance connected with this family, that its two sections, or subfamilies, have been mingled together by all authors, owing to the very close resemblance of many of their species. Analogies between the two subfamilies have been mistaken for affinities. It is sometimes difficult to understand in these cases which is the imitator and which the imitated. We have, however, generally a sure test in the one set exhibiting a departure from the normal style of colouring of their congeners, whilst the other are conformable to their generic types. The species of *Napeogenes* are, by this criterion, evidently all imitators of *Ithomiæ*; they are also rare insects, like the *Leptalides*. The mimetic species of *Heliconius* must be, for the same reason, imitators.

These imitative resemblances, of which hundreds of instances could be cited, are full of interest, and fill us with the greater astonishment the closer we investigate them; for some show a minute and palpably intentional likeness which is perfectly staggering. I have found that those features of the portrait are most attended to by nature which produce the most effective deception when the insects are seen in nature. The faithfulness of the resemblance, in many cases, is not so striking when they are seen in the cabinet. Although I had daily practice in insect-collecting for many years, and was always on my guard, I was constantly being deceived by them when in the woods. It may be asked, why are mimetic analogies so numerous and amazingly exact in insects, whilst so rare and vague in the higher animals*? The only answer that I can suggest is, that insects have perhaps attained a higher degree of specialization, after their type, than most other classes: this seems to be shown by the perfection of their adaptive structures and instincts. Their being more numerous and striking in tropical than in temperate countries is perhaps attributable to the more active competitive life, and the more rapid succession of their generations, in hot than in cold countries.

It is not difficult to divine the meaning or final cause of these analogies. When we

* Two instances of mimicry in birds, quite as wonderful as those between *Leptalis* and *Ithomia*, have just been communicated to me by my old travelling companion, Mr. A. R. Wallace. He has observed two species of *Oriolidæ* (perverted from the normal facies of the family) attendant on two species of *Meliphagidæ*, and mimicking them in the most curiously minute way in colours and in general figure. The associated pairs inhabit separate islands, as follows:—
—I. Bourou, *Mimeta* (*Oriolidæ*) *Bouroënsis*, *Tropidorhynchus* (*Meliphagidæ*), n. sp.; I. Ceram, *Mimeta Forstini*, *Tropidorhynchus subcarinatus*.

see a species of Moth which frequents flowers in the daytime wearing the appearance of a Wasp, we feel compelled to infer that the imitation is intended to protect the otherwise defenceless insect by deceiving insectivorous animals, which persecute the Moth, but avoid the Wasp. May not the Heliconide dress serve the same purpose to the *Leptalis*? Is it not probable, seeing the excessive abundance of the one species and the fewness of individuals of the other, that the Heliconide is free from the persecution to which the *Leptalis* is subjected?

I think it clear that the mutual resemblance in this and other cases cannot be entirely due to similarity of habits or the coincident adaptation of the two analogues to similar physical conditions. This is a very abstruse part of our subject; for I think the facts of similar variation in two already nearly allied forms do sometimes show that they have been affected in a similar way by physical conditions. A great number of insects are modified in one direction by a seaside habitat. I found, also, the general colours of many widely different species affected in a uniform way in the interior of the South American continent. But this does not produce the specific imitation of one species by another; it only prepares the way for it.

It is perhaps true that the causes (to be discussed presently) which produce a close or mimetic analogy cannot operate on forms which have not already a general resemblance, owing to similarity of habits, external conditions, or accidental coincidence. Species or groups which have this kind of resemblance to each other have been called by Dr. Collingwood recurrent animal forms. The English Bee-Moths owe the narrow and pointed shapes of their wings, which already approximate them to Bees, to their blood-relationship to the Hawk-Moth family. Their Bee-like size, form, and flight doubtless arise from their Bee-like habits. A close specific analogy between any one of these and a Bee, such as exists between the insects discussed in this memoir, could scarcely be due to an accidental resemblance like that between the Hawk-Moth and a Bee, or to similarity of habits. It would mean an adaptation of the Moth with especial reference to the Bee.

I believe, therefore, that the specific mimetic analogies exhibited in connexion with the *Heliconidæ* are adaptations—phenomena of precisely the same nature as those in which insects and other beings are assimilated in superficial appearance to the vegetable or inorganic substance on which, or amongst which, they live. The likeness of a Beetle or a Lizard to the bark of the tree on which it crawls cannot be explained as an identical result produced by a common cause acting on the tree and the animal.

Some of the imitations by insects of inanimate and living objects are very singular, and may be mentioned in this place. Many caterpillars of Moths, but sometimes the cases only which are manufactured and inhabited by the caterpillars, have a most deceptive likeness to dry twigs and other objects. Moths themselves very frequently resemble the bark on which they are found, or have wings coloured and veined like the fallen leaves on which they lie motionless. The accidental general resemblance between the shape of Moths' wings and leaves here gives nature the ground-work for much mimetic analogy. It has been pointed out by Rössler* that the Buff-tip Moth, when at rest, is intended to represent a broken piece of lichen-covered branch,

* In an article on resemblances between insects and vegetable substances (Wiener Entomol. Monatschrift, 1861,

—the coloured tips of these wings, when they are closed, resembling a section of the wood. Other Moths are deceptively like the excrement of birds on leaves. I met with a species of Phytophagous Beetle (*Chlamys pilula*) on the Amazons, which was undistinguishable by the eye from the dung of Caterpillars on foliage. These two latter cases of imitation should be carefully considered by those who would be inclined to think that the object of mimetic analogies in nature was simply variety, beauty, or ornament: nevertheless these are certainly attendants on the phenomena; some South-American *Cassidæ* resemble glittering drops of dew on the tips of leaves, owing to their burnished pearly gold colour. Some species of Longicorn Coleoptera (*Onychocerus scorpio* and *concentricus*) have precisely the colour and sculpture of the bark of the particular species of tree on which each is found. It is remarkable that other species of the same small group of *Longicornes* (*Phacellocera Buquetii*, *Cyclopeplus Batesii*) counterfeit, not inanimate objects, like their near kindred just cited, but other insects, in the same way as the *Leptalides* do the *Heliconidæ*.

Amongst the living objects mimicked by insects are the predacious species from which it is the interest of the mimickers to be concealed. Thus, the species of *Scaphura* (a genus of Crickets) in South America resemble in a wonderful manner different Sand Wasps of large size, which are constantly on the search for Crickets to provision their nests with. Another pretty Cricket, which I observed, was a good imitation of a Tiger Beetle *, and was always found on trees frequented by the Beetles (*Odontocheilæ*). There are endless instances of predacious insects being disguised by having similar shapes and colours to those of their prey; many Spiders are thus endowed: but some hunting Spiders mimic flower-buds, and station themselves motionless in the axils of leaves and other parts of plants to wait for their victims.

The most extraordinary instance of imitation I ever met with was that of a very large Caterpillar, which stretched itself from amidst the foliage of a tree which I was one day examining, and startled me by its resemblance to a small Snake. The first three segments behind the head were dilatable at the will of the insect, and had on each side a large black pupillated spot, which resembled the eye of the reptile: it was a poisonous or viperine species mimicked, and not an innocuous or colubrine Snake; this was proved by the imitation of keeled scales on the crown, which was produced by the recumbent feet, as the Caterpillar threw itself backwards. The Rev. Joseph Greene, to whom I gave a description, supposes the insect to have belonged to the family *Notodontidæ*, many of which have the habit of thus bending themselves. I carried off the Caterpillar, and alarmed every one in the village where I was then living, to whom I showed it. It unfortunately died before reaching the adult state.

p. 164). The author enumerates many very singular cases of mimicry; he also states his belief that the mimicry is intended to protect the insects from their enemies.

There is an interesting note, by the Rev. Joseph Greene, in the 'Zoologist,' 1856, p. 5073, on the autumn and winter Moths of England, whose colours are shown by the author to be adapted to the prevailing tints of nature in the season in which the species appear.

* A remarkable instance of deceptive analogy relating to a Cricket and a species of *Cicindela* is described by Westwood in Trans. Lin. Soc. vol. xviii. p. 419. In this memoir, Mr. Westwood has enumerated many curious cases of mimetic analogy.

I think it will be conceded that all these various kinds of imitative resemblances belong to the same class of phenomena, and are subject to the same explanation. The fact of one species mimicking an inanimate object, and another of an allied genus a living insect of another family, sufficiently proves this. I do not see how they differ from the adaptations of organs or instincts to the functions or objects they relate to. All are adaptations, either of the whole outward dress or of special parts, having in view the welfare of the creatures that possess them.

Every species in nature may be looked upon as maintaining its existence by virtue of some endowment enabling it to withstand the host of adverse circumstances by which it is surrounded. The means are of endless diversity. Some are provided with special organs of offence, others have passive means of holding their own in the battle of life. Great fecundity is generally of much avail, added to capabilities, active or passive, of wide dispersion; so that when the species is extirpated in one part of its area of distribution, the place is refilled by migration of individuals from another part. A great number have means of concealment from their enemies, of one sort or other. Many are enabled to escape extermination, or obtain subsistence, by disguises of various kinds: amongst these must be reckoned the adaptive resemblance of an otherwise defenceless species to one whose flourishing race shows that it enjoys peculiar advantages.

What advantages the *Heliconidæ* possess to make them so flourishing a group, and consequently the objects of so much mimetic resemblance, it is not easy to discover. There is nothing apparent in their structure or habits which could render them safe from persecution by the numerous insectivorous animals which are constantly on the watch in the same parts of the forest which they inhabit. It is probable they are unpalatable to insect enemies. Some of them (*Lycorea*, *Ituna*) have exsertible glands near the anus, which are protruded when the insects are roughly handled; it is well known that similar organs in other families (*Carabidæ*, *Staphylinidæ*) secrete fetid liquids or gases, and serve as a protection to the species. I have noticed also that recently killed specimens of Danaoid *Heliconidæ*, when set out to dry, were always less subject than other insects to be devoured by vermin. They have all a peculiar smell*. I never saw the flocks of slow-flying *Heliconidæ* in the woods persecuted by birds or Dragon-flies, to which they would have been easy prey; nor, when at rest on leaves, did they appear to be molested by Lizards or the predacious Flies of the family *Asilidæ*, which were very often seen pouncing on Butterflies of other families. If they owe their flourishing existence to this cause, it would be intelligible why the *Leptalidæ*, whose scanty number of individuals reveals a less protected condition, should be disguised in their dress, and thus share their immunity.

This explanation, however, would not apply to the imitation of Danaoid *Heliconidæ* by other species of the same subfamily. Moreover, there are several genera of other groups (*e. g.*, *Heliconius*, *Papilio*) which contain mimetic species side by side with species that are the objects of mimicry by members of other families, as will be seen by reference to the Table at p. 503. There is no reason to conclude that some of these possess the peculiar means of defence of the Danaoid *Heliconidæ*, whilst their near kindred are de-

* Mr. Wallace tells me the *Euplœæ* of the Eastern Archipelago have also this peculiar smell.

prived of them. It is not unreasonable to suppose that some species are taken by insectivorous animals, whilst others flying in company with them are avoided. I could not, from their excessive scarcity, ascertain on the spot that the *Leptalides* were thus picked out. I noticed, however, that other genera of their family (*Pieridæ*) were much persecuted. We have proof, in the case of Sand-Wasps, which provision their nests with insects, that a single species is very generally selected out of numbers, even of the same genus, existing in the same locality. I was quite convinced in the case of *Cerceris binodis* of South America, which destroys numbers of a *Megalostomis* (family *Clythridæ*), that the great rarity of the Beetle was owing to its serving as prey to the *Cerceris*. We cannot point out all the conditions of life of each species concerned in these mimetic analogies. All that we can say is, that some species show, by their great abundance in the adult state, that during this period, before they propagate their kind, they enjoy by some means immunity from effective persecution, and that it is therefore an advantage to others not so fortunate, and otherwise unprovided for, if they are so like as to be mistaken for them.

The process by which a mimetic analogy is brought about in nature is a problem which involves that of the origin of all species and all adaptations. What I have previously said regarding the variation of species, and the segregation of local races from variations, the change of species of *Heliconidæ* from one locality to another, and the probable vital necessity of their counterfeits which accompany them keeping to the exact imitation in each locality, has prepared the way to the explanation I have to give. In the cases of local variation of the *Heliconidæ*, there was nothing, as before remarked, very apparent in the conditions of the localities to show why one or more of the varieties should prevail in each over their kindred varieties. There was nothing to show plainly that any cause of the formation of local varieties existed, other than the direct action of physical conditions on the individuals, although this might be seen to be clearly incompetent to explain the occurrence of several varieties of the same species in one locality. We could only conclude, from the way in which the varieties occur in nature, as described in the case of *Mechanitis Polymnia*, that the local conditions favoured the increase of one or more varieties in a district at the expense of the others—the selected ones being different in different districts. What these conditions were, or have been, was not revealed by the facts. With the mimetic species *Leptalis Theonoë* the case is different. We see here a similar segregation of local forms to that of *Mechanitis Polymnia*; but we believe we know the conditions of life of the species, and find that they vary from one locality to another. The existence of the species, in each locality, is seen to depend on its form and colours, or *dress*, being assimilated to those of the *Ithomiæ* of the same district, which *Ithomiæ* are changed from place to place, such assimilation being apparently its only means of escaping extermination by insectivorous animals. Thus we have here the reason why local races are formed out of the natural variations of a species: the question then remains, how is this brought about?

The explanation of this seems to be quite clear on the theory of natural selection, as recently expounded by Mr. Darwin in the 'Origin of Species.' The local varieties or races cannot be supposed to have been formed by the direct action of physical conditions

on the individuals, because, in limited districts where these conditions are the same, the most widely contrasted varieties are found existing together, and it is inexplicable how they could have produced the nice adaptations which these diverse varieties exhibit. All the varieties figured on Pl. LV. figs. 2, 7, 9, and on Pl. LVI. figs. 1, 2, 3, 4, 6, are found at St. Paulo, within a mile of each other, in the same humid forest. Neither can these adapted races, as before remarked, have originated in one generation by *sports* or a single act of variation in each case. It is clear, therefore, that some other active principle must be here at work to draw out, as it were, steadily in certain directions the suitable variations which arise, generation after generation, until forms have resulted which, like our races of *Leptalis Theonoë*, are considerably different from their parent as well as their sister forms. This principle can be no other than natural selection, the selecting agents being insectivorous animals, which gradually destroy those sports or varieties that are not sufficiently like *Ithomiæ* to deceive them. It would seem as though our *Leptalis* naturally produced simple varieties of a nature to resemble *Ithomiæ*; it is not always so, as is proved by many of them figured in the places above quoted. There is some general resemblance, it is true; and this is not purely accidental; for it is quite natural that the parent *Leptalis* should produce offspring varying in the direction of *Ithomiæ*, being itself similar to an *Ithomia*, and having inherited the property of varying in this manner through a long line of ancestors. We cannot ascertain, in this case, whether changed physical conditions have had any effect, quantitative or qualitative, on the variability of the species after migrating to a new district. At any rate, the existing varieties of our *Leptalis* show that the variations of *Leptalis* and *Ithomia* are not quite coincident, and that the agency of natural selection is required to bring the slowly forming race of one to resemble the other. I do not forget that at each step of selection the forms of *Leptalis* must have had sufficient resemblance to an *Ithomia* to lead to their preservation, or, at least, to prevent their complete extinction: as, however, the two analogues so much resemble each other at the commencement of the process, these steps would not be numerous. In many cases of mimetic resemblance, the mimicry is not so exact as in the *Leptalides*. This would show either that the imitator has only inherited its form from remote ancestors who were actively persecuted, the persecution having ceased during the career of its immediate ancestors; or it would show that the persecutor is not keen or rigid in its selection; a moderate degree of resemblance suffices to deceive it, and therefore the process halts at that point. I leave out of consideration all resemblances which can only be accidental, or which are resemblances of affinity.

If a mimetic species varies, some of its varieties must be more and some less faithful imitations of the object mimicked. According, therefore, to the closeness of its persecution by enemies, who seek the imitator, but avoid the imitated, will be its tendency to become an exact counterfeit,—the less perfect degrees of resemblance being, generation after generation, eliminated, and only the others left to propagate their kind. The actual state of *Leptalis Theonoë* is not the same in all of its three districts. A few varieties, or *sports*, are seen at Ega (65° W. long.) and St. Paulo (69° W. long.), namely, those figured Pl. LV. figs. 4, 5, 7, 8, and 9, which have an indeterminate resemblance. On the Cuparí

(55° W. long.) the resemblance is perfect (Pl. LV. fig. 1); and this is the only form of the *Leptalis* known in the locality. The varieties figured Pl. LVI. figs. 1, 2, 3, show different degrees of resemblance to *Ithomia Chrysodonia* (fig. 3 *a*); these, therefore, exhibit the selection in process. Thus, although we are unable to watch the process of formation of a new race as it occurs in time, we can see it, as it were, at one glance, by tracing the changes a species is simultaneously undergoing in different parts of the area of its distribution.

The fact of one of the forms of *Leptalis Theonoë*, namely *L. Lysinoë*, mimicking at Ega, not an *Ithomia*, but a flourishing species of another quite distinct family (*Stalachtis Duvalii*), shows that the object of the mimetic tendencies of the species is simply disguise, and that, the simple individual differences in that locality being originally in the direction, not of an *Ithomia*, but of another object equally well answering the purpose, selection operated in the direction of that other object. This point is well illustrated by the species of a small group of Longicorn Beetles already cited, some of which mimic a piece of bark, and others insects of another family—and by hunting Spiders, many of which wear the form of insects, and many that of inanimate objects amongst which they seek their prey.

When the persecution of a variable local form of our *Leptalis* is close or long continued, the indeterminate variations naturally become extinct; nothing then remains in that locality but the one exact counterfeit, whose exactness, it must be added, is henceforward kept up to the mark by the insect pairing necessarily with its exact counterpart, or breeding *in and in*. This is the condition of *Leptalis Theonoë* (Pl. LV. fig. 1) in its district; and it is the condition of all those numerous species of different orders which now appear fixed and distinct. When (as happens at St. Paulo, where a greater abundance of individuals and species, both of *Ithomia* and *Leptalis*, exists than in the locality of the last-named) many species have been in course of formation out of the varieties of one only, occasional intercrossing may have taken place; this would retard the process of segregation of the species, and, in fact, aid in producing the state of things (varieties and half-formed species) which I have already described as there existing.

In what way our *Leptalis* originally acquired the general form and colours of *Ithomiæ* I must leave undiscussed. We may conclude (if we are to reason at all from existing facts) that, as the antecedent forms of our races of *Leptalis* which are still undergoing change were themselves similar to *Ithomiæ*, the form has been inherited through a long line of ancestors, which have been more or less subjected to similar conditions. The instance of one of our forms leaving the *Ithomiæ* to mimic a species of another family may show us how a new line of mimetic analogy and gradual modification may have been originally opened.

Such, I conceive, is the only way in which the origin of mimetic species can be explained. I believe the case offers a most beautiful proof of the truth of the theory of natural selection. It also shows that a new adaptation, or the formation of a new species, is not effected by great and sudden change, but by numerous small steps of natural variation and selection. Some of the mutual resemblances of the *Heliconidæ* already mentioned seem not to be due to the adaptation of the one to the other, but rather, as they

have a real affinity, the genera to which they belong being throughout very similar in colours and markings, and all equally flourishing, to the similar adaptation of all to the same local, probably inorganic, conditions. The selecting agent, which acts in each locality by destroying the variations unsuitable to the locality, would not in these cases be the same as in *Leptalis*; it may act, for anything we know, on the larvæ; in other respects, however, the same law of nature appears, namely, the selection of one or more distinct varieties by the elimination of intermediate gradations *. The conditions of life of these creatures are different in each locality where one or more separate local forms prevail, and those conditions are the selecting agents. With regard to the *Leptalides*, I believe we may be said to know these conditions. To exist at all in a given locality, our *Leptalis Theonoë* must wear a certain dress, and those of its varieties which do not come up to the mark are rigidly sacrificed. Our three sets of *Leptalides* may be compared to a variable flowering plant in the hands of a number of floriculturists, whose aims are different, each requiring a different colour of flower, and attaining his end by "roguing" or destroying all variations which depart from the standard.

It may be remarked that a mimetic species need not always be a rare one, although this is very generally the case; it may be highly prolific, or its persecution may be intermitted when the disguise is complete.

The operation of selecting agents, gradually and steadily bringing about the deceptive resemblance of a species to some other definite object, produces the impression of there being some innate principle in species which causes an advance of organization in a special direction. It seems as though the proper variation always arose in the species, and the mimicry were a predestined goal. This suggested the only other explanations that I have heard of, namely, that there may be an innate tendency in the organization to become modified in a given direction—or that the parent insect, being powerfully affected by the desire of concealment from the enemies of its race, may transmit peculiarities to its offspring that help it to become modified, and thus, in the course of many generations, the species becomes gradually assimilated to other forms or objects. On examination, however, these explanations are found to be untenable, and the appearances which suggest them illusory. Those who earnestly desire a rational explanation, must, I think, arrive at the conclusion that these apparently miraculous, but always

* Some of the close resemblances amongst the *Heliconidæ* themselves seem to be kept up by their varying in a precisely similar way. There is a very singular instance in three species of three different genera, *Melinæa*, *Mechanitis* (*Mothone*), and *Heliconius*, which are all, in East Peru, orange and black in colour, and in New Granada orange, black, and yellow. This seems to be a case of coincident, simple variation; for if three forms are quite alike in colours, it is conceivable that they may vary alike when placed under new conditions by migration. Our *Leptalides* have been shown not to vary precisely like their models; and therefore the case just quoted does not throw any difficulty in the way of the explanation I have given; but it is a very extraordinary one.

I have not thought it necessary to mention cases of close resemblances in insects which are only accidental, or which are explicable by the blood-relationship or affinity existing between the species which display them. Some orders of insects contain an almost infinite variety of forms, and it will not be wonderful, therefore, if species here and there be found to resemble each other, although inhabiting opposite parts of the earth, and belonging to widely different families. Such analogies are accidental, and can have nothing at all to do with the evidently intentional system of resemblances, carried on from place to place, which I have discussed. Some cosmopolitan families present very similar species in all parts of the earth; it can scarcely be necessary to say that close resemblances between New and Old World forms in these cases are resemblances of affinity, and not mimetic analogies.

beautiful and wonderful, mimetic resemblances, and therefore probably every other kind of adaptation in beings, are brought about by agencies similar to those we have here discussed.

HELICONIDÆ.

I have mentioned, in a note at p. 496, that I should follow the example of Dr. Felder in separating the Danaoid *Heliconidæ* from the remainder of the family, and combining them with the *Danaïdæ*. I shall, however, consider these groups as subfamilies, instead of families. The modifications in the classification thus introduced will be seen by the following synopsis of the section Rhopalocera.

Order LEPIDOPTERA.

Section RHOPALOCERA.

Family 1. HESPERIDÆ. Six perfect legs in ♂ ♀; hind tibiæ, with few exceptions, having two pair of spurs. Larva inhabiting a rolled-up leaf; pupa secured by many threads, or enclosed in a slight cocoon. (These characters approximate the family to the Moths, or Heterocera).

Family 2. PAPILIONIDÆ. Six perfect legs in ♂ ♀. Wing-cells (at least, of the hind wings) closed by perfect tubular nervules. Hind tibiæ with one pair of spurs. Pupa secured by the tail and a girdle across the middle in an upright position. (The *Papiliones* have a leaf-like appendage to the fore tibiæ, as pointed out recently by Dr. Adolf Speyer; the character approximates the family to the Hesperidæ and Moths.)

Family 3. LYCÆNIDÆ. Six perfect legs in ♀; four in ♂; the fore tarsi wanting the tarsal claws, but densely spined beneath. Wing-cells (except in *Eumæus*) not closed by perfect nervules. Pupa secured by the tail and a girdle across the middle.

Family 4. ERYCINIDÆ. Six perfect legs in ♀; four in ♂; the fore tarsi consisting only of one or two joints, and spineless.

Subfam. 1. ERYCININÆ. Pupa recumbent, flattened beneath, secured by the tail and a girdle across the middle.

Subfam. 2. STALACHTINÆ. Pupa not flattened beneath, secured rigidly by the tail in an inclined position, without girdle.

Subfam. 3. LIBYTHÆINÆ. Pupa suspended freely by the tail.

Family 5. NYMPHALIDÆ. Fore legs imperfect in both sexes; in the ♀ wanting the tarsal claws; in the ♂ the fore tarsi aborted, consisting of one or two joints. Pupa suspended freely by the tail.

a. Lower disco-cellular nervule, especially of the hind wing, more or less atrophied.

Subfam. 1. NYMPHALINÆ (*Nymphalidæ, Ageronidæ, Eurytelidæ,* and *Morphidæ,* part, of authors).

b. Lower disco-cellular nervule perfect.

Subfam. 2. HELICONINÆ.

Subfam. 3. ACRÆÏNÆ.

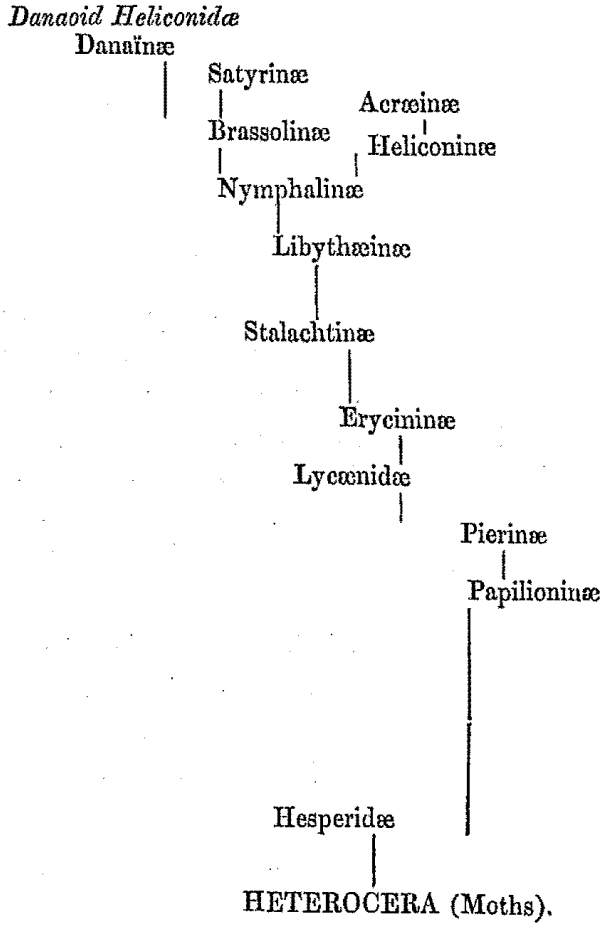
Subfam. 4. BRASSOLINÆ.

Subfam. 5. SATYRINÆ.

Subfam. 6. DANAÏNÆ.

The *Danaoid Heliconidæ*, as before mentioned, are considered to stand at the head of

the order Lepidoptera, as being the perfection of the Lepidopterous type. This position might be disputed with them by the *Satyrinæ* on account of the degree of atrophy of the fore legs, which is perhaps as great in some species of *Satyrinæ* as it is in the most advanced genera of Danaoid *Heliconidæ*. The order of affinities does not range in a line; there are branches; and so it may happen that two groups may be nearly equal in their grade of perfection through each standing at the head of its branch. The true relationships of the groups of Rhopalocera may be therefore better explained by a diagram.



Subfamily DANAÏNÆ.

A. DANAÏNÆ proper
(*Danaïdæ* of authors).

Genus DANAÏS, Latreille.

1. DANAÏS ERIPPUS, Cramer.

Papilio Erippus, Cram. Pap. Exot. t. 3. f. A, B.

A common and well-known insect. It is found in waste grounds and open places everywhere throughout the region of the Lower Amazons. Its larva feeds on *Asclepias Curassovica*.

2. DANAÏS GILIPPUS, Cramer.

Papilio Gilippus, Cram. Pap. Exot. t. 26. f. C, D.

This is a rarer species than the foregoing. It is found in similar situations at Pará.

3. Danaïs Eresimus, Cramer.

Papilio Eresimus, Cram. Pap. Exot. t. 175. f. G, H.

This is the common species in the interior of the country. It is very abundant at Ega, on the Upper Amazons, where *D. Erippus* did not occur.

B. Danaoid Heliconidæ

(*Heliconidæ*, part, of authors).

Genus Lycorea, Doubleday.

Doubleday and Hewitson, Gen. Diurn. Lepid. p. 107.

The six described species of this genus differ from each other by such slight characters (small differences in colours, and in the arrangement of the pattern on the wings, being the only points which distinguish them), that they might fairly be considered as varieties of one only. I have not yet seen specimens, however, which connect all the forms together, and these are mostly the products of different geographical areas; it will be more convenient therefore to treat them independently, than to combine them under the head of one polymorphic species. A good collection of specimens from all parts of the area of distribution of the genus would here be very instructive. We should then be able to ascertain the metropolis and probable area of origination of each of the various forms. I have seen only *L. Halia* in collections from S.E. Brazil. *L. atergatis* is peculiar to Columbia and the Upper Amazon region; but a striking variety of it prevails over the type in this last-mentioned district, and another, *L. Pales* (Felder), occurs on the Rio Negro. *L. Cleobæa* (which is scarcely more different from *L. atergatis* than the just-mentioned *L. atergatis*, var., is from its type) is reputed to occur in the West India Islands. At Pará three forms, including *L. Halia*, are found together; and here some intermediate varieties occur, making it probable that the segregation of the quasi-species is not in that district complete.

1. Lycorea Ceres, Cramer.

Papilio Ceres, Cramer, Pap. Exot. t. 90. f. A.

This species occurs in the Amazon region at Pará, and on the banks of the Tapajos. It is also an inhabitant of Surinam. Cramer's figure is made from an example rather aberrant in the markings of the hind wings; otherwise it agrees very well with the specimens I have before me. I have a variety from Pará which connects this form with *L. Halia*.

2. Lycorea Pasinuntia, Cramer.

Papilo Pasinuntia, Cram. Pap. Exot. t. 316, A, B, C.

This form occurs throughout the whole of the Amazon region, from 48° to 70° W. long. The extreme western examples, found at St. Paulo on the Upper Amazons, show a change of colour in the yellow irregular belt of the fore wing, which has acquired the same orange-tawny shade as the rest of the wing. The same substitution of colour