Mr. Meldola communicated the following translation of a paper by Dr. Fritz Müller,† published in 'Kosmos,' May, 1879, p. 100:—

"Ituna and Thyridia; a remarkable case of Mimicry in Butterflies.";

"The genera Ituna and Methona were erected by Doubleday in 1847, and placed between Eutresis and Thyridia in the family Heliconiidae, from which they were subsequently removed, with Ithomia and its allied genera, and transferred to the Danaidae. Methona has since been united with Thyridia, Hüb., next to which genus Ituna still stands in Kirby's 'Synonymic Catalogue' (1871). These two genera appear, therefore, to have been always regarded, and are still recognised, as closely allied. Their resemblance, however, is not due to consanguinity, but has been acquired through imitation, and is remarkable, inasmuch as the insects have not only deceived casual collectors, but even skilled observers, after careful comparison. The resemblance of the genera named is the more worthy of notice since it occurs between insects both belonging to the group of butterflies which are protected by distastefulness. The explanation which applies in ordinary cases of mimicry—and no other has, so far as I know, been offered—cannot obtain for this imitation among protected species.

"Ituna, Ilione and Thyridia Megisto, the wings of which are here represented (Figs. 1 and 2), are with us two rather rare butterflies. In addition to the similarity of the wings, which is to be found in the arrangement of the transparent yellowish spots and of the black veins and bands which intersect and divide these spots, and also in that of the white spots which ornament the black wing-borders, may be added the long yellow antennæ and the black and white marking of the body in both species. Both butterflies

† [I am indebted to Mr. Charles Darwin for drawing my attention to this paper, and to Dr. Ernst Krause, of Berlin, one of the Editors of 'Kosmos,' for permission to reproduce it in our 'Proceedings,' as also for having kindly placed at my disposal electrotypes of the wood-cuts.—R. M.]
‡ "This paper, as also that on Epipalia Acontius ('Kosmos,' iv., p. 285) was in our hands before the appearance of Wallace's paper on the colours of plants and animals, which explains why the author has not taken Mr. Wallace's later views into consideration."—Note by the Editor of 'Kosmos.'
show, like the Ithomiae, a preference for the small white flowers of an *Adenostemma*, which grows on the borders of woods and on the edges of forest-paths; but they also visit other flowers, especially white ones, of the same order (Compositae), such as *Vernonia*, *Mikania* and *Baccharis*. I do not remember to have seen them on flowers of other orders.

"The characters by which Doubleday separated the genus *Ituna* from the apparently similar *Melitona* and *Thyridia* are such as would not prevent these genera from being regarded as most closely related, and the differences to which I am about to refer may appear very insignificant; they become of importance, however, from the fact that they recur in long series of allied species, one group of which agrees with *Ituna* and the other with *Thyridia*; it thus appears that the Danaid. long ago underwent separation into two groups, one being related to *Ituna* and the other to *Thyridia*, so that these two genera must have undergone a correspondingly ancient separation.

"In the next place, on the hind wings in both sexes, between two of the veins, there are always two white spots situated between the nervures 1b and 2 (i.e., between the submedian and first branch of the median), but in *Thyridia* these spots are double. The wing-cell between these two nervures appears double, as indeed it is. Originally, as shown by moths and the pupae of butterflies, the wings of butterflies had three veins on the inner margin, the foremost of which (1c) has disappeared, although sometimes to be found in a rudimentary condition. Thus, in *Aerona Thalia*, for example, the course of this vein on the hind wing is indicated by a row of
black hairs similar to those marking the courses of the other well-developed nervures. In many other cases there is scarcely anything of the missing vein (1 c) to be seen, but its former existence is indicated by the markings of the wings, which make the cell between the veins 1 b and 2 appear double. In other cases this indication of the original state is also lost, and the cell which was formerly double shows the same number of spots as the others. The wing-cell in question, as in Thyridia, still appears double in Dirceina, Ceratinia, Mechanitis, Melinae, and in all the allies of the Ithomiae; on the other hand it is single in Lycorea and Danais, as in Ituna (and also, judging from figures, in Hestia and Euplaca).

"A second distinguishing character between the genera Ituna and Thyridia consists in the presence of a small 'basal cell' (Wurzelzelle), as Herrich-Schäffer calls it, at the base of the hind-wing in Ituna, and also in Lycorea and Danais, but which is wanting, on the other hand, in Thyridia and in all the allies of the Ithomiae. Herrich-Schäffer made use of the 'basal cell,' where he found it, as a family character. Thus, by its absence or presence, he distinguishes between the families Heliconidae and Danaidae, which latter he limited to the genus Danais; if he had not therefore overlooked the certainly very small 'basal cell' in Ituna and Lycorea, he would have separated these genera from the Ithomiae and have associated them with Danais.

"In the next place, in the production of odour, the male Thyridia allies itself to the Ithomiae, Ituna to Lycorea and Danais. The males of Ithomiae and its allies are known to possess an odoriferous 'tuft of hair on the upper side of the hind-wing on the subcostal vein' (Herrich-Schäffer), and this character served that author for distinguishing the genus. In Thyridia Megisto the odour of this tuft is very powerful, and it is the only species known to me in which the character acquired by the male has been transferred to the female: in the latter it is certainly much less developed and emits a weaker odour. In Ituna this tuft is wanting on the hind-wings; on the other hand, as shown by Doubleday, the males have two finger-shaped processes at the end of the abdomen, which can be protruded and withdrawn at pleasure. They carry a tuft of stiff black hairs, which can be spread out like a round brush, and emit what appears to me to be a strong repugnant
smell of snuff. These scent-brushes at the end of the finger-shaped processes are similarly found in *Lycæra*, and also (although less developed and smelling weaker) in *Danais Gilippus* and *D. Erippus*, in which species they appear to have been hitherto overlooked.

"Thus, on the ground of the foregoing characteristic differences, and especially of the former, which, being obviously of no advantage to the species, may be taken as sure indications of a common origin, the Ithomiae and the true Danaides (*Danais, Lycæra* and *Ituna—Hestia* and *Euphia*, I know only from figures) must be regarded as two groups which long ago underwent separation, and which are at least as far apart as, perhaps, the Acræinae and the Maracuja butterflies. These last groups are also distinguished by the wing-cell between the veins 1b and 2 of the hind-wing, which is double in the Acræinae as in the Ithomiae, and single in the Maracuja group as in the Danaides. The caterpillars of Acræinae accord completely in character with those of the Maracuja butterflies, but not with those of the Danaidæ and Ithomiae: the former so well known as living on Asclepiadaceæ have on the back two (*Danais Erippus*), three (*D. Gilippus*), or four (*Euphia Midamus*) pairs of long, thread-like, unprotrusible 'tentacles.' The *Ithomia* caterpillars, which feed on Solanaceæ or the nearly-allied Scrophulariaceæ, are either entirely without appendages or have below the spiracles fleshy spherical protuberances (*Mechanitis Lyonsia*)."

"If, in accordance with all characters, *Thyridia* is thus related to *Ithomia*, and *Ituna* to the Danaides (if the latter is not, as in Kirby's 'Catalogue,' separated from *Lycæra* by the Ithomian genus *Athesis*), the resemblance of these two genera could only be ascribed to descent from a common ancestor if they had preserved the original colouring and marking of the ancestors of all the Ithomiae and Danaide. But this cannot be maintained. If the progenitors of these two groups had possessed wings with large transparent spaces, it is improbable that such a large number of the existing species of the said groups should have reverted to a still earlier type of wing completely clothed with scales. It might be maintained, with equal right, that *Lycæra* and the various Ithomiae, so similar to this genus in marking and colouring, indicate the original marking and colouring of the groups in question.

"A case of acquired resemblance—one of imitation or mimicy—is thus presented. But which of the two species, *Ituna Hione* or *Thyridia Megisto*, is the original form, and which the mimic? On this point there should surely be no doubt. Does not a species which serves as a model occur...

* The caterpillar represented by Boisduval (Spec. Gen. Lepidopt., pl. 4, fig. 9), ascribed to *Stalacthis (Nerias) Enterpe*, appears to be that of a *Mechanitis*; in hairiness it resembles that of *M. Lyonsia*. A glance at this figure and figs. 10 and 11 of the same plate, which represent caterpillars of true Danaides, shows immediately the great difference between the caterpillars of the Danaides and Ithomiae.
always in countless swarms, while the mimic is a hundred times more rare? Does not the model bear the hereditary colouring of its genus and family, while the mimic appears in borrowed plumes? And, finally, is not the model unpalatable on account of its repulsive taste and odour, being for these reasons safe from foes, while the mimic finds protection in its disguise, without which it would be devoured as a tasty morsel? It is much to be regretted, however, that all these characters sometimes leave us in the lurch.

"The imitating species may, at least in some districts, be more common than its model. If both the latter and its mimic extended into a new district the conditions might be more frequently unfavourable to the model and favourable to the rarer species, and thus the original proportional numbers might be reversed; indeed, this may happen, in course of time, in the old habitat of the species. In the province of Santa Catharina, Archonias (Enterpe) Tereas is common in the forest-paths almost throughout the entire year, while its model, Papilio Nephalion, is, on the other hand, a rare butterfly. Occasionally the relative numbers of different species change very considerably in successive years, and may be entirely reversed in comparatively adjacent districts. Here in Itajahy Colanis Julia is far commoner than the deceptively similar but smaller Eueides Aliphera; some months ago, however, to the north of our province on the high land at Sao Bento, I found Eueides Aliphera in such numbers that I sometimes caught eight with a single sweep of the net, whilst in the course of a week I saw Colanis Julia but two or three times.* Indeed, it is conceivable that the model species may become extinct while the mimicking species remains unaffected. Thus, according to Mr. Trimen and Mr. A. G. Butler,† Papilio Antimachus and P. Zalephoxis might be imitations of gigantic extinct or still unknown species of Aereia. In the case of the Ituna and Thyridia, under consideration, both species are rare, at least in Santa Catharina, and their relative numbers give no clue, therefore, as to which is the model.

"The second indication, viz., that the model species bears its own characters, and the mimic acquired ones is found with ease and safety in the fact that the more widely-separated the groups to which the two species belong the further does the imitating species depart from the ordinary characters of its allies. Thus, if certain locusts (Scaphura) are disguised as wasps (Pepsis)—if others (Phylloocyrtus) are disguised as beetles, while others again are disguised as spiders;—there cannot be the least doubt, in such

* [See also Trans. Ent. Soc., 1877, p. 223.—R. M.]
‡ I have never seen this disguise mentioned; I observed it on one occasion. An insect, which I at first took to be a spider, but which nevertheless had a strange appearance, was resting on a leaf; I looked at it on all sides without being clear as to what it was until it jumped up and flew away. The most remarkable feature in it was the long spider-like legs.
cases, which is the imitating species, as the object of the disguise is immediately apparent.*

* With many other species, also, which are less widely separated such characters are of great service. Thus the black Archonias Tereus, with the white spots on the margin of the fore-wings and the rose-red of the hind-wings, presents a strange appearance among its congenerous, whilst Papilio Neptunus belongs to a long series of similarly colored species, so that where this Papilio is rare and the Archonias common, we cannot for this reason regard the latter as the model of the former.

"The more closely related are the two species which resemble one another, the more alike were they ab initio, and the more uncertain in consequence is this second indication of mimicry; it becomes perfectly useless in cases where the nearest allies of the two species are without a common, peculiar, sharply defined form of marking and colouring. Colantis Julia and Eueides Alphera will again serve as examples. In the genus Colantis, near the fiery-red Julia, there stands the green Vido, and other species with still different colors and form of wing, whilst in the genus Eueides, the spotted Isabella and the Acraea-like Parana stand near the fiery-red Alphera.

"Of the two genera under consideration, Thyridia possesses a rather larger number of similar allies (Dircenna, for instance) than does Ituna, and we might perhaps consider the latter to be the imitating species since, with respect to flowers, it appears to possess the taste of the Ithomiae, and not that of the blood-related Danaides.

"With regard to the third and last indication of mimicry, viz., that the model is protected from enemies by unpleasant taste and odour, whilst the imitator is without such protection, and thus derives benefit from its resemblance to the distasteful model, it is to be remarked that model and mimic could be distinguished from one another with certainty if all distasteful species possessed for insectivorous birds, as well as for us, a repulsive odour, and if also butterflies malodorous to us did not occur as mimics.

"The Ithomiae of the Amazons and their allies (e.g., Mechanitis), as Bates observed, are imitated by so many butterflies belonging to the most different families that they may certainly be correctly regarded as quite safe

* And yet this seemingly impossible misconception has occurred to a German Professor. Prof. Vitus Graber, in his recent interesting book, "Die Insekten," which is rich in new facts and ideas (but which certainly misrepresents foreign species and much else), speaks (vol. ii. 1, p. 72) of "certain sand wasps which, in order the more readily to deceive their prey, the genus of crickets, Sphacura, disguise themselves in the form of their victims." The "genus of crickets, Sphacura," must certainly be the locust genus, Sphacura. The author has distorted the name as well as the fact. Wasps do not resemble locusts, but the latter mimic wasps, which certainly carry in locusts (but not in the perfect state) for their young, and never Sphacura, as far as I have seen. Their deceptive resemblance to wasps serves them as a protection.
from the pursuit of birds on account of their distastefulness and yet, so far as I know, a repulsive smell has not yet been detected in them. The odour emitted by the odoriferous tufts of the males is generally very faint and far from being unpleasant, but is rather like that of vanilla or roses, so that the cause of the distastefulness cannot be sought therein, the less so since it emanates from the wings, which are not eaten. We have thus numerous imitators taking for models species without any distastefulness recognizable by us.

"On the other hand, among the numerous mimics which appear elsewhere (Itajahy) suddenly in swarms twice in the year are Acrea Thalia and the much rarer Eueides Pavana, which possesses the same odour-emitting appendages at the extremity of the abdomen and the same repulsive smell as the remainder of the Maracuja butterflies. Of the same nature is the resemblance of the three related and similarly smelling species, Eueides Aliphera, Colanis Julia, and Dione Juno, of which the odoriferous power is certainly possessed in the highest degree by the smallest species, although this appears to have been acquired, in most part at least, subsequently. Further, the strongly smelling Eueides Isabella and Heliconius Eurete have either individually or together acquired a resemblance to Mechanitis Lysimnia, which (apart from the extremely faint, and to us scarcely perceptible, odour of the male) is to us inodorous; and, among the numerous butterflies which sufficiently resemble the three above-named species as to be occasionally mistaken for them are species belonging to the Ithomia group (Melinae) and to the true Danaides (Lycorea).

"Thyridia and Ithomia both belong to the class of cases in which the two species which resemble one another appear to be equally well protected by distastefulness. The former belongs to the Ithomia group, the distastefulness of which has been just referred to, and the latter to the Danaides, which play the same part as models of imitating species in the Old World as the Ithomiae in the New. They appear even after death to defy the ravages of time and the attacks of mites, &c., by virtue of their distastefulness. Last year Mr. Raphael Meldola exhibited to

* [The fact that no odour has been detected cannot be considered as conclusive evidence that none is emitted. Just in the same manner as there are sounds and odours both above and below the limits of our sensual perceptions, so there may be odours inappreciable by our sense of smell.—R. M.]

On what authority does Prof. Delbouef state (‘ Kosmos,’ vol. ii., p. 106) that "the Heliconide (the subject treated of referred to Ithomia, not to Heliconius) when in danger emit a disgusting fluid, which makes them the most distasteful of all food"? It probably proceeded from the pen of one of the numerous followers of Bates and Wallace, who so easily tread the path laboriously beaten out by these unsurpassed observers of mimicry and protective resemblance. [Here follows a severe criticism of Mr. A. W. Bennett's objections to the explanation of mimicry by natural selection; ride ‘Natura,’ vol. iii., p. 30.]
the Entomological Society the remains of an old Indian collection which had been destroyed by mites, &c., 'the surviving specimens all belonged to protected genera (Euphaea, Danaus and Papilio), proving that the quality which rendered these insects distasteful was, to a certain extent, retained after death.'*

"Now what does the mimicry of protected species signify? What advantage can it be to the rare Eueides Paraná to be so wonderfully like the common Acraea Thalia, and what benefit can one species derive from resembling another, if each is protected by distastefulness. Obviously, none at all if insectivorous birds, lizards, &c., have acquired by inheritance a knowledge of the species which are tasteful or distasteful to them—if an unconscious intelligence tells them what they can safely devour and what they must avoid. But if each single bird has to learn this distinction by experience, a certain number of distasteful butterflies must also fall victims to the inexperience of the young enemies. Now if two distasteful species are sufficiently alike to be mistaken for one another, the experience acquired at the expense of one of them will likewise benefit the other; both species together will only have to contribute the same number of victims which each of them would have to furnish if they were different. If both species are equally common, then both will derive the same benefit from their resemblance—each will save half the number of victims which it has to furnish to the inexperience of its foes. But if one species is commoner than the other, then the benefit is unequally divided, and the proportional advantage for each of the two species which arises from their resemblance is as the square of their relative numbers.† For instance, let us suppose that in a given region during one summer 1200 butterflies of a distasteful species have to be destroyed before it becomes recognised as such, and that in this region there exist 2000 individuals of one (A) and 10,000 of another (B) distasteful species. If they are quite different each species


+ Let \( a_1 \) and \( a_2 \) be the numbers of two distasteful species of butterflies in some definite district during one summer, and let \( n \) be the number of individuals of a distinct species which are destroyed in the course of a summer before its distastefulness is generally known. If both species are totally dissimilar, then each loses \( n \) individuals. If, however, they are undistinguishably similar, then the first loses \( \frac{a_1 n}{a_1 + a_2} \), and the second \( \frac{a_2 n}{a_1 + a_2} \). The absolute gain by resemblance is therefore for the first species \( n - \frac{a_1 n}{a_1 + a_2} = \frac{a_2 n}{a_1 + a_2} \); and in a similar manner for the second, \( \frac{a_1 n}{a_1 + a_2} \). This absolute gain, compared with the occurrence of the species, gives for the first, \( \frac{a_2 n}{a_1 (a_1 + a_2)} \), and for the second species, \( \frac{a_1 n}{a_2 (a_1 + a_2)} \), whence follows the proportion, \( \frac{1}{1} = \frac{1}{2} = \frac{a_2}{a_1} : \frac{a_1}{a_2} \).
will lose 1200 individuals; but if they are deceptively alike, then this loss will be divided among them in proportion to their numbers, the first (A) will lose 200, and the second (B) 1000. The former (A) accordingly gains 1000 (or 50 per cent.) of the total loss, and the latter (B) only 200 (or 2 per cent.) of this number. Thus, whilst the relative number of the two species is in the ratio 1 : 5 the advantage derived by those possessing the resemblance is 25 : 1.

"If two species are concerned, of which the one is very common and the other very rare, then the advantage falls almost entirely on the rarer species. If, for example, *Acrea Thalia* were a thousand times commoner than *Eueides Pavana*, the latter would derive a million times greater benefit from the resemblance of the two species, whilst for the *Acrea* the benefit is practically nil. Thus *Eueides Pavana* might by natural selection be converted into one of the most exact mimics of *Acrea Thalia*, although it is just as distasteful as the species imitated.

"On the other hand, if two or even several distasteful species are about equally common, resemblance brings them a nearly equal advantage, and each step which the other takes in this direction is preserved by natural selection—they would always meet each other numerically so that finally one would not be able to say which of them has served as the model for the others. In this manner are explained those cases where several allied distasteful species (e.g., *Colenis Julia*, *Eueides Aliphera*, and *Dione Juno*) resemble one another—cases where such resemblance cannot be regarded as inherited, and yet where neither of the species appears to claim to have served as a model for the others.

"To this category *Ituna* and *Thyridia* may belong, although the first has probably made the greater step in passing from the former dissimilarity to the present resemblance of the two species."

With reference to Dr. Fritz Müller's remarks on the inexperience of young birds, Mr. Jenner Weir stated that from the numerous experiments which he had made on the subject of larvae which are eaten or rejected, he had always been profoundly impressed with the utter disregard paid by birds to larvae which were inedible. He had never but once seen a distasteful larva even examined by a bird. When, day by day, he had thrown into his aviary various larvae, those which were edible were eaten immediately; those which were inedible were no more noticed than if a pebble had been thrown before the birds. It was Mr. Weir's opinion that the experience of birds in this respect had become hereditary in the species, and was not the result of the experience of individual birds, but was rather to be regarded as an act of 'unconscious cerebration.'

Mr. Bates, whilst acknowledging the great value of the numerous facts adduced from his own personal observation by Dr. Fritz Müller, could not agree with him in his proposal to separate, as a distinct family, *Ituna* and
Lycorea (with Danais) from Thyridia and the remainder of the Ithomia group; the characters mentioned by him only went to prove that Ituna and Lycorea were the connecting links between Danais and the Ithomia, thus justifying the views of those Lepidopterists who first defined this important group nearly twenty years ago. With regard to the still incompletely solved problem of mimicry, he could not see that Dr. Müller’s explanations and calculations cleared up all the difficulties. The numerous cases where species which are themselves apparently protected by their offensive secretions evidently mimic other species similarly protected still form a great stumbling-block. The excessive complexity of the question must be evident to all who read Dr. Fritz Müller’s writings on this subject. The phenomena with regard to the Heliconiæ, stated broadly, were these:—In Tropical South America a numerous series of gaily-coloured butterflies and moths, of very different families, which occur in abundance in almost every locality a naturalist may visit, are found all to change their hues and markings together, as if by the touch of an enchanter’s wand, at every few hundred miles, the distances being shorter near the eastern slopes of the Andes than nearer the Atlantic. So close is the accord of some half dozen species (of widely different genera) in each change that he (Mr. Bates) had seen them in large collections classed and named respectively as one species. Such a phenomenon was calculated to excite the interest of the travelling naturalist in the highest degree. Although the accordant changes were generally complete, cases occurred in which intermediate varieties were still extant, and the study of these had given him, when he was in South America, the clue to an explanation which, however, does not embrace the whole of the problem.

July 2, 1879.

Sir John Lubbock, Bart., M.P., V.-P.R.S., President, in the chair.

Donations to the Library were announced, and thanks voted to the respective donors.

Election of a Member.

Mr. Vincent Robert Perkins, of 54, Gloucester Street, South Belgravia, was ballotted for and elected an ordinary Member.

Exhibitions, &c.

Mr. S. Stevens exhibited living specimens of Tillus unifasciatus and Teretrix picipes, from the same fence, at Norwood, where these insects were captured last year, this being the fourth season of capturing the first, and the third season of taking the second species in this locality. (See also Proc. Ent. Soc., 1878, p. xli).