TABLE II.

Specific heat of liquid nitrogen.							
No.	Quantity of nitrogen in grammes	Mean temperature	Temperature increase	Heat capacity of nitrogen + flask and core K_{III} in joules/degree K.	Heat capacity of flask + core K_{III} in joules/degree K.	Specific heat of nitrogen in cal_{15}/degree K.	Atomic heat in cal_{15}/degree K.
29 Nov.							
II	41.7	63.95	0.585	112.6	29.5	0 476	6.67
III	„	69.15	0.564	116.2	32.8	0.478	6.70
IV	„	69.73	0.566	115.9	33.2	0.474	6.64
VI	41.6	75.46[5]	0.727	121.9	36.4	0 490	6.87
V	„	76.49	0.752	117.6	37.0	0 462[5]	6.48

The values of the atomic heat of liquid nitrogen are also given in Fig. 4.

The sudden increase of the atomic heat at the triple point appears to amount to 1.3 cal.

The value found by us for the specific heat of liquid nitrogen is considerably higher than that given by ALT[1]): 0.430 for the mean specific heat between 65° and 77° K.

Zoology. — "*On the phylogenetic significance of the Wing-markings in Hepialids*". By J. F. VAN BEMMELEN.

(Communicated in the meeting of January 29, 1916).

My previous investigations of the colour-markings on the wings of Lepidoptera have led me to certain conclusions, which may be briefly summarised here, as they are needed for the better understanding of the phenomena on the wings of the primitive Hepialid family.

The first conclusion is that the colour-pattern is to be looked upon as a mixture of components of different phylogenetic age, and consequently of unequal systematic value.

Of the facts on which this conclusion is based, three may be mentioned here:

1. During the development of the wings inside the pupal sheath

[1]) H. ALT, Ann. d. Phys. (4) 13 (1904), p. 1010.

the imaginal colour-pattern arises rather suddenly in the last days of the chrysalid period, but this pattern is preceded by a different one, which passes only partially into the definite pattern, and for the rest is obliterated by it.

This preliminary, original or primary pattern is distinguished from the imaginal one by its greater regularity, simplicity and at the same time completeness. Moreover it is identical in different nearly related species.

2. On the wing sheaths of those pupae which are not simply of a brown or black hue, but show an elaborate colour-pattern, these markings form a design, which corresponds to the above mentioned primitive pattern, and consequently is similar in a number of related species.

3. A comparison of the imaginal forms of the said related species shows, that the principal features of similarity from which this relationship is deduced, are especially furnished by those elements of the primitive pattern, which have been retained in the definite pattern.

The second conclusion is, that the above mentioned simplicity, regularity and completeness of the primitive pattern depend on its connection with the course of the wing-veins, the markings either following these veins, or being arranged in the interspaces between them, without transgressing their boundaries. As a proof of this connection the fact may be mentioned, that in many cases the course of veins which become obliterated during the development of the wings, still remains visible in the colour-pattern. For it must be noted that the system of wing-veins likewise undergoes a process of metamorphosis: the definite wing-skeleton arises from the modification of a provisional and more primitive one, which shows smaller differences between fore- and hindwings, and greater similarity to a general ground-plan, holding good for all different groups of Lepidoptera. In those families, which for different reasons are considered the most primitive, the imaginal system of wing-veins shows the least degree of deviation from this general plan, and for the same reason the greatest similarity to the distribution of wing-veins in other insect-orders nearly related to the Lepidoptera, such as the Trichoptera.

The third conclusion is connected with the fact that in the bulk of imaginal patterns the markings on the upper side differ from those on the underside, and those of the forewing from those of the hind one (especially on the upper surface). This fact may be contrasted with the similarity existing, as remarked before, between

upper- and underside, fore- and hindwing in the primitive pattern during the greater part of the pupal period, as well as on the wings of a certain number of imaginal forms in different families, which bear the character of primitiveness. The conclusion drawn is that the said uniformity of the markings in different wing-parts may depend on the preservation of the primitive pattern.

Should these conclusions be well-founded, it may be fairly expected that the investigation of the most primitive Lepidopterous families will probably confirm them. As such may be considered the Micropterygids, Hepialids and Castniids. Of these the second family was investigated by me, with regard to their imaginal or definite colour-markings.

The Hepialids are a small family of moths, sharply delineated by definite characteristics, which stamp them as a very primitive group of Lepidoptera, more intimately related to the Trichoptera than the bulk of the remaining moths and butterflies. The family is divided into a number of genera, which for the greater part are well characterised by the general appearance of the species composing them, though it might prove exceedingly difficult to found this difference on constant, sharply delineated features, which could be described in strict terms.

Some of the genera consist of one single species, others contain only a very few, but there are also some, which are richer in members, and the species of these latter may be said to resemble each other very closely, the specific distinction again depending more on the general appearance than on certain well marked. constant features. I therefore presume, that in many cases (e.g. the genus Charagia) a careful survey of large series of specimens from different habitats will lead to a reduction of the number of species to a few types, each with its local races and constant varieties.

As to individual modifications the Hepialids show an extraordinary degree of variability, especially with regard to the wing-markings, which provide the more obvious features for the identification and description of the insect. In every species, where I had at my disposal a relatively large number of specimens, I found without exception, that not two of them could be said to be even approximately alike.

Yet the differences may all be classed under the category of more or less: e.g. a larger or smaller number of spots arranged in the same row, greater or less dimensions of these spots (leading to a greater or less tendency to coalesce with their neighbours, either of the same row or with those of the next, by means of protrusions in

that direction), darker or lighter hue of one and the same colour, sharper or more effaced traces of the same design.

This phenomenon is a necessary consequence of a general fact, which I was able to establish by comparison of the different individuals and sexes of the same species, as well as by that of different species belonging to the same genus, or by the genera among themselves, viz. that the colour-pattern of all Hepialids can be deduced from one ground-form, or, expressing it in evolutional terms, that all Hepialid wing-markings have developed as modifications of the same original form.

Now on reconstructing the latter, it is found to conform to the rules, formulated for the original colour-pattern of Lepidopterous wings in general. It consists of a regular alternation of biconvex and biconcave markings, filling up the interspaces between the wing-veins and rigorously keeping within these boundaries. This arrangement is uniformly repeated on fore- and hindwings, upper- and underside, yet there exists a considerable contrast between the upper side of the forewings and the rest of the wing-surface, in so far as the former shows the markings sharply delineated and vividly coloured, while on the remaining wing-surfaces they are faint and diluted, often almost effaced. This may go so far, that only by observation of the wing-surface under a very oblique angle, or by careful inspection of photographs, the presence of spots on an apparently unicolorous surface can be detected (in the same way as the characteristic pantherine pattern can be distinguished on the skin of the black leopard by looking at it under a very acute angle).

I must acknowledge, that for want of material up to this moment I have not been able to investigate the development of the Hepialid wings in their pupae and so to give additional proof of the primitive character of their colour pattern. Neither have I succeeded in discovering traces of markings on the pupal wing-sheaths.

In some species the above mentioned primitive colour-design is present in its entirety, in others it is more or less modified and reduced to fragments. The modifications are different in character: sometimes the entire wing-surface has been uniformly influenced by them, e.g. when the markings have disappeared and one single hue prevails. In other cases part of the surface has deviated from the original plan, while this has remained unaltered on the rest of the wing, in which case the proximal part usually shows the modified plan, the distal one the original design. Judging by the complication or simplicity of the design, a distinction between progressive and regressive changes may be made.

The latter occur especially on the lower surface of the forewings and on both sides of the hindwings, while the former show themselves in different aspects on the upper surface of the forewing.

Now could these different types of modification be proved to correspond to the distinctions between the genera, they certainly would be of important assistance in tracing the boundaries of the latter. As a matter of fact this seems to be the case to a certain extent, and undoubtedly the founders of the genera have been led amongst other features by the different character of the colour pattern. So for instance I do not doubt that the author of the genus Charagia, WALKER, has been influenced by the conspicuous green shade, which in the majority of species colours the upper surface of the forewings. In the same way it cannot be denied that Leto venus, the single species of the South African genus Leto, is distinguished from all other Hepialids by the large silvery blotches, more or less regularly arranged in transverse rows all over the upper side of the forewings.

Again we might be led to suppose that the members of the genus Dalaca might be easily recognized by the exceedingly curious character of their wing-markings, looking like the letters of an antique inscription standing out in high relief upon the brown-grey background, with which they contrast by their lighter shade as well as by the greater size and different shape of the wing-scales, which enter into their composition. Finally to cite one more instance the genus Pielus seems to differ from other groups of Hepialids not only by its special slender build and elegantly pointed wings, showing a certain superficial similarity to Sphingidae, but moreover by the longitudinal white streak of fantastically broken contours, running from base to tip over the middle of the wing-surface.

Yet all these peculiarities as well as other special features of the colour-pattern can be shown to be the ultimate degrees of modification of the original design, occurring in a less grade in other genera or to be for other reasons lacking in importance for the determination of generic boundaries.

The latter case is illustrated by the green shade in the majority of the Charagia-species, for not only do we find this shade replaced by a brown one in others, but this may be even the case with specimens of the same species (Ch. thermistis and virescens). Moreover in Ch. lignivorus the forewings are partly green, partly brown.

As to the relation between these two shades, I think it the most probable supposition to consider green as a modification of brown, instead of the reverse. For in a number of families and genera of Lepidoptera a certain percentage of green forms occurs beside

a majority of differently coloured ones, and gives rise to the supposition that this green has arisen as an adaptation to surroundings, and in so doing has obscured an older and more elaborate colour-pattern. This is a general rule, applicable not only to Lepidoptera, but likewise to other insects, and even to all groups of animals. Turning our attention to the silvery marks of Leto, we meet them in other genera of Hepialids as well, though smaller in shape and number, e.g. Hepialus, Phassus, Phassodes, Charagia, Hepialiscus, Pielus. For here they occur in corresponding places, and often show the same arrangement in transverse rows. Moreover on comparing the different species of the above-named genera and looking over series of specimens, we become convinced that the silvery shine of these spots is not essential. It varies not only with the species, but even with the sex and in the individuals. Ch. ramsayi for instance. especially in the female sex, shows a good number of well-developed, very conspicuous silvery spots, the most so in the variety chrysomallon, in which again the ground-colour is brown instead of green, and devoid of all remaining primary markings. But the male sex possesses fewer and smaller silvery markings, and this is also the case with Ch. mirabilis ♂ to an even greater extent. Yet the tendency to silvery lustre must be present there as well as in the ♀, for the smaller groups of lustrous scales occur in just the same places as in the latter.

In the female of mirabilis on the contrary, this tendency seems at first sight to be altogether absent. Yet the place of the lustrous spots is occupied by markings of a special character, viz. dark spots, composed of a deep-blue dumbbell-shaped centre situated between two brown rounded blotches. Perhaps the fact that the metallic blue gives a sharp white image on the photographic plate, and that the same is the case to a less degree with the brown blotches, is not without deeper significance, as it gives evidence that these two colours emit active chemical rays.

Sundry other species of Charagia have the lustrous spots of some individuals replaced in others by dark brown blotches (Ch. virescens, eximia). The same occurs in species of other genera, as is shown by the series:

Phassus chamyli, purpurascens, giganteus.

Phassodes guthrei ♂, odorivalvula ♂, vitensis, rewaensis, nausori ♂.

Pielus hyalinatus, var. leucochiton ♂. hyalinatus ♀ var. bursa.

Trictena labyrinthica ♂ & ♀.

Hepialus humuli ♂ (totally lustrous white), fusconebulosus, hectus, humuli ♀.

As most of the remaining genera also contain many or at least some species, showing the lustrous spots to a greater or less extent, we come to the conclusion, that a hereditary tendency to the production of lustrous spots over the whole forewing-surface must be present in all Hepialids, but by other factors is either repressed (which leads to the diminution or total suppression of the silver-spots), or modified (blue or brown spots), or restricted to certain wing-areas. In other cases on the contrary, it is fully displayed, producing complete metallism.

These restraining factors must differ in character as well as in intensity of influence, according to genera, species, varieties, local forms, sexes and individuals. Yet as they lead to similar chains of modifications in different genera, it is obvious that we may not found the system of the different features of our genera on the peculiarities of the links in this chain.

In order to justify this conclusion, let us once more compare the species of one genus, and afterwards this genus as a whole with others, taking as our starting point a form with a wing-design of a primitive character.

As such several species of the genus Charagia may be chosen, for the upperside of their forewings shows that regularity and simplicity of pattern, which I take to be an indication of primitivity. The wing-design is composed of alternating biconcave and biconvex markings, arranged in transverse rows, parallel to the external margin of the wing. In Ch. mirabilis ♀ the pattern is seen in its simplest and most complete form. Nowhere do the spots trespass on the course of the veins; in different wing-areas they agree with one another in shape as well as in size. It is only along the margins that inconsiderable deviations from these general rules occur, especially along the anterior wing-border. Moreover the discoidal cell shows slight variations of the hourglass-shapes and disturbances of the regular arrangement, which latter thereby only strengthens the impression of its primitivity, as the said wing-areas are those which have suffered the strongest modifications in their venous system.

This impression is furthermore strengthened by the repetition of the same pattern on the underside of the forewings and both surfaces of the hindwings, differing only by being less sharply traced, and coloured in lighter hues. As already remarked, this indistinctness without doubt may be ascribed to a tendency towards total disappearance. But besides, this pattern differs from that of the upper side of the forewings by its simplicity, all spots and blotches being alike in shade and hue, instead of the rows of darker and differently

stained markings, which alternate with the lighter ones, the latter thereby giving the impression of a background. These conspicuous rows constitute what I call the secondary pattern, the same which in other species is still more prominent by its silver lustre. In some of these latter, for instance Ch. ramsayi ♀, the contrast with the primitive markings is moreover enhanced by the silvery blotches obtaining jet-black borders and deviating in size and shape both from each other and from the general original type of the primary markings. This deformation may lead to the obliteration of some members of a row, or at least their reduction to mere points, the rest of them at the same time increasing in bulk to such an extent, that they coalesce with their neighbours. When these changes go hand in hand with the evanescence of the primary markings by their immergence into the ground colour, a really unicolourous background is left, strewn with black-bordered silverblotches of different size and irregular shape, as in Ch. ramsayi var. chrysomallon.

A somewhat different modification of the same original arrangement leads to the coalescence of all the white or dark markings in one secondary row (principally the submarginal one), so that an unbroken transverse band or bar ensues. Sometimes its original composition from separate spots remains clearly visible, in other cases it is quite effaced. This modification occurs in different species, and is more developed in males than in females.

A third differentiation is likewise common to a number of species: it consists of a longitudinal lightcoloured bar, starting from the forewing-root, and reaching to beyond the middle of the hind margin. By this bar a triangular narrowbased hinder area is separated from the rest of the wing. Probably it passes along the demarcation line between two wing-areas of different constitution, which are distinct from each other in several insect-orders, and have been indicated by the names "folded part" (Faltenteil) and "spread part" (Spreitenteil). As the bar runs nearly parallel to the hindmost wing-veins, it meets the above mentioned transverse secondary bar at nearly right angles, and in so doing circumscribes a proximal and anterior wing-area, which in its shade and markings often contrasts with the rest of the wing. Ch. lignivorus, lewini and splendens form instances of this "triangle"-modification, which again is more pronounced in males than in females. Yet some faint indications of it may be observed in the colour-pattern of Ch. mirabilis ♀. So characteristic is this modification for Hepialids, that it is spoken of as the Hepialid-triangle.

On comparing with Charagia other genera, e. g. the very charac-

teristic genus Phassus, the three types of colour-pattern described above, can again be distinguished, and the connection between them is seen to be the same. For instance Ph. giganteus corresponds to Charagia mirabilis ♀ in the regular alternation of biconcave and biconvex markings over almost the whole space of the wing-surface. Ph. chamyl is the counterpart of Ch. ramsayi ♀ in the occurrence of silver markings of different shape and size spread over the wingsurface in an apparently irregular manner, and in the great contrast between these conspicuous blotches and the rest of the design, which for the greater part is indistinct, the markings showing a tendency to coalesce.

Finally several species of Phassidae, e. g. purpurascens, herzi signifer, and also the just mentioned chamyl, possess the Hepialid triangle, in the same position as Ch. splendens, liguivorus and lewini.

The same is the case in many species of the genus Hepialus, where it is often combined with transverse rows of secondary and primary markings. Nevertheless in H. behrensi, the primary markings have completely vanished, and nothing is left of the pattern but two rows of secondary silver-markings, strongly contrasting with the uniform dark ground-colour (ramsayi ♀ type). H. hectus tends to the same type, but less perfectly, and within the specific limits of H. fusconebulosus a variety gallicus occurs, in which the reduction of the markings has led to almost complete unicolourism, though the type possesses a very elaborate pattern. Again in the male of H. humuli all traces of pattern have given way to a uniform coloration of silvery shade, the female at the same time showing red markings on a yellow ground, which by careful analysis can be deduced from the general Hepialid plan.

Though a well known fact, it nevertheless is worth remembering, that in the Shetland-islands a race of humuli is found, in which the males agree in colour-pattern with the females.

Pielus and Trictena are two Hepialid genera, whose colour-pattern is modified in the same remarkable way, leading to a close similarity between the two groups, so much so that I still doubt the validity of their separation. In all cases it is easily shown that also this highly complicated colour-pattern may be deduced from the same groundform as that of other genera, and has developed from it along similar lines.

The characteristic longitudinal white streak, running from wing-root to tip, with its fantastically crooked and vacillating contours, is evidently the result of the deformation, coalescence and partial obliteration of spots, originally arranged in transverse rows and similar to each other in form and size.

Though the most primitive type, that which is preserved to us in forms like Charagia mirabilis ♀, Phassus giganteus and Dalaca assa, is not met with in the genus Pielus, yet stages corresponding to Ch. ramsayi ♂ and Ch. splendens, can be recognized among the different degrees of modification belonging to it, which culminate in a form like Pielus hyalinatus var. barcas, where the above mentioned white bar stands out against an almost unicolourous dark background. And even this characteristic bar is seen to occur as well in some forms of the New-Zealand genus Porina.

The result, to which this comparison of the Hepialid genera leads us, is the independence of the colour-pattern in its original form as well as in its various modifications, of generic differences. For this fact no other explanation can be found. in my opinion, than the assumption, that phylogenetically the colour-pattern in all its manifestations is older than the division of the Hepialid family into genera, or, otherwise expressed, that the whole complex of modifications of the wing-design belonged to the inherent properties of the ancestry of the present Hepialids.

Supposing this conclusion to be right, we are forced to assume that in all species of the different genera the hereditary factors for all these colour-modifications are present. Otherwise we should be obliged to believe, that in each genus, independently of the remaining ones, one and the same series of modifications of the common original pattern had developed, which means that as many cases of parallel evolution had occurred as genera of Hepialids exist.

The latter supposition cannot be said to appear very probable, even for the genera of one family, but it becomes decidedly absurd as soon as we realise, that also in other families of Lepidoptera, akin to the Hepialids, the same types of modification, derivable from an identical groundform, are met with.

If, however, our first assumption should prove justified, we cannot avoid the conclusion that also those specific forms in which the original pattern demonstrates itself with the least amount of secondary changes (Charagia mirabilis ♀, Phassus giganteus, Dalaca assa, Porina characterifera, Oxycanus fusconebulosus, Phassodes nausori) cannot for that reason be considered really to possess a more original constitution than the farthest advanced modifications. The predisposition for these modifications must be equally present in their hereditary outfit, as in that of the other forms, whose outer aspect attains the highest degree of specialisation, or at least this hereditary tendency must originally have belonged to it. In cases of

total unicolourism (albinism, melanism,xanthism, erythrism, chlorism) nobody doubts the original presence of the factors for an elaborate colour-pattern, although it remains invisible. Why then should the same supposition be inadmissible in the case of other deviations from the original pattern, and why should not the latter manifest itself, if the secondary modifications to which it is subject are suppressed.

The above mentioned parallelism in the series of colour-patterns in different Hepialid genera may therefore be considered as a proof that these chains of modifications are phylogenetically older than the genera themselves. We may even push their origin still further back, to beyond the branching point of the Lepidopterous order into its different families.

This supposition is supported by the evident correspondence between the original colour-pattern and the distribution of the wing-veins, because the regular arrangement of uniform spots along these veins and along their interspaces may probably be considered as a last trace of the primordial communication of neighbouring veins by series of connections, which disappeared almost completely; the so called discoidal vein forming a last remnant. Such systems of transverse connecting veins occur in the wings of primitive insects, e.g. Ephemerids and Neuroptera, which fact certainly strengthens the hypothesis of their former presence in Lepidoptera.

Nor are we restricted to wing-veins when seeking connections of the original colour-pattern (composed of a single motive of decoration regularly repeating itself) with other organic structures of the wings. It might also be related to the branching of the nervous system over the wing-membrane, and the distribution of the sense organs which are situated at the end of these branches. For we know by the investigations of VOGEL, F. KÖHLER and others regarding scent-scales on the wings of butterflies, that these smell-producing dermal appendages are originally distributed between the veins in patches at regular distances, each patch being provided with a nerve-branch. In many other groups of the animal kingdom we meet with numerous instances of an original connection between colour-distribution and that of sense organs with their nerve tracts, therefore the supposition that such a connection primitively existed in insect wings also, cannot be qualified inadmittable.