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Mayflies from Japanese Torrents

- X. Life Forms and Life Zones of Mayfly Nymphs
- II. Ecological Structure Illustrated by Life Zone Arrangement

By

Kinji IMANISHI

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X. Life Forms and Life Zones of Mayfly Nymphs

II. Ecological Structure Illustrated by Life Zone Arrangement*

By

Kinji IMANISHI (今西錦司)

(Institute of Zoology, Kyoto Imperial University)

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In a preceding, introductory paper** the author adopted three terms: life form, synusia and life zone. At the beginning of this paper it will be convenient to explain concisely these concepts once more, because this paper deals with some generalizations based upon such concepts with references to the distribution of mayfly nymphs in Japanese torrents, to which the author have devoted many years in observation and study.

These three concepts were proposed by different investigators. The concept of life form was proposed by RAUNKIAER, that of synusia by GAMS and that of life zone by MERRIAM. Each one of these concepts was defined to have a special reference to different sets of phenomena so that the inherent relation between these concepts has not yet been properly emphasized. There has been an apparent lack of endeavour to correlate the results of researches on the problem of distribution of organisms carried out from the taxonomic as well as the ecological standpoint.

By *life form* is not meant any structure of such organism as a lifeless museum specimen which used so long to be the sole object of study in taxonomy, but it refers to a mode of life that is manifested by that living organism because of such a structure. Numerous organisms with the similar structural plans manifest a similar life form. This is an important fundamental point in the life-form principle. When there are various structural plans there may be various life forms. Organisms with different structural plans do not, as a rule, coexist on the earth surface in a chaotic and ever-

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lasting struggle. If the organisms with different life forms coexist it may be taken as an evidence of the biotic community as a whole, being an organized system with a definite structure. The fact that various organisms are able to coexist in a given situation is chiefly due to the habitat segregation within that space according to the difference in life form among them. The general fact that organisms with similar structures are most frequently found in similar habitats is only natural because they have a similar life form. Since many, if not all, structures of the organism are more or less correlated to its habitat, it is plain that the question of habitat forms a principal part of the concept of life form.

Now, assuming that the organisms with a similar life form have a similar bodily structure and live in a similar habitat, the analysis of a biotic community in terms of life forms requires a taxonomic procedure on one hand and an analysis of habitats on the other hand. The possibility of recognition of a tree layer within the plant community, in the same way, is evidently due to the fact that the structure of each constituent tree of that layer and the space occupied by it are recognized by us as such. Such a tree layer included within, and forming an integral part of, the plant community under consideration is called a *synusia* by some plant ecologists. This term is taken to signify an aggregation of organisms with a similar life form and therefore naturally with a similar life habitat forming a social structure with the organic life of the community to which this *synusia* belongs. In this sense the term *synusia* may be of some use in animal ecology too, so that it is adopted in the present paper.

SMUTS (1926) has employed a very suggestive term, 'field', in connection with the environment of organisms. In my opinion the habitat may be interpreted as a field of life with an individual organism at its center. The interwoven complex of life fields constitutes a spatial stage for the unfolding of the life activities of a *synusia*. In short a *synusia* may be regarded as a socially organized life form.

The ecological analysis of a biotic community in terms of *synusiae* must inevitably reach the final category or the final unit of the community. This final unit is found in the *synusia* consisting of the life form of a taxonomically defined species, and may be designated as *specific synusia*. On reaching this stage of analysis, our ecological study of community may be called to have achieved a concrete result. Such idea of specific *synusia* fills up a logical gap between autoecology and synecology.

The part is recognized as such only when the whole, in which the part is included, is anticipated. As a part of the whole it has a definite function and structure of its own. When a *synusia* is recognized as a part of the community as a whole, it must have a function correlated with structure of its own as its concrete content. The presence or the absence of such a concrete content forms a criterion for judging whether the analytical procedure adopted is based on an objective, that is, scientific foundation or on a subjective, that is, mere philosophical foundation. As to the

categories and the number of categories of synusia above the specific synusia to be expected in an ecological analysis of a biotic community, future investigations alone will be able to establish on a general basis.

Proceeding to the case of the mayfly nymphs as the bottom inhabitants of torrents, the specialization in life forms may correspond with the differences in environmental conditions and in that case the correlation between the taxonomic differentiation and the habitat segregation is not hard to be recognized. Such facts have suggested to the author that the synusia may be interpreted to be constructed of many specific synusia as their parts and they reveal their own structures in the arrangement of these specific synusia. To elucidate these points with an especial reference to the Japanese ECDYONURIDAE is the central concern of this thesis. To apply the term *life zone* to such an arrangement of specific synusia is not only in conformity with the original meaning of the term but also useful in clarifying its contents by restricting it to rational usage.

In the latter part of this paper, a classification of river types is attempted on the basis of an ecological structure, namely, life zone arrangement, and two types are recognized in regard to the Japanese torrents. I am aware of that any synecological efforts can not be complete unless all environmental factors, physical as well as biotic, are consulted. In the present paper, however, all physical and chemical natures of the water such as turbidity, acidity and H-ion concentration, are neglected for simplicity's sake. Neither the food complex nor the spatial relation between the mayflies and the other groups of animal or plant are considered, so that all conclusions proposed in the present paper are of preliminary and more or less hypothetical and must be checked and worked out further and more accurately in future works of myself or some other ecologists of Japan.

It is with great pleasure that I offer my grateful thanks to Prof. T. KAWAMURA for his constant interest and advices in my work which made these series of reports possible. My sincere thanks are also due to Dr. H. YUASA for reading through the manuscript and for giving valuable suggestions. I must also heartily thank those gentlemen whose names are already mentioned in the previous paper for their valuable helps.

Two series of life zones

In the preceding paper I have pointed out the following life zones in terms of specific synusia forming the *Ecdyonurus-Epeorus* synusia which are arranged according to the velocity of the stream:

Ecd. yoshidae→*Ep. latifolium*→*Ep. curvatulus*→*Ep. uenoi*.

Although that paper was not accompanied by any sufficient statistical data this series of life zones was ascertained to be really existing, for instance they are easily recognizable at any time between April and October in the Kamogawa River at Shimogamo, Kyoto. Whether all four of the specific synusia are found or some of them is lacking in any cross-section there, granting other situations to be satisfied, seems to be correlated not

directly to the distribution of the absolute quantity of the velocity of the stream in that cross-section, but to the relative arrangement of the velocity in that cross-section as well as to those in the surrounding sections. In other words, it means that life zones found at a set of habitat arrangement remain in a relatively stationary state in spite of the considerable change in the velocity of the stream from the high water of the spring flood to the low water of the midsummer, when the water is much drawn into the rice-fields for irrigation. Perhaps each specific synusia is not rigid but rather plastic in itself to any environmental change. When any shifting of life zones corresponding to such an environmental change as the change of the velocity of water stream is not visible, it is highly probable that each specific synusia does regulate itself against the existence of its neighbouring specific synusiae in constantly changing environmental conditions.

The river always changes its character, physical or chemical, as its water travels seaward, so that there occur also the changes of its biological character between in its course. Naturally there arises a question as to what extent the same set of life zones is found in so far as there is found the corresponding set of habitat arrangement in such a variable nature of a river system. I have chosen the Kamogawa* River for the purpose of solving this question and have surveyed it up to the source of one of its tributaries, just below the Seryô Pass (690 meters), 10 kilometers NNW of our university as the crow flies, after following up the Ichiharagawa and Kibunegawa throughout, each of which is a part of the surveyed river system named after the village that the river passes through. Other large tributaries as the Kumogahatagawa and the Shizuharagawa, and some small valleys as well as those of other river systems contiguous to the Kamogawa River have been surveyed in case of necessity or when I made an excursion there. My investigation has brought to light the fact that the distributional range of each of specific synusiae of mayfly nymphs is not identical but most of them are succeeded by other equivalent specific synusiae in the upper region of the river at some distance from its source. Here I wish again to illustrate this phenomenon by the *Ecdyonurus-Epeorus* synusia as I consider it as the most characteristic one among various synusiae of mayfly nymphs found in Japanese torrents.

Ecdyonurus yoshidae gradually disappears while other species of *Ecdyonurus*, *Ecdyonurus kibunensis* or *Ecdyonurus tobiironis* begins to appear in the upper region, roughly speaking, about Kibune. *Epeorus latifolium* disappears before or after *Ecdyonurus yoshidae* does but is not succeeded by other species during the summer. *Epeorus curvatulus* is succeeded by such mayfly nymphs that are very similar to itself in general appearance and habits. They are destitute of the typical C-shaped markings of *Epeorus curvatulus* on the frontal part of their head as well as other lighter mark-

* The suffix 'gawa' means a river in the Japanese language.

ings of *Epeorus curvatulus* on their thorax and abdomen, so they appear darker in colour than *Epeorus curvatulus*. I have reared these nymphs and obtained imagines. When compared with the typical form of imagines of *Epeorus curvatulus*, I found that their imaginal characters examined seem to be not enough to separate them as a distinct species from *Epeorus curvatulus*. Moreover, there have been sometimes collected transitional forms between these nymphs and those of *Epeorus curvatulus* in their transitional belt or their transitional season of appearance. Therefore I consider them as merely a form of *Epeorus curvatulus* and describe them in the present study under the name of *Epeorus curvatulus cumulus*. And at last individuals of *Epeorus uenoi*, the inhabitant of the most rapid part of the stream, are succeeded by those of another *Epeorus* species, an equally competent inhabitant of the rapid water with equally enlarged first gill-lamelae as *Epeorus uenoi*, viz., *Epeorus hiemalis* in the upper mountain region.

Consequently, in some upper region of the river system surveyed, life zones in the *Ecdyonurus-Epeorus* synusia arranged according to the velocity of the stream may be recognized as follows:

Ecd. kibunensis or *Ecd. tobiironis*→*Ep. curvatulus cumulus*→*Ep. hiemalis*. But again, in *Epeorus curvatulus cumulus* and *Epeorus hiemalis* the latter disappears first when the survey proceeds further upward, because the river is becoming smaller and smaller as it approaches to its source and the habitat occupancy by *Epeorus hiemalis* is becoming more and more difficult relating to the habitat arrangement there than in other species. By the same reason, *Epeorus curvatulus cumulus* should be excluded next where their habitats are no more available in the trickling rivulet of the head-water, and further above, *Ecdyonurus* only find their habitats. But *Ecdyonurus kibunensis* is not distributed so far as to such an upper region, as they are succeeded by another *Ecdyonurus* species, *Ecdyonurus tigris*, at some distance below the source. Then we may find in the uppermost region or the true, spring-fed source of the river, where the velocity of the stream is much reduced and large boulders are scarcely present, two *Ecdyonurus* species, *Ecdyonurus tigris* and *Ecdyonurus tobiironis*, the former outnumbering the latter.

Then the life zone arrangement as the arrangement of specific synusiae recognized along the course of the river may be represented, for instance, in the slowest part of the stream, from the lower region to the upper region as follows:

Ecd. yoshidae→*Ecd. kibunensis* or *Ecd. tobiironis*→*Ecd. tigris*.

Although we should now recognize two series of life zones in the same *Ecdyonurus-Epeorus* synusia, it is of significance that this series of life zones is different in its character from the other series of life zones which is arranged according to the velocity of the stream and has been mentioned to be recognizable in the direction across the stream, for instance:

Ecd. yoshidae→*Ep. latifolium*→*Ep. curvatulus*→*Ep. uenoi*.

The difference between this and the foregoing series of life zones appears

at first sight to exist in the difference of the direction of the arrangement. But as life zones correlating to the velocity of the stream is not only arranged in the direction across the stream but also may be arranged in the direction along the stream if the set of habitat arrangement corresponding to the velocity of the stream is found in that direction. Hence the essential difference between these two series is not in the direction of the arrangement. On the other hand, we may find a considerable difference between these two series when we examine the life form arrangement corresponding to the life zone arrangement. The series of life zones correlating to the velocity of the stream reveals a more remarkable change between respective life forms than in another series of life zones, the change which often corresponds with the difference between the genera considered from the structural or taxonomic point of view. In the foregoing instance we see a change from *Ecdyonurus* to *Epeorus* and also a change from *Epeorus* without enlarged first gill-lamellae to *Epeorus* with enlarged first gill-lamellae. While in another series the change between respective life forms is much smaller, usually confined in the same genus as in the case of the change of

Ecd. yoshidae→*Ecd. kibunensis* or *Ecd. tobiironis*→*Ecd. tigris*.

or in the same species as in the case of the change between *Epeorus curvatulus* and *Epeorus curvatulus cumulus*.

I have already mentioned that in the evolution of the life form many structural differentiation can be considered in connection with any habitat segregation. If the taxonomic treatment is ideal, i. e. the group of animal is classified according to true natural affinities any structural differentiation such as comprehended in a conception of the genus shall be prior to that which is comprehended in a conception of the species and it shall be recognized that the habitat segregation corresponding to the generic differentiation is prior to that corresponding to the specific differentiation among the same genus. That is to say that in two series of life form arrangements corresponding to two series of life zones, one correlating to the velocity of the stream is in general more fundamental in the study of distribution as a problem relating to the occupancy, for it is indicative of the habitat segregation pretty well corresponding to the generic differentiation. Under such consideration I wish now to distinguish these two series of life zones by describing the one series correlating to the velocity of the stream as 'life zones of the first order', and the other series recognized in tracing the similar set of the habitat arrangement in the course of a river as 'life zones of the second order'.

The above mentioned generalization that the generic differentiation is always prior to the specific differentiation may appear to prove too much, since there may be some exceptional cases of this rule in which the generic characters are too poor to cover the different characters of all species in that genus and accordingly there exist no fair parallelism between the taxonomical differentiation and the habitat segregation. But as far as I

know such exceptional cases have never been found in the mayfly nymphs of our running waters and I believe that my conclusion proposed in the present paper is quite true and good enough to be applied to the synecology of the mayflies of all streams and torrents.

Seasonal change in life zones

Before entering the discussion of distributional problems concerning our mayfly nymphs it may not be out of place to mention here an outline of the seasonal change of the fauna of these insects. The seasonal change of any fauna is attributable to the difference in the life histories among its constituents. If a species needs an interval of more than a year for its nymphal stage, this nymph should be found throughout the year. If a species completes one generation in one year, the season of the appearance of its nymphs should naturally be connected with the season of the emergence of its imagines. Thus, nymphs of most spring mayflies such as *Ameletus costalis*, *Heptagenia kihada*, *Epeorus ikanonis*, *Ephemerella basalis*, *Ephemerella longicaudata* and so on, will commence to appear in the late autumn forming important constituents of the winter fauna. If a species completes two generations a year and the emergence of its imagines takes place twice each year, in the spring and the autumn, such as *Ecdyonurus tobiironis*, then its nymphs will be found either in the winter or the summer. If a species completes more than two generations in one year and the emergence of its imagines takes place at any time between the spring and the autumn, such are the case with *Ecdyonurus yoshidae* and *Epeorus latifolium*. Their nymphs are found in all seasons i. e. almost continuously.

Indeed, the nymph of *Baetis thermicus*, for instance, is found throughout a year, but that of *Ecdyonurus yoshidae* or *Epeorus latifolium* is not found in winter. In such a species as *Ecdyonurus yoshidae*, the emergence of which imagines takes place continuously in the warmer season, its generation are always overlapping or in other words, there are always found individuals in various stages of its life history. And as this condition continues till the late autumn and again appears in the spring, we may expect there are also individuals in various stages in any place during the winter. In reality, I have often found the nymphs of *Ecdyonurus yoshidae* in the mud under stone in midwinter, although I could not find them in their normal habitats. It seems likely that *Epeorus latifolium* does not hibernate in the nymphal stage like *Ecdyonurus yoshidae* but in the egg stage, as there are found no nymphs till next spring after its synchronous swarming occurring every year in the late autumn. In other families, the nymph of *Siphonurus sanukensis* also hibernates in the muddy bottom of a pool along the side of the stream.

During the hibernation such species may cease their development, but will their places remain unoccupied after they recede to their hibernating places? There is no *Ecdyonurus* which takes the place of *Ecdyonurus yoshidae* in winter, whereas *Epeorus latifolium* is fairly succeeded by another

species, *Epeorus ikanonis*, which develops in winter in the habitat formerly occupied by *Epeorus latifolium* and emerges in the early spring before *Epeorus latifolium* again appears. In this way, *Epeorus curvatulus* seems to be succeeded also by *Epeorus ikanonis* in the lower region and to *Epeorus napaesus* in the upper region of the river system under consideration, while *Epeorus hiemalis* of the upper region gives its place to *Epeorus aesculus* after its emergence in the late autumn. But as exceptions, there are *Epeorus uenoi* and *Epeorus curvatulus cumulus*, which are found throughout the year as they remain in their normal habitats even in winter, and there are no more *Epeorus* to take their places in this season. Although the former seems to perform scarcely any development in this season as in other hibernating species, it is noticeable that the latter is active and develops as in the nymph of the winter form of *Baetis thermicus*. If there is found the seasonal dimorphism in one species, one form which appears in the cooler season is usually darker in its coloration than the other form which appears in the warmer season. I have already reported on such a dimorphism found in the imagines of *Epeorus latifolium* and *Baetis thermicus*. Considering from these facts, *Epeorus curvatulus cumulus* may possibly be recognized as a melanistic form of *Epeorus curvatulus*, found in the oligotrophic, clear, cool water of the upper region, even if it is not yet safe to say that it represents the winter form in the seasonal dimorphism of that species.

I should like to mention here two more examples before I finish the description of the seasonal change of species belonging to the *Ecdyonurus*—*Epeorus* life form group. In winter there are sometimes found *Ecdyonurus tobiironis* and *Heptagenia kihada* together in the spring-fed source of the river where in summer *Ecdyonurus tobiironis* and *Ecdyonurus tigris* live. In this connection, the life form of *Heptagenia kihada* seems to demonstrate a relation to the life form of *Ecdyonurus*, although it may be properly anticipated from the morphological affinity of these two genera. But it is more interesting that in winter some species belonging to the genus *Cinygma*, say, *Cinygma hirasana*, occupies the habitat where *Ecdyonurus kibunensis* lives in the warmer season. Consequently, it may be concluded that the life form of some *Cinygma* species is equivalent to that of *Ecdyonurus kibunensis*. However, it does not follow that the life form of *Cinygma* species is accordingly also equivalent to that of *Ecdyonurus yoshidae*. That is to say that the life form of *Ecdyonurus kibunensis* is not exactly equivalent to that of *Ecdyonurus yoshidae*, as the former is much smaller in size than the latter and is the inhabitant of smaller stones than those which the latter prefers to as its habitat.

In the preceding paper I have emphasized the difference between two life form groups of the family ECDYONURIDAE, viz., the *Ecdyonurus*—*Epeorus* life form group and the *Cinygma*—*Rhithrogena* life form group on the basis of life forms. But from further ecological consideration I must point out here the close affinity between these two groups which justifies the inclusion of these two groups in the family ECDYONURIDAE, a higher category of

the life form group, since as mentioned above, even two species belonging to the different groups are considered as only complementary to each other through the seasonal adjustment in their occupancy of the same habitat.

Table 1.

Spatial distribution of some mayfly nymphs in the Kamogawa river system.

Species	Survey section										
	Headwater	Kibune V	Kibune IV	Kibune III	Kibune II	Kibuneguchi	Ichihara	Sodegatani	Kurumazaka	Kamo II	Kamo I
<i>Ameletus kyotoensis</i>	*	*	*
<i>Ecdyonurus tigris</i>	*	*	*
<i>Epeorus curvatulus cumulus</i>	*	*	*
<i>Ecdyonurus tobiironis</i>	*	*	*	*	*
<i>Ephemera japonica</i>	*	*	*	*	*	*
<i>Epeorus hiemalis</i>	.	*	*	*	*	*
<i>Epeorus aesculus</i>	.	*	*	*	*	*
<i>Epeorus napaeus</i>	.	*	*	*	*	*
<i>Cinygma dorsalis</i>	.	.	*	*	*	*
<i>Paraleptophlebia chcorata</i>	*	*	*	*	*	*	*	*	*	.	.
<i>Ecdyonurus kibunensis</i>	.	*	*	*	*	*	*	*	*	*	.
<i>Cinygma hirasana</i>	*	*	*	*	*	*	*	*	*	*	.
<i>Baetis thermicus</i>	*	*	*	*	*	*	*	*	*	*	*
<i>Ephemerella nigra</i>	*	*	*	*	*	*	*	*	*	*	*
<i>Ephemerella basalis</i>	*	*	*	*	*	*	*	*	*	*	*
<i>Ephemerella trispina</i>	.	*	*	*	*	*	*	*	*	*	*
<i>Baetiella japonica</i>	.	*	*	*	*	*	*	*	*	*	*
<i>Ameletus montanus</i>	.	.	*	*	*	*	*	*	*	*	*
<i>Ameletus costalis</i>	.	.	*	*	*	*	*	*	*	*	*
<i>Epeorus curvatulus</i>	.	.	*	*	*	*	*	*	*	*	*
<i>Epeorus latifolium</i>	.	.	*	*	*	*	*	*	*	*	*
<i>Epeorus uenoi</i>	*	*	*	*	*	*	*
<i>Ecdyonurus yoshidae</i>	*	*	*	*	*	*
<i>Epeorus ikanonis</i>	*	*	*	*	*	*
<i>Ephemerella rufa</i>	*	*	*	*	*	*
<i>Ephemera strigata</i>	*	*	*	*	*	*
<i>Siphonurus sanukensis</i>	*	*	*	*	*
<i>Potamanthodes kamonis</i>	*	*	*	*

Table 2.

Seasonal distribution of some mayfly nymphs in the Kamogawa river system.

Species \ Month												
	January	February	March	April	May	June	July	August	September	October	November	December
<i>Potamanthodes kamonis</i>	*	*	*	*
<i>Bleptus fasciatus</i>	.	.	.	*	*	*	*	*	*	.	.	.
<i>Ecdyonurus tigris</i>	.	.	.	*	*	*	*	*	*	.	.	.
<i>Ephemerella rufa</i>	.	.	.	*	*	*	*	*	*	.	.	.
<i>Epeorus curvatulus</i>	.	.	.	*	*	*	*	*	*	*	*	.
<i>Ecdyonurus kibunensis</i>	.	.	.	*	*	*	*	*	*	*	*	.
<i>Ecdyonurus yoshidae</i>	.	.	*	*	*	*	*	*	*	*	*	.
<i>Epeorus latifolium</i>	.	.	*	*	*	*	*	*	*	*	*	.
<i>Siphonurus sanukensis</i>	.	.	*	*	*	*
<i>Paraleptophlebia chocorata</i>	.	.	*	*	*	*
<i>Ameletus montanus</i>	.	*	*	*	*	*
<i>Ephemerella trispina</i>	.	*	*	*	*	*
<i>Epeorus aesculus</i>	*	*	*	*	*
<i>Ephemerella strigata</i>	*	*	*	*	*
<i>Cinygma hirasana</i>	*	*	*	*	*	*
<i>Epeorus napaesus</i>	*	*	*	*	*	*	*
<i>Ephemerella basalis</i>	*	*	*	*	*	*	*
<i>Ephemerella nigra</i>	*	*	*	*	*	*	*
<i>Ameletus kyotoensis</i>	*	*	*	*	*	*	*
<i>Heptagenia kihada</i>	*	*	*	*	*	*
<i>Epeorus ikanonis</i>	*	*	*	*	*
<i>Ameletus costalis</i>	*	*	*	*	*
<i>Ecdyonurus tobiironis</i>	*	*	*	.	*	*	*	*	*	*	*	*
<i>Epeorus uehnoi</i>	*	*	*	*	*	*	*	*	*	*	*	*
<i>Epeorus curvatulus cumulus</i>	*	*	*	*	*	*	*	*	*	*	*	*
<i>Baetis thermicus</i>	*	*	*	*	*	*	*	*	*	*	*	*
<i>Baetiella japonica</i>	*	*	*	*	*	*	*	*	*	*	*	*
<i>Epeorus hiemalis</i>	*	*	*	*	*	*

Once the seasonal change of the fauna concerning and within the family ECDYONURIDAE is clearly understood, then we should be able to understand the seasonal change of the life zone arrangement in reference to the species of the same family without further explanations. Life zones are recognized

as specific synusiae are opposed to each other, but they are also synthesized into a higher synecological or biosociological category corresponding to the synusia of the family ECDYONURIDAE, as specific synusiae are complementary to each other in space and in season, as if they occupy and maintain their common habitat as a part of that of a family, by means of their common life form which is descended from their common ancestor, standing against the synusiae of other animals of different life forms or different phylogenies.

I have hitherto concerned with the family ECDYONURIDAE almost exclusively and have mentioned life zone phenomena citing instances from it, but of course such phenomena may be recognized in other synusiae corresponding to that of the family ECDYONURIDAE. The above two tables, the one representing the spatial distribution of some important species of mayfly nymphs found in the river system surveyed by myself, the other representing their seasonal distribution, are offered hoping to help to establish the general concept of life zone phenomena.

Further investigation of life zones of the second order

I have pointed out that the life zone arrangement can be considered as the structure of a synusia, in which each specific synusia as the component adjusts itself to its succeeding ones in its spatial as well as its temporal distribution. And although there are two series of life zones in the same synusial extension, it has been considered that the life zones of the first order is arranged according to the velocity of the stream. Now it is the purpose of this section to examine the life zones of the second order more closely.

1. Distribution within the given river system

That the life zones of the second order are arranged from the upper region to the lower region in the direction of the course of the river is suggestive of a kind of the altitudinal distribution of fauna or flora in a mountainous country such as Japan. But in our case the altitude is not always correlated with the life zone arrangement, since the segregation of life zones of the second order is also observed even at an almost equal level, when we select a section of the river with various tributaries, large and small, and examine the fauna of each tributary. The study makes it soon evident that the smaller the tributary, the more its fauna bears resemblance to that of the upper region of the main stream and vice versa. I will give here an example obtained from the survey section "Ichihara-Kurumazaka" at an altitude of about 140-150 meters high, which is represented the summer fauna of the *Ecdyonurus-Epeorus* life form group of the family ECDYONURIDAE.

- | | |
|-----------------------------|--|
| a) spring | <i>Ecd. tigris</i> |
| b) smallest tributary | <i>Ecd. tigris</i> , <i>Ep. curvatulus</i> |
| c) somewhat large tributary | <i>Ecd. kibunensis</i> , <i>Ep. curvatulus</i> , |

d) main stream

Ep. hiemalis
Ecd. yoshidae, *Ep. latifolium*,
Ep. curvatulus
Ep. uenoi

SHELFORD* discussed the distribution of fishes in the North Shore stream of Lake Michigan and concluded that the fish fauna of any section in a stream is dependent on the stage of that section reached by the developmental processes in the physiography of the stream itself, as had originally been pointed out by C. C. ADAMS. Hence it followed that the smaller and shorter the stream, the more closely its fauna resembles to that of the upper course of the larger and longer stream, and in this respect my result seems to coincide with the scheme of SHELFORD in the superficial comparison. But he did not try any analysis of life forms of fishes, so that he naturally did not touch upon the question of synusia and life zones which I am emphasizing in this study. Although his data are homogeneous at that point that they are all fishes, is it justifiable to consider that each species of them belongs to the same synusia? Is there any recognizable arrangement of life zones of the second order as I have mentioned above? For instance, the horned dace (*Semotilus atromaculatus*) which is described as a fish characteristics of the headwater or the youngest section of a stream, is found distributed also in the lower course of the stream or the older section of the stream, according to his comment. The successive appearance of species in his case is no more than the superposition of different synusiae, or at best as a phenomenon within the extent of the life zone phenomena of the first order, corresponding to the ever increasing depth of the stream or anything else in the change of the stream taking place as it follows its downward course. I have already mentioned a similar case observed in the *Ecdyonurus-Epeorus* synusia in the upper region of my surveyed river system, in which *Ecdyonurus tigris*, *Epeorus curvatulus cumulus* and *Epeorus hiemalis* appear successively from the headwater downwards. In both cases the phenomena do not contain any arrangement of specific synusiae recognized as life zones of the second order as defined above.

Though I do not hesitate to recognize the common fact in his and my cases that the similar physiographic condition is occupied by the similar fauna, it is recognizable from my case that each fauna is not always composed by the superposition of species. At the same time it is also recognizable that every component in a fauna is not always replaced by a new one in the other fauna. When the fauna d is compared with the fauna c, it is observed that *Ecdyonurus yoshidae* and *Epeorus uenoi* are replaced by *Ecdyonurus kibunensis* and *Epeorus hiemalis* respectively, while *Epeorus latifolium* is absent in the latter fauna and *Epeorus curvatulus* is common in both faunas. Then it follows that the segregation of life zones of the second order does not always take place simultaneously in each series of specific

* SHELFORD, V. E., 1913, Animal communities in temperate America, pp. 108-113.

synusiae situated in the similar position in the life zone arrangement of the first order. In this way, *Ecdyonurus* series are considered in this example to be segregated into three specific synusiae which may be recognized in the life zone arrangement as *Ecdyonurus tigris* zone, *Ecdyonurus kibunensis* zone and *Ecdyonurus yoshidae* zone at an almost equal level, whereas they are arranged in turn in the course of the main stream from its headwater downwards. Life zone arrangement may be regarded as discontinuous when tracing a river from the main stream to its small tributary, because of the lack of some intervening zone as the *Ecdyonurus kibunensis* zone in this example, and such a discontinuous arrangement of life zones is always observed corresponding to the discontinuous conjunction in the river system itself.

I consider that such segregation of life zones of the second order may be more properly exemplified in the classically known successive distribution of three species of planarians in Europe, viz., *Planaria alpina*, *Polyceris cornuta* and *Planaria gonocephala*, and in the similar case in our country, represented in the following species as *Planaria vivida*, *Polyceris auriculata* and *Planaria gonocephala*, which has been already studied by KABURAGI* and UENO,** rather than in the example of the distribution of fishes cited above. Various theories have hitherto been proposed to explain the successive distribution of planarians, but the water temperature, taking its annual change into consideration, seems to be accepted by most authors as a primarily important factor for this problem. To be sure, it will not be sufficient to consider that the similarity observed between the fauna of the small tributary flowing into the main stream at an altitude of only 150 meters high and that of the headwater of the main stream at an altitude of more than 550 meters high, depends upon the mere physiographic similarity, for there is also the clearly recognizable similarity of the water temperature between these two places, which may be to the distributional problem of mayfly nymphs as important as to that of planarians. My another paper*** is referred for the details of this similarity, in which the distribution of the water temperature within the surveyed river system in the summer of 1936 is mentioned.

But to what extent is the life zone segregation correlated to the distribution of the water temperature? Granted that the appearance of the headwater inhabitants such as *Ecdyonurus tigris*, *Heptagenia kihada* and *Ameletus kyotoensis* at so low an altitude as the foot-hill line, is correlated to the water temperature in the small tributary there, it is but natural that

* KABURAGI, T., 1922, On some Japanese freshwater Triclad; with a note on the parallelism in their distribution in Europe and Japan. Jour. Coll. Sci. Tokyo Imp. Univ., vol. 44, art. 2.

** UENO, M., 1931, On the distribution of planarians in mountain streams. Chikyu, vol. 15, pp. 260-279. (In Japanese).

*** IMANISHI, K., 1937, On the stream water temperature in the vicinity of Kyoto. Jap. Jour. Limnology, vol. 7, pp. 173-183. (In Japanese).

the water temperature decreases, in as much as the air temperature decreases, according to the increase of the altitude. Then we should expect some other segregation of life zones of the second order in the high altitude of the Japanese Alps where the highest summit reaches over 3100 meters high, though in the Kamogawa river system hitherto considered, it does not reach to even an altitude of 900 meters.

2. Distribution in the Northern Japanese Alps

That the life zone arrangement of the second order is not directly correlated to the altitude has already been discussed above. Now it will be assumed as a working hypothesis that the arrangement of the second order is correlated to such an environmental arrangement as represented by the water temperature, just as that of the first order is correlated to the habitat arrangement as represented by the velocity of water stream. Then any species which is distributed at a limited altitude in the Kamogawa river system may appear again in the river system based on the higher altitude, if there is found the proper arrangement of habitat and temperature. The typical inhabitants of the lower region of the Kamogawa such as *Siphonurus sanukensis*, *Ecdyonurus yoshidae* or *Epeorus ikanonis* are known from some streams flowing in the Matsumoto basin at an altitude of 700-900 meters, or from the Kisogawa at Kisofukushima at an altitude of 750 meters. It seems probable that the physiographic maturity of the river system itself in each of these collecting places combined with its relatively high water temperature enables them to be distributed there in spite of its relatively high altitude.

Having dealt with the survey of the distribution of mayfly nymphs in the district of Kyoto as well as the district of the Northern Japanese Alps since 1927, I should like to consider it as a general phenomenon that the limit of distribution of any species of the freshwater fauna in a river system is usually pushed up to the higher altitude according as the mountain system containing the river system becomes higher and more massive, and in reality, this phenomenon may be only a special case of the phenomena due to the so-called 'Massenerhebung', originally recognized in the Alps of Europe, which mean that the limit of distribution of the component of the terrestrial fauna and flora is pushed up to the higher altitude according that the mountain system with such fauna or flora becomes higher and more massive. Then it follows that the mayfly nymphs in the small tributary at some low altitude are found again in the headwater of the main stream, within the same river system, for example the Kamogawa river system, is not considered to be a phenomenon theoretically different from that of the mayfly nymphs in the lower region of the Kamogawa appearing again in some larger river systems such as the Shinanogawa at some higher altitude like the Matsumoto basin. Presumably in this way, *Epeorus uenoi* is found in a tributary of the Nakabusagawa at an altitude of 850 meters, while *Epeorus latifolium* is found in a still higher place as Kami-

kôchi, at an altitude of 1600 meters. The limits of distribution of these species are notably higher in these cases than those in the Kamogawa.

It is, however, premature to conclude from the above description that the life zone arrangement of the second order in some river system in the district of the Northern Japanese Alps is no more than the reproduction of that in the Kamogawa River on a mere larger scale, even if these two districts are regarded to belong to a common faunal region. It is sufficient to notice here that such a consideration is a prejudice as it does not take into consideration the difference between the stream of the mountain system of high altitude and that of low altitude in their physiographic appearances as well as their temperature characteristics. Once entering into the high mountain system proper, we shall find there usually the constantly turbulent but terribly dashing water of its wild stream where is scarcely any room for such a swimming life form as *Ameletus* to live, though *Ameletus montanus* is still found at 2300 meters in some case, distributed in its habitat condition, occasionally found there, while the distribution of *Ameletus costalis*, one of the spring mayflies, is mainly limited to 1000 meters or thereabout.

Now, the arrangement of life zones in the *Ecdyonurus-Epeorus* synusia in such a situation must be considered. I find it convenient to take the summer aspect of the fauna of the Azusagawa in Kamikôchi at an altitude of 1600 meters, as an example. Here is found in the slowest part of the stream no more species belonging to the genus *Ecdyonurus*, but a species of the genus *Cinygma*, *Cinygma kurobensis*, which is closely allied to *Cinygma hirasana* in the district of Kyoto. *Epeorus latifolium* is found as has been mentioned but is restricted in its distribution to the less wild stream of the side-valley as Tokusawa. *Epeorus curvatulus* is represented normally by the form *Epeorus curvatulus cumulus*, which is, however, not abundant in its individual number. And at last, *Epeorus uenoi*, an inhabitant of the most rapid part of the stream, is not replaced by *Epeorus hiemalis* as in the upper region of the Kamogawa, but by another *Epeorus* species with equally enlarged first gill-lamellae, *Epeorus aesculus*, which appears in the district of Kyoto before *Epeorus hiemalis* does there. Hence the arrangement of life zones of the first order may be recognized as follows:

Cinygma kurobensis→*Ep. curvatulus cumulus*→*Ep. aesculus*.

Where the stream is still wilder, there is found *Epeorus curvatulus cumulus* less and less abundant and life zones are ultimately arranged from *Cinygma kurobensis* to *Epeorus aesculus* directly. In this case, *Epeorus aesculus* is distributed to almost the whole stretch of the cross-section of the stream except the marginal zone where *Cinygma kurobensis* occupies, although the stream itself is, in all respects, larger than in the Kamogawa at Shimogamo. And such an arrangement may be observed continuously until we come up to the headwater which is often situated above the timber line. I collected these two representatives from a rapid emerging from the névé in the cirque of Mt. Kurobegorô, at an altitude of 2450 meters and

also *Epeorus curvatulus cumulus* from another more slowly flowing rivulet at the same altitude of the same locality.

On the contrary, where the stream is less wild as in the Ôtakigawa or the Kusarigawa*, each of which is situated in the more southern portion of the mountains, there appears *Epeorus hiemalis*, accompanied not only with *Epeorus latifolium* and *Epeorus curvatulus* but also with *Epeorus aesculus*. Then, will it not mean some destruction of the life zone arrangement adjusted in the seasonal distribution between *Epeorus aesculus* and *Epeorus hiemalis* in the occupancy of the most rapid part of the stream? But the question will be sometimes applicable to the transitional belt in which the *Epeorus uenoi* zone is adjacent to the *Epeorus aesculus* zone or the *Epeorus hiemalis* zone as well. In this connection, I recognize after the careful scrutiny of life form that where two equivalent species are obliged to coexist, there is also an adjustment in themselves. For instance, where *Epeorus aesculus* coexist with *Epeorus hiemalis*, the former usually gives the occupancy of the more rapid part to the latter, as if *Epeorus latifolium* usually gives the occupancy of the more rapid part to *Epeorus curvatulus* when these two species coexist. My observations on the adjustment of the life zone arrangement among three equivalent species under consideration may be schematically stated in the following sequence:

Ep. aesculus < *Ep. hiemalis* < *Ep. uenoi*.

But to what reason will the coexistence of *Epeorus aesculus* and *Epeorus hiemalis* be attributable? Will it not be explicable on the basis of retardation of the appearance on the part of *Epeorus aesculus* owing to the retardation of the season in high mountains, which, in turn, implies the retardation of the increasing of the water temperature there? In reality, the arrangement of life zones of the first order such as

Cinygma kurobensis → *Ep. curvatulus cumulus* → *Ep. aesculus*

is no more than that recognized in the spring in some upper region of the Kamogawa, if *Cinygma kurobensis* is only regarded as an alpine form of its closely allied *Cinygma hirasana*. The water temperature at the lower limit of the *Epeorus aesculus* zone in the Kamogawa in May is roughly identical with those in the streams of the Northern Japanese Alps in August; this temperature is scarcely over 15°C. in both cases. And this fact seems to justify the hypothesis that the arrangement of life zones of the second order in a river system is correlated to the arrangement of the water temperature in that river system, for it is more natural to explain the correlation between the spatial and the seasonal distribution of an organism by the temperature of its medium, and it may be said from above considerations that the seasonal change in life zones is in itself no other than a kind of the life zone arrangement of the second order. Of course, there is a physiological temperature limit to any species, but that the life

* This river was surveyed by Mr. T. KANI. I am indebted to him for his kindness who delivered me many valuable materials collected by him.

zone arrangement of the second order is an adjustment to a given temperature arrangement of the medium among different specific synusia, which are opposed to each other but also complementary among them, much as that of the first order is an adjustment to a given velocity arrangement of the habitat, and in each case, the fact that the mere environmental determinism is by no means competent for its explanation, is emphasized here once more.

If the mountain system from which the Kamogawa emerges is higher and more massive, there is surely found *Epeorus aesculus* even in summer in its imaginary upper region, as found in the streams of the Northern Japanese Alps. On the other hand, in the season when it is found in the district of Kyoto, life zones in the Northern Japanese Alps are also considered to descend to some low altitude, since I was able to collect *Epeorus aesculus* from every stream flowing into the Matsumoto basin in the middle of April, together with nymphs of some typical spring mayflies common in the district of Kyoto such as *Ameletus costalis* and *Ephemerella basalis*. Although, in such places, *Epeorus aesculus* as well as its fellow spring mayflies, is monogeneric as in the district of Kyoto, it may be polygeneric in the higher region where no longer the seasonal change in life zones takes place, but it may be again monogeneric in the still higher region like the region above the timber line by reason of the shortage of the available season. Recognizing that such a seasonal shifting of life zones is also attributable to the adjustment to the temperature arrangement of a given river system in space and in season, I will take again the summer aspect as a standard of comparison in my further investigation.

It is not yet possible to take up the question of life zones of the second order concerning the biota in general to which the designation of 'the life zones' was originally applied by C. H. MERRIAM. In practice, however, the segregated as well as the successive distribution among some species called the 'life zone indicators' arbitrarily selected from the components of the given biota was alone recognized, in so far as the consideration of life zones of the second order should be primarily based upon the comparison of series of specific synusia situated in the similar position in the life zone arrangement of the first order as I have already mentioned. In other words, it should be based upon the comparison of the equivalent specific synusia analysed by the application of the life form principle. SHELFORD and KENDEIGH* have rightly pointed out the weakness of MERRIAM's temperature laws, but the existence of some life zone arrangement of the second order recognized by MERRIAM and which formed the basis of his concept of 'life zones' is an obvious fact which after all no one may deny or ignore.

* SHELFORD, V. E., 1932, Life zones, modern ecology and the failure of temperature summing. *Wilson Bulletin*, XLIV, pp. 144-156.

KENDEIGH, S. C., 1932, A study of Merriam's temperature laws. *Ibid.*, pp. 129-143.

I* have recently published an opinion concerning the 'Höhenstufen' of the Northern Japanese Alps, in which I recognized four vertical regions by means of the combination of life zones of such physiographically and ecologically dominant trees of the climax forest as those belonging to the genus *Abies* or *Fagus*. These regions are defined as follows:

- 1, the alpine region as equivalent to the zone above the timber line,
 - 2, the subalpine region as equivalent to *Abies Mariesii* or *Abies Veitchii* zone,
 - 3, the montane region as equivalent to *Abies homolepis* or *Fagus crenata* zone,
 - 4, the submontane region as equivalent to the evergreen *Quercus* zone.
- In this case, such species were used as 'regional indicators' rather than as 'life zone indicators', or at least they were expected to be useful as a standard, with which the life zones of the second order belonging to the different synusiae are compared. Then, to what extent do the life zones of the second order here considered in the distribution of mayfly nymphs exhibit correspondence with such a standard?

There is, of course, few species belonging to the swimming life form groups in the torrents of the Northern Japanese Alps. *Ameletus montanus* has been mentioned as being distributed to the relatively high altitude, though it is not succeeded by *Ameletus kyotoensis* as in the Kamogawa, in such a high altitude, but by another *Ameletus* species, probably the nymph of either *Ameletus subalpinus* or *Ameletus croceus*, found in the headwater of the spring origin. It may be said that *Ameletus kyotoensis* is only equivalent to such a *Ameletus* species, if strictly speaking from the life form concept, but *Ameletus montanus* forms a characteristic synusia by itself with no equivalent one, therefore, it is not participating in the life zone segregation of the second order or it may be regarded as monozonal, as in *Epeorus latifolium* synusia. Other species belonging originally to the same life form groups such as *Baetis thermicus* and *Baetiella japonica*, which are equally known from the high altitude, are also monozonal in regard to the life zone arrangement of the second order in the mountain torrent. In the genus *Ephemerella*, only two large sized species, *Ephemerella basalis* and *Ephemerella trispina*, are common in the torrents of the Northern Japanese Alps, but these two are successive in the seasonal appearance as in the district of Kyoto, and in summer the latter is also monozonal. In the family ECDYONURIDAE, the relation between *Cinygma adusta* and *Cinygma kurobensis* seems to be the same one, and the headwater inhabitants such as *Ecdyonurus tobiironis*, *Ecdyonurus tigris* or *Heptagenia kihada* are not yet found in the Northern Japanese Alps proper. Consequently, there remain two examples which hold good for the intended comparison, the life zone arrangement represented by *Epeorus curvatulus* and *Epeorus curvatulus cumulus*, and that represented by *Epeorus uenoi* and *Epeorus aesculus*.

* IMANISHI, K., 1937, Über die Höhenstufen der japanischen Nordalpen. San-gaku, vol. 31, pp. 269-364. (In Japanese).

Judging from these two available examples, it seems to me fairly certain that the correspondence with the given standard is not recognized in the distribution of mayfly nymphs in the torrents of the Northern Japanese Alps. In the headwater region situated in the cirque and fed by the cold water from the melting snow even in high summer, no mayfly nymphs are found and *Scopura longa* of the order PLECOPTERA, one species of the trichopterous larvae belonging to the family SERICOSTOMATIDAE and *Planaria vivida* are the only components of its fauna. If this region is considered to correspond with the alpine region above defined, the number of recognizable zones becomes three in contrast to the four zones of the standard. In this connection, it is interesting to note that the studies worked out by DODDS and HISAW* in Colorado show a highly definite correlation to MERIAM's life zones.

But if the life zone arrangement of the second order recognized in the above examples, is considered as correlated to the temperature arrangement, then *Epeorus curvatulus cumulus* or *Epeorus aesculus*, the inhabitant of the upper region as well as the small tributary, should be found in the main stream flowing at the low altitude in the high latitude, provided that the other habitat conditions be satisfactory, as it is also but natural that the water temperature decreases in as much as the air temperature decreases in the high latitude. This temperature relation offers another criterion for the validity of the given hypothesis.

3. Distribution in the high latitude compared with that in the high altitude

Some observations and collections of mayfly nymphs in Saghalien were made by myself in the summer 1932, but in my second visit to Saghalien and Hokkaido last summer (1937) with an aim of studying primarily the distributional problem of mayfly nymphs as shown in the heading. From these experiences it is provisionally concluded that some species common in the district of Kyoto as well as in the district of the Northern Japanese Alps such as *Epeorus curvatulus* which is hitherto known from Yakushima to Yamagata, or its life form equivalent *Epeorus curvatulus cumulus*, is found neither in Hokkaido nor in Saghalien, while other species not yet found in Honshû occur there, but in general, the number of species tends to decrease in the case of latitudinal increase, just corresponding, in this respect, to the case of altitudinal increase.

It will be, however, desirable to mention the more concrete example for interpreting the latitudinal distribution, and I will begin with some examples from Hokkaido. In the Ishikarigawa at Sôunbetsu, at an altitude of about 600 meters, following species were collected from its main stream, namely, *Epeorus uenoi*, *Epeorus aesculus*, *Epeorus latifolium*, *Rhithrogena*

* DODDS, G. S. & F. L. HISAW, 1925, Ecological studies of aquatic insects, IV. Altitudinal range and zonation of mayflies, stoneflies and caddisflies in the Colorado Rockies. Ecology, vol. 6, pp. 380-390.

sp., *Ecdyonurus kibunensis*, *Ephemerella trispina*, *Baetis thermicus* and *Baetiella japonica*. This list immediately suggests to us on resemblance with that of the late spring fauna in some upper region of the Kamogawa by reason of the presence of *Epeorus aesculus* and *Ephemerella trispina*, or more appropriately, to the summer fauna in some torrents in the Northern Japanese Alps except for the presences of *Epeorus latifolium* and *Ecdyonurus kibunensis*, and the absence of *Cinygma kurobensis*. It is also worthy of notice that *Epeorus uenoi* and *Epeorus aesculus* coexist at this height in the main stream, so that one may suppose from this fauna such a familiar arrangement of life zones of the first order in the *Ecdyonurus-Epeorus* synusia as

Ecd. yoshidae → *Ep. latifolium* → *Ep. uenoi*

in some lower region of this river or at least of other ones located in the lower latitude than this one in Hokkaido.

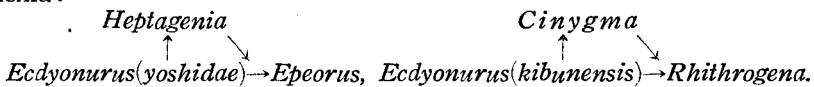
In reality, *Ecdyonurus yoshidae*, one of the commonest mayfly nymphs in the Kamogawa at Shimogamo, Kyoto, was found in the Toyohiragawa at Sapporo, though in this case it was associated with *Ecdyonurus kibunensis* and its individual number was far less than that of the associate. But it was found neither in the Tonbetsugawa at Matsuneshiri, Kitami nor in the Teshiogawa at Shibetsu, Teshio, each of which is located in the north of the Ishikarigawa. In these places a species belonging to the genus *Heptagenia* was found together with *Ecdyonurus kibunensis*. The taxonomic position of this *Heptagenia* has not yet been determined, so that it is conveniently denoted by *sp. A*. This species has been found recently also in Mr. Katô's collection* from the Hôrenga, Manchoukuo. Judging from the life form, it seems to me that this species is truly a northern equivalent of *Ecdyonurus yoshidae*, which is widely distributed in Southern Japan and was collected by Dr. Miyadi in the Rôkei, Formosa as its southernmost locality hitherto known. On the continent, it was collected by Mr. M. Yamasaki in the Taishiga, Manchoukuo, together with *Ecdyonurus kibunensis*, and also by Mr. Katô in the Tôjiga, Manchoukuo, the northernmost habitat hitherto known.

If it is accepted that this *Heptagenia sp. A*. is recognizable as a life form equivalent of *Ecdyonurus yoshidae*, then it must be a disclosure of another link between the two genera, *Heptagenia* and *Ecdyonurus*, which are morphologically so closely allied, through the application of the life zone concept derived from the life form principle. At the same time, it follows that in so far as the *Ecdyonurus* synusia is concerned, the latitudinal distribution is not a mere projection of the altitudinal distribution as simply convinced by some biogeographers, because it is admissible to consider that *Ecdyonurus yoshidae* in its latitudinal distribution is not only succeeded by *Ecdyonurus kibunensis* as already recognized in the arrangement of life zones of the second order in the Kamogawa, but also succeeded by *Heptagenia*

* Acknowledgement is offered to Mr. Y. KATÔ for favouring me with specimens collected in his journey of the summer 1937.

sp. A which is not distributed in the Kamogawa. This reason seems to be clear from the fact that although, considering from the temperature arrangement alone, the altitudinal arrangement of temperature indeed exhibits the general similarity to its latitudinal arrangement, the habitat arrangement as a whole in the high altitude is not exactly the same as that in the plain of the high latitude. Therefore, that some species found in the lower region of the northern stream, such as here discussed *Heptagenia sp. A*, is not found in the mountain torrent of Central Japan because of some difference in the habitat arrangement, is no less reasonable than that some species found in the latter is not always found in the former because of the same reason. These species may be said respectively as 'plain species' and 'mountain species' against the species which, if present, appears both in the former and in the latter, so that its distribution may be treated as primarily correlated to the temperature arrangement.

Moreover, to recognize this *Heptagenia sp. A*. as a reasonable equivalent of *Ecdyonurus yoshidae* is to deny the recognition of *Ecdyonurus kibunensis* as the life form equivalent of that species, if critically analyzed, though I have already mentioned some opinion about this point in the preceding pages. Now it seems to me that the family ECDYONURIDAE as a category of the life form group can, after all, be divided at least into two life form subgroups through the genus *Ecdyonurus*, and each of these life form subgroups tends to form an independent subsynusia in the family ECDYONURIDAE as a synusia, that is to say that *Ecdyonurus yoshidae* takes part in the structure of the *Ecdyonurus-Heptagenia-Epeorus* synusia, probably including the hygropetric *Bleptus*, while *Ecdyonurus kibunensis* is considered to be concerned in the structure of the *Cinygma-Rhithrogena* synusia. In spite of the recognition of such a difference that *Heptagenia sp. A*. is the northern equivalent of *Ecdyonurus yoshidae*, while *Cinygma hirasana* is the seasonal equivalent of *Ecdyonurus kibunensis*, the structure of each synusia represented in the life zones may be better understood in the following schema:



By means of such interpretations, we can find more satisfactory an expression of the life zone phenomena. For instance, the fauna of the family ECDYONURIDAE in the Toyohiragawa at Sapporo may be described as follows:

$$\begin{cases} \text{Ecd. yoshidae} \rightarrow \text{Epeorus latifolium} \\ \text{Ecd. kibunensis} \rightarrow \text{Rhithrogena sp.} \end{cases}$$

In this connection, it follows as a matter of course that one of the arrangements of life zones of the second order observed in the Kamogawa and described such as

Ecd. yoshidae → *Ecd. kibunensis* or *Ecd. tobiironis* → *Ecd. tigris*,
is ambiguous unless it is analysed further and redescribed as follows:

$$\begin{cases} \text{Ecd. yoshidae} \rightarrow \text{Ecd. tobiironis} \\ \text{Ecd. kibunensis} \rightarrow \text{Ecd. tigris} . \end{cases}$$

At the same time the arrangement of life zones of the first order, in which *Ecdyonurus kibunensis* and *Ecdyonurus tobiironis* were included together, should be also analysed and redescribed properly as follows:

{*Ecd. tobiironis*→*Ep. curvatulus cumulus*→*Ep. hiemalis*
 {*Ecd. kibunensis*→*Rhithrogena* sp.

Then it is naturally concluded that, in this case the life form equivalent of *Ecdyonurus yoshidae* is not *Ecdyonurus kibunensis* but is *Ecdyonurus tobiironis*, therefore it may be called a montane equivalent of *Ecdyonurus yoshidae* in contrast with its northern equivalent, *Heptagenia* sp. A. And here we should recognize once more that *Ecdyonurus yoshidae* has two equivalents, the montane one and the northern one, is only interpreted by reason of the difference in the characteristics of the habitat arrangement between the case of the altitudinal increase and that of the latitudinal increase, even if the life zone segregation itself may be considered in either case as correlated to the temperature arrangement.

As for the absence of *Epeorus uenoi* in the above-mentioned places as the lower regions of rivers in Hokkaido, it can not be attributed to the temperature arrangement. It was ascertained that this species as well as its life zone associates, *Epeorus curvatulus*, *Epeorus latifolium* and *Ecdyonurus yoshidae*, is able to live even in the highest water temperature of about 34°C. observed in the Kamogawa at Shimogamo, Kyoto, but this species and *Epeorus curvatulus* will disappear sooner or later if the survey is extended to further downwards, although the environmental conditions seem to be still tolerable for the maintenance of the usual arrangement of life zones of the first order. To my regret, I cannot give here the more satisfactory explanation of these phenomena based on a more thorough investigation, but it may be said that *Epeorus uenoi* as well as *Epeorus curvatulus* is probably too much of a mountain species comparing with *Epeorus latifolium* or *Ecdyonurus yoshidae* to live in such a lower region.

In order to observe the arrangement of life zones of mayfly nymphs in the upper region of rivers in Hokkaido, I visited the Hidaka range and traversed it from the Totsutabetsugawa to the Nukabiragawa, ascending *en route* the highest summit of that range, Mt. Poroshiri, 2025 meters. In this survey it was ascertained that the faunas of these two rivers are not only similar to each other but also similar to the fauna of the Ishikarigawa at Sôunbetsu, though they are to be distinguished from it by the absence of *Ecdyonurus kibunensis*.

To summarize, life zones of the first order in the ECDYONURIDAE is arranged in the middle course of these rivers as follows:

{*Ep. latifolium*→*Ep. uenoi*
 {*Rhithrogena* sp.

Of course this arrangement may show some change as the survey proceeds up stream or down stream. In down stream, it is usually observed that *Epeorus uenoi* drops out of this structure and this is considered as a normal phenomenon already discussed. In upper stream, however, it is observed

that *Epeorus uenoi* is replaced by *Epeorus aesculus* at about 750 meters. *Rhithrogena* sp. also disappears at about this height, but on the other hand *Cinygma* sp. appears and is distributed up stream together with *Epeorus aesculus*—a combination which we are already familiar with in some torrents in the Northern Japanese Alps. It is, however, worthy of mentioning in comparison with my previous experience that *Epeorus latifolium*, together with *Epeorus aesculus* and *Cinygma* sp. is also distributed in these streams to so high an altitude, that the upper limit of distribution of the former is only about 100 meters lower than that of the latter two. Then, in the uppermost stream, which flows on the cirque floor as in the Japanese Alps, no mayfly nymphs are found but *Scopura longa* and the trichopterous larvae of the family SERICOSTOMATIDAE, are found same as in the Japanese Alps.

If such changes themselves should be recognized as the arrangement of life zones of the second order required, then there is no other means to verify the validity of the hypothesis that the arrangement of life zones of the second order is essentially correlated to the temperature arrangement than to take as an example the arrangement of life zones observed in the most rapid part of the stream, namely the arrangement between the *Epeorus uenoi* zone and the *Epeorus aesculus* zone, for concerning the genera *Rhithrogena* and *Cinygma* the identification between the nymphal stage and the imaginal stage has been only incompletely studied. Furthermore, any systematic measurement of the physical environment has not yet been attempted as regards these rivers, much less such a particular problem as the life zone arrangement or the life zone boundary. But even if this is done, it should be anticipated that the correlation between the life zone arrangement of the second order and the temperature arrangement is verified only in the statistical exactness, in so far as it is considered that the distributional range of any organism is not determined by the temperature alone but the temperature arrangement itself is included in the set of the environmental arrangement as well as in the case of the correlation between the life zone arrangement of the first order and the arrangement of the velocity of the stream, and emphasis has been laid upon this point already repeatedly. Then it may be said that the temperature of 13.3°C., measured at noon at the life zone boundary between the *Epeorus uenoi* zone and the *Epeorus aesculus* zone in Hokkaido is not so seriously different from the temperature of 15°C. at noon, the temperature which I have provisionally regarded as a temperature of roughly indicating the boundary under consideration, judging from my previous experiences in Central Japan.

Above descriptions are based upon the observation in the main stream which I selected as the course of my journey. Is the phenomenon also recognizable in Hokkaido that the fauna of the upper region of the main stream reappears in the fauna of such a small tributary that flows into the main stream at some considerable low altitude? Yes, it was recognized

in a tributary of the Totsutabetsugawa—that is to say that both of the upper region inhabitants of the main stream, *Epeorus aesculus* and *Cinygma* sp., were present in the cool water of this tributary united with the main stream at an altitude of about 400 meters. As regards the distribution of *Epeorus aesculus* within a given river system, this relation is quite similar to that recognized in the Kamogawa, but that is recognized in the late spring in the Kamogawa while this is recognized in midsummer in the Totsutabetsugawa. Then, roughly speaking, does it not mean that the temperature arrangement in the late spring in the Kamogawa, Kyoto, is similar to that in midsummer in the Totsutabetsugawa, Hokkaido? This will be only explicable by the temperature decrease according as the latitudinal increase. Then if we proceed further north, we can properly anticipate there a river system in which *Epeorus aesculus* appears in midsummer at the level height so far as it is concerned with the tributary. And at last may we anticipate the existence of a river system in which *Epeorus aesculus* appears at the level height even in the main stream? In other words, does the boundary between the *Epeorus uenoi* zone and the *Epeorus aesculus* zone in the main stream decrease according as the latitudinal increase by reason of the temperature decrease, if considering a similar river system? It is a question I could not solve in Hokkaido.

On the other hand, it seemed to me that it is no longer reasonable to assume the appearance of any new zone in the life zone arrangement in the northern rivers when the life zone arrangement investigated in Hokkaido is compared with that in Central Japan, especially that in the Northern Japanese Alps. For instance, *Epeorus aesculus* is able to inhabit the cold stream in the high altitude originating from the melting snow, in so far as the temperature is concerned, therefore if the arrangement of life zones of the second order is correlated to the temperature arrangement, it seems to be not necessarily to anticipate another life zone which succeeds the *Epeorus aesculus* zone in the upper region of the main stream of some river system situated further north, even though *Epeorus aesculus* appears already in its lower region. Thus I went over to Saghalien with such problems in mind.*

In Saghalien the Horogawa in part and the Odasamugawa up to the source of one of its tributaries were surveyed in the summer 1937, but for the sake of simplicity only the summary of these surveys will be mentioned. Justifying my expectation, *Epeorus aesculus* was found in the main stream of each of these rivers in its lower region, a few kilometers away from its estuary at the coast of the Sea of Okhotsk while *Epeorus uenoi* was not found, though it was once collected by Dr. Miyadi in a stream of the Iturup Island, Kuriles. The water temperature measured is rather high, its

* In this opportunity I wish to express my cordial thanks to Messrs. M. HORI and K. TAMANUKI, the Central Experimental Station of Saghalien, Konuma; Mr. S. KOBAYAKAWA, the Forest Station of the Tokyo Imperial University, Ochiai, for their valuable helps delivered to my survey in Saghalien, 1937.

maximum being 18°C., at 1. 10 P. M. in the lower region of the Odasamugawa. Judging from this temperature alone, *Epeorus uenoi* may still be found here, and in reality, even in Saghalien in so far as my survey is concerned, *Epeorus aesculus* is found more numerous in the small tributary flowing directly out of the surrounding mountains than in the main stream, though these two habitats are located on the same level of only thirty or forty meters high. Then apart from the absence of *Epeorus uenoi*, it seems that such a distribution of *Epeorus aesculus* is an indication of its characteristic as a mountain species as in the case of *Epeorus uenoi*. At any rate, we can conclude at last from these facts that the arrangement of life zones of the second order thus reduced to a phenomenon of almost purely horizontal or latitudinal distribution is correlated to the temperature arrangement of the environment as it is only logical to explain such a zonal arrangement as correlated primarily to the zonal arrangement of the temperature on the earth surface. As a consequence, if the same life zone arrangement of the second order is observed in any one river system, it may be also explained as correlated to the temperature arrangement of that river system. In this connection if the seasonal change of life zone arrangement of the second order in a river system is recognized as the same life zone arrangement which appears in any other river system as a spatial arrangement, then it may be recognized only as a temporal arrangement of the same life zone arrangement, correlated to the seasonal change of the temperature arrangement of that river system. Thus it is considered that the seasonal distribution, the vertical distribution and the horizontal distribution are not separable from each other, or each of them is recognized as a different phase of the same arrangement of life zones of the second order. At the same time this interpretation is supported also by my confirmation of the absence of any life zone which succeeds the *Epeorus aesculus* zone in the survey of the Odasamugawa, even though the highest summit belonging to that river system, Mt. Odasamu, is only 924 meters high.

Such a generalization has been prevalent since older times among biogeographers, especially among plant geographers. If any parallelism to my conclusion from the distributional phenomena of other animals is needed, then the case of *Salvelinus pluvius*, a salmoniid fish, may be cited. This fish is not only associated with *Epeorus aesculus* in the fauna of the torrents of the Northern Japanese Alps and in that of Hokkaido, but also its appearance in the lower altitude at the higher latitude seems to be roughly coinciding with that of *Epeorus aesculus*, and if a locality is recognized as belonging to the different geographical region according as whether these species are present or absent in its fauna, then in the vertical distribution, the existence of these species will indicate the equivalence to the subalpine region and in the horizontal distribution, it will indicate the equivalence to the boreal region as their distribution is also, roughly speaking, regarded

as parallel to the existence of true subalpine or boreal coniferous forests. But it is worthy to notice here once more that this generalization is to regard the life zone arrangement of the second order as correlated primarily to the temperature arrangement, and it does not mean, on the contrary, that the same life zone arrangement is always to be found exactly where the same temperature arrangement exists, as in the case of my examples, from which, however, this generalization was induced. The discussion on this point will be taken up again in the next section concerning the distribution of *Epeorus latifolium*.

In Saghalien, a different form of *Epeorus latifolium* is found in place of the typical *Epeorus latifolium* distributed in Central Japan inclusive of Kiushu and Hokkaido and probably also Southern Korea. It is distinguishable from the latter by the following points: 1) its larger size, 2) the shape of its paired lighter marks situated in the middle of the frons, which is an inversed triangle in this form, but a rectangle in the typical form. I cannot yet determine whether it is a form of or a species independent of *Epeorus latifolium*, but it rather resembles *Epeorus napaesus* in its size than *Epeorus latifolium*. *Epeorus napaesus* may be regarded as a montane equivalent of *Epeorus latifolium* in Central Japan, then will this form be not regarded as a northern equivalent of the same *Epeorus latifolium*? Interesting enough, this form was also collected by Mr. Y. Katô in the Tôjiga, Manchoukuo—another northern locality. Consider that such a life zone segregation as represented in the arrangement between this form and *Epeorus latifolium* is correlated to the temperature arrangement, then one can expect some southern locality where such a northern form may appear and emerge before *Epeorus latifolium* appears and emerges; that is to say that there may be recognized a seasonal adjustment between these two. Time has come that it is proven when I had an opportunity to examine Prof. T. Kawamura's Collection from Korea. The examination revealed that in a collection in early June from the Nandaisen at Kisshû, North-eastern Korea, at a lower region of about 120 meters high, this form was included together with the typical *Epeorus latifolium*, but the former was full grown while the latter was almost immature—namely, the former will emerge earlier than the latter will do. I cannot safely say that the same phenomenon should be also recognizable in some part of Hokkaido as my observation is hitherto limited to the midsummer, and it should not be explained by reason of its characteristic of a non-mountain species that this form is not found in that season in the upper region of rivers in Hokkaido as *Epeorus aesculus* does, for it is distributed in the upper region as well as in the lower region of rivers in Saghalien. But by what reason is *Epeorus napaesus*, which is distributed together with *Epeorus aesculus* or *Cinygma* sp. in the district of Kyoto as well as in the Northern Japanese Alps, not also found there instead of *Epeorus latifolium*? In this connection for the first time in this paper, the importance of the existence of the Tsugaru Straits as well as the Sôya Straits as a barrier of distribution is pointed out

and this absence of *Epeorus napaesus*, in turn, may be regarded as the explanation of the abnormal phenomenon that *Epeorus latifolium* is distributed to so high an altitude in the stream in Hokkaido.* But how can we deny it from the absence of *Epeorus napaesus* in Hokkaido that this species may be distributed in Saghalien, judging from the fact that this species is found even in some streams of the Matsumoto basin in April, or the form under consideration is rather closely allied to *Epeorus napaesus* than to *Epeorus latifolium*? Nevertheless, the morphological characters inclusive of the colour pattern on the wing venation of the female imagines which I fortunately collected and examined, leads me to conclude that this form is to be considered meanwhile as a form of *Epeorus latifolium*. Therefore I wish to describe it as *Epeorus latifolium borealis* in this paper.

In the marginal part of the main stream with the slowest velocity of the stream as well as in the non-torrential tributaries, there was found *Ecdyonurus kibunensis* as in the river of Hokkaido except for those of the Hidaka range, but it seems that there exist in these northern rivers at least two forms belonging to this species, judging from the comparison of the nymphal structure alone, namely, a typical one as distributed in the district of Kyoto and a somewhat smaller one. In spite of such a differentiation of the size of the body, I will treat these two forms as belonging to the same life form in this paper, for I could not as yet find in them any habitat segregation corresponding to their structural differentiation. Then the life zone arrangement in the ECDYONURIDAE synusia at the middle course of the Horogawa may be represented as follows:

{ *Ep. latifolium borealis* → *Ep. aesculus*
Ecd. kibunensis → *Rhithrogena* sp.

On proceeding upstream, *Cinygma* sp. will be found in places of *Ecdyonurus* and *Rhithrogena* as usual. Then, even though *Epeorus latifolium* is replaced by *Epeorus latifolium borealis*, the life zone arrangement in Saghalien is not essentially different from that observed in Hokkaido, or in other words, the structure of the ECDYONURIDAE synusia hitherto mentioned remains, in the result, unaltered provided that the replacement of one member by its very closely allied member be recognized. And it is the relation between such two species that is properly defined as equivalent to each other in the life zone arrangement. The equivalent species constitutes in most cases

* It has been well known among plant ecologists that in the Hidaka range *Betula Ermani* is very dominantly distributed, forming a zone by itself upon the forest of *Abies sachaliensis* and *Picea jezoensis*, and its upper limit being corresponding with the timber line of that range, about 1700 meters. Comparing however, this distribution of *Betula Ermani* with that in the Northern Japanese Alps, it seems doubtless to me that the absence in Hokkaido of *Abies Mariesii*, which is overwhelming *Betula Ermani* in that mountains, is the explanation of this phenomenon, for *Abies sachaliensis*, more closely allied to *Abies Veitchii* than to *Abies Mariesii*, seems to be not so much a mountain species as *Betula Ermani* or *Abies Mariesii*. It is cited here as an example which is to be compared with the case of *Epeorus latifolium*.

the complementary species at the same time. Thus *Epeorus latifolium* ascends to the abnormal height in Hokkaido in the absence of its antecedent equivalent, *Epeorus napaesus* or *Epeorus latifolium borealis*, while the presence of *Epeorus aesculus* in the considerable high temperature in Saghalien may be explained by the absence of its subsequent equivalent, *Epeorus uenoi*. But what is meant by the similarity or the dissimilarity of the ecological structure of synusia? Does it not indicate the similarity or the dissimilarity of the type of the river system itself? Now I have to turn my attention to this hitherto untouched problem.

On the river type

I have already mentioned that the life zone arrangement of the second order is recognized as the seasonal arrangement in some habitat within one river system, or as the vertical arrangement in one river system, or as the horizontal arrangement among different river systems, if they are pursued polewards, and each of these zonal arrangement should be understood as correlated primarily to the zonal arrangement of the temperature of the medium. Then one may separate such a region as indicated by the presence of *Epeorus aesculus* as a cool river type, whether it is situated in the higher altitude at the middle latitude or in the lower altitude at the high latitude, in contrast to such a region as indicated by the presence of *Epeorus uenoi* as a warm river type, as illustrated in the preceding section. To classify the river types in this way is to submerge this problem in the broad problem concerning the recognition of the geographical regions. What I would like to suggest here is the possibility of a classification of the river types on some specific basis inherent to this particular problem. I wish to find the criterion of the difference of the river types between two rivers which differ radically from each other in their ecological structure even if they belong to the same geographical region. In other words the question of the river type belongs to the problem of ecological structure or that of the arrangement of life zones of the first order than to the problem of geographical region or that of the arrangement of life zones of the second order, though the type of a river as a whole is, indeed, only recognizable from these two approaches.

Following the above descriptions, I will cite examples mostly from the ECDYONURIDAE as a synusia, and in this respect I consider that the presence or the absence of the zone of the *Epeorus latifolium* group inclusive of *Epeorus latifolium*, *Epeorus latifolium borealis* and *Epeorus napaesus* in a river is very significant in the recognition of the type of that river. As already mentioned, *Epeorus latifolium* is scarcely found in the upper region of some rivers emerging from the Northern Japanese Alps where *Epeorus aesculus* and *Cinygma spp.* are dominant, though it is found in its lower region as well as in some more southerly rivers in that range. Such a peculiar distribution may seem at first sight to be correlated to the difference of the snow accumulation in the mountain system. The nearer a mountain

is situated to the Sea of Japan, the deeper the winter snow as it is carried by the north-west wind of the winter monsoon, and it follows that the more the winter snow accumulated the longer it takes to melt, consequently the slower the rise of the air temperature as well as the water temperature; also the longer a river is fed by the winter snow the longer its water is cooled. Therefore in the northern part of the Northern Japanese Alps where the winter snow is deepest and where the high mountains slope down suddenly to the coastal plain as in the Toyama Prefecture, water reaches the very low lands in still low temperature even in the midsummer and accordingly both invertebrate and vertebrate animals which are accustomed to live in the cool water of the upper region are also found in the very low altitude. For instance, *Salvelinus pluvius*, a salmoniid fish, is found in such a region at an altitude of about 300 meters high. *Epeorus aesculus* and *Cinygma kurobensis* are also found in the midsummer at about 600 meters or probably further below. But *Epeorus latifolium* is not found even in such a lower region, though it is found at 1600 meters in the Tokusawa at Kamikôchi, in the more southern part of that range, as already mentioned elsewhere.

We can understand the occurrence of *Salvelinus pluvius* or *Epeorus aesculus* at an unusually low altitude in the northern part of the Northern Japanese Alps simply as the general fall of the life zone arrangement of the second order correlated to the temperature arrangement and this tendency is obviously in conformity with that of lowering down towards the Sea of Japan of the snow line as well as the timber line in that mountain system, on which I have already reported.* But this explanation will not be applicable to the distribution of *Epeorus latifolium*, as it is distributed to an altitude of about 1000 meters in some rivers of the very same part of that range where it is quite absent in other rivers. As already seen from the survey of Hokkaido, there is no doubt about that it can live in the relatively cool water associated with *Epeorus aesculus* and this also holds good for the distribution of its allied species, *Epeorus napaensis* as well as *Epeorus latifolium borealis*.

Now another explanation will be proposed. It is well known that in Central Japan the climatic character on the side of the Sea of Japan is so different from that of the Pacific side, owing to its winter precipitation as the heavy snow fall, so that in the Northern Japanese Alps stretching in the north-south direction the climatic character of its northern part differs naturally from that of its southern part in the same manner. This is well demonstrated by the distribution of some characteristic plants, for instance, the gradual disappearance in the northern part of that range of *Picea*

* IMANISHI, K., 1933, Über die Schneegrenze der japanischen Alpen. Sangaku, vol. 28, pp. 193-226. (In Japanese).

IMANISHI, K., 1935, Über die Waldgrenze der japanischen Nordalpen. Sangaku, vol. 30, pp. 217-264. (In Japanese).

jezoensis, a spruce, or *Betula Tauschii*, a birch, which becomes, however, abundant in the more southern part but manifests its cold resisting character well in its northerly distribution beyond 50°N, seems to be attributable to this difference of the regional climatic characters.* As for the distribution of *Abies Veitchii*, a fir, in Central Japan, it is also very rare or absent under the prevalence of the typical snow climate of the Sea of Japan, while its northern equivalent *Abies sachaliensis* is found in the most parts of Hokkaido and Saghalien where the climate is more continental in winter. Among insects, for instance, the distribution between *Aporia hippia*, a butterfly and its northern equivalent *Aporia crataegi* corresponds more or less with such a discontinuous distribution between *Abies Veitchii* and its equivalent *Abies sachaliensis*. Doesn't the distribution of *Epeorus latifolium* group also correspond with such a distribution? But negative evidences are at hand. There are also some rivers in the district of Kyoto, where either *Epeorus latifolium* or *Epeorus napaesus* is absent, while these species are present in some rivers which is situated in the typical snow climate of the Sea of Japan. In this connection, it seems to me that the distribution of *Epeorus hiemalis* is to be rather considered as limited by such a climatic character, which is as yet found neither in the northern part of the Northern Japanese Alps nor in the northern land in so far as I have surveyed, because the early arrival of the snow fall as well as the prolongation of the snow cover in these regions means the shortage of the developmental season necessary to the unique life history of this species, as it hatches in summer and emerges in the early winter.

Then, it is interesting to see in what kind of river *Epeorus latifolium* is absent. Although in the district of Kyoto it is quite common in the river which emerges out of the mountain consisting of the sedimentary rock, it is absent in the river which comes out of the mountain consisting of the igneous rock, in this case mainly the granite. Superficially it seems as if its distribution is correlated to the kind of rocks to which the boulders of the substratum belong. In the Northern Japanese Alps too, it is not found, at where the substratum is composed mainly of the boulders of the igneous rock as in the Kurobegawa, in the Kashimagawa or in the Azusagawa at Kamikôchi, while it is common where the substratum is composed of the boulders of the sedimentary rock as in the Kusarigawa or in the Tokusawa at Kamikôchi, though it should be remembered that this insect was also found at an altitude of about 1350 meters in one of the tributaries of the Takaragawa, descending from Mt. Norikura, where the substratum is composed of the andesite, the volcanic rock. And this seems to hold good also for the distribution of *Epeorus napaesus*. In the Matsukawa there was found neither *Epeorus napaesus* nor *Epeorus uenoi*, while in the Himekawa both of them were found. *Epeorus napaesus* was also collected in the Magawa at an altitude of 1600 meters, the substratum of which is likewise composed of the boulders of the sedimentary rock.

* IMANISHI, K., 1937, Über die Höhenstufen der japanischen Nordalpen, opt. cit.

However, this geological explanation is not always applicable. *Epeorus latifolium* as well as *Epeorus napaesus* is found even on the granite boulders, for instance, in the Kisogawa at Kisofukushima, and this fact seems to suggest that the presence or the absence of these species in a river is indifferent to the kind of rocks to which the boulders of the substratum belong. Then, that these species are not found in the upper region of the granite valley in the district of Kyoto or in elsewhere but may be found in its lower region, is considered to have some correlation with the phenomenon that the appearance of the upper region of such a valley is usually very wild on account of the rapid disintegration of the bed rock, especially intensified in recent years by quarrying, while its lower region is not so conspicuous in its wildness that it is not distinguished from that of the other valleys composed of the different bed rock. The stream must reflect such a wildness, from which it emerges, in its violent water flow, in its unstable bottom, in its constant burden of fine mineral particles, in its scarce content of the organic matter and so on. Such are the characteristics of the 'wild torrent' in which life will be precarious at every rain fall due to the raging water.

It may be considered that the presence or the absence of *Epeorus latifolium* or its allied species in a habitat or a river is, in reality, determined by the presence or the absence of their specialized food in that habitat or in that river, and such a physical condition of the environment as the arrangement of the velocity of the stream or the arrangement of the water temperature may influence the distribution of the algal vegetation on the boulders. If so, physical factors influence only indirectly the distribution of animals dependent on the algal vegetation as their food. Furthermore the distribution of the algal vegetation itself may not be directly dependent on such a physical condition but primarily on the quality and quantity of its nutriment viz. dissolving chemical substances. Although I have not yet studied closely such a correlation between the life zone arrangement of mayfly nymphs and that of the algal vegetation, it is quite recognizable that the algal flora in the upper region of a river, for instance the Kamo-gawa, is different from that in its lower region, therefore such a phenomenon that the habitats of *Epeorus napaesus* of the upper region are not completely replaced by *Epeorus latifolium* in summer, may be explained in future by some of such correlations. In general, the greater the quantity of the discharge of the water in a river, the greater the downward extension of the condition of its upper region, whether it is the physical one or the chemical one, then its biological one as the fauna or the flora will be also pushed downwards. And the effectiveness of this downward push is increased according as the steepness of the mountain slope on which the river flows is increased. In the northern part of the Northern Japanese Alps where the high mountains rise up abruptly over the coastal plain, therefore the downward push of the life zone arrangement can be expected also from such an environmental condition. The same phenomenon may

be also expected in every wild torrent, the existence of which is attributable to some extent to the steepness of the mountain, but in the case of the life zone arrangement between these species under consideration, this explanation is evidently not complete since in the typical wild torrent where *Epeorus latifolium* seems to be absent owing to this downward push of the life zone arrangement, there is also absent *Epeorus napaesus* in its upper region as well as in its lower region.

In this paper I do not intend to ascribe the above-mentioned wildness of a river, in which *Epeorus latifolium* or its allied species is not found, to any one kind of environmental factors obtained from the analytical method. As already mentioned, I wish rather to recognize the difference of the life zone arrangement of the first order as the difference of the river type, for the presence or the absence of *Epeorus latifolium* is no more than the problem of the life zone arrangement of the first order. However, so far as the life zone arrangement of the first order is recognized as correlated to the arrangement of the velocity of the stream, it can be said that such a river type as proposed in this paper is also recognized as correlated to the arrangement of the velocity of the stream. Now, we will see what type of the river can be supposed in the absence of *Ecdyonurus tobiironis*, for instance, in the following life zone arrangement of the first order.

Ecd. tobiironis→*Ep. latifolium*→*Ep. curvatulus cumulus*→*Ep. aesculus*.

Taking a step further, what type of the river may we suppose in the absence of both of *Ecdyonurus tobiironis* and *Epeorus latifolium* in this same arrangement? We saw the former instance in the Tokusawa at Kamikôchi and the latter instance in the Azusagawa at Kamikôchi. Is such a change of the life zone arrangement not regarded as correlated to some change of the arrangement of the velocity of the stream, or in short, is it not regarded as correlated to the increase of the wildness of the river?

It is such a modification of the life zone arrangement that the exclusion begins from that of the inhabitants of the slowest part of the stream according as the wildness of the river increases, or it may be considered that such a modification indicates the degree of wildness of the river, which is, in fact, nothing but the degree of torrentialness of the river. As already seen, the inhabitants of the most rapid part of the river disappear first, when the river flows downwards into the plain. In this case also, the same idea may be applied but if so, it goes without saying that the degree of wildness is reduced and that of mildness increased. The river is not a closed system as recognized in the case of a lake. Every river may change its degree of wildness more or less in the course between its source and its estuary. To investigate the degrees of wildness of a river is by itself quite interesting and significant. But when a river is taken up in its entirety throughout its entire course it may be difficult to classify the river into different types according to the degrees of wildness. A river is, however, divisible into individually recognizable sections each of which may be designated as a river, stream or torrent. For practical purposes if we

succeed in discovering within the *Ecdyonurus-Epeorus* synusia suitable index organisms or indicators which will indicate by their presence the types of the sections of a river with reference to the degrees of wildness, then a direct consistent classification will be achieved. I wish to point out the significance of *Epeorus latifolium* group as such a type indicator. My field experiences indicate that there are two distinct types of the river, the stream or the torrent; one type is characterized by the presence of *Epeorus latifolium* and its allies; the other type is characterized by their absence; the latter is wilder and probably more oligotrophic than the former.

Although I have come to recognize two types of the river in reference to the *Ecdyonurus-Epeorus* synusia as it is the most characteristic synusia of mayfly nymphs in the mountain streams so common in our country, the *Ecdyonurus-Epeorus* synusia is not the only synusia of mayfly nymphs in the mountain stream nor even in the wild torrent of the mountain. As has been shown, such a swimming life form as *Ameletus montanus* is also widely distributed there in so far as there is found its available habitat. But such a classification as proposed seems to be justified to a certain extent even if it is applied to other synusiae, judging from the following facts. In the wild river, the wild stream or the wild torrent as typified by the absence of the *Epeorus latifolium* group, I have never found so far *Ecdyonurus yoshidae* or *Ecdyonurus tobiironis* which usually inhabits the slower side of the stream next to *Epeorus latifolium* and likewise such significant species as *Bleptus fasciatus*, *Epeorus ikanonis*, *Ecdyonurus kibunensis*, *Ecdyonurus tigris*, *Heptagenia kihada*, *Ameletus kyotoensis*, *Dipteromimus tipuliformis*, *Ephemerella nigra*, and probably also such burrowing life forms as *Ephemera japonica*, *Ephemera strigata* and *Potamanthodes kamonis* are not found in such habitats.

Recently, A. THIENEMANN* recognized three types of the river, namely, the high mountain river, the middle mountain river and the transitional river situated between the preceding two. My classification cannot be immediately compared with it owing to the difference in so many respects of the nature between Japan and Germany. However it seems to be common in both countries that the high mountain river is always the wild river, although it is worthy to notice that the wild river in Japan is not always the high mountain river. Some of the important species, which are not found in the wild torrent, are known as the headwater inhabitants of a river emerging from and flowing through the forest as the Kamogawa. In other words, there is no habitat in the headwater of the wild torrent fit to be occupied by them as in that of the less wild or much mild forest stream. In this respect such a stream or a river may be contrasted with the so-called middle mountain river of European investigators, which also emerges from the forest-covered land. However, it will be emphasized once more

* THIENEMANN, A., 1936, Alpine Chironomiden. Archiv f. Hydrobiol., Bd. 30, SS. 167-261.

before closing this section that the classification of a river into geographical regions seems to be rather satisfactorily accomplished in reference to the life zone arrangement of the second order, that is the faunal change even in the region of the same ecological structure, but the classification of the river types under consideration is different from the geographical classification of a river since the former is accomplished in this paper in reference to the life zone arrangement of the first order, or in short, the change of the ecological structure even in the same faunal region.

Summary of the present paper

1. In this paper the life zone is interpreted from the synecological point of view as an arrangement of specific synusia and is considered as a structure of synusia of a higher category, in which each specific synusia as the component adjusts itself to its succeeding ones in its spatial as well as its temporal distribution. Such generalizations are illustrated in the first place in reference to the synusia of the family ECDYONURIDAE, for it is considered as the most characteristic one among various synusia of mayfly nymphs found in Japanese torrents. Then two subsynusia of this family, the *Ecdyonurus-Epeorus* synusia and the *Cinygma-Rhithrogena* synusia, are again recognized by means of the life zone analysis.

2. There are recognizable two kinds of life zones within the same synusial extension of mayfly nymphs. The life zone arrangement of the first order is considered as correlated to such an environmental arrangement as represented by the velocity of the stream, and that of the second order to the arrangement as represented by the water temperature, although in each case any environmental determinism should be carefully rejected. In these two kinds of life zones that of the first order manifests a more fundamental character than that of the second order, because the velocity of the stream is more directly correlated with the substratum on which the animals under consideration live and on which their life forms are primarily dependent, than with the water temperature. In other words, as an environmental factor the velocity of the stream seems to be more selective or exclusive in regard to the distribution of the animal than the water temperature, since the former is more specifically related to the question of the occupancy of the habitat than the latter. Nevertheless, the distribution of the velocity of the stream is more universal than the distribution of the temperature, at least under the geographical conditions prevailing in our empire. Thus, the distribution of a species can be always seen from two quite different angles, and species belonging to the same life form group are woven into a synusia through these two kinds of life zone arrangements as warp and woof, a synusia being one of the real categories analysed out from the biotic community as a whole.

3. The life zone arrangement of the second order is further discussed under the following headings: the distribution within the given river system, the distribution in the Northern Japanese Alps and the distribution in the

high latitude compared with that in the high altitude. In this connection it is considered that the seasonal distribution, the vertical distribution and the horizontal distribution are not separable from each other, or each of them is recognized as a different phase of the same arrangement of life zones of the second order. However, that the vertical distribution in some river system in the Northern Japanese Alps is no more than a reproduction of that in the lower altitude as the district of Kyoto on a mere larger scale, and distribution in the high latitude is not always a mere projection of that in the high altitude, is admitted by reason of the difference in the characteristics of the habitat arrangement as a whole in each of these regions, even if the life zone segregation itself may be regarded in either case as correlated to the temperature arrangement.

4. There are recognizable two types of the river, the stream or the torrent; one type is characterized by the presence of the zone of *Epeorus latifolium* or its allies; the other type is characterized by their absence; the latter is wilder and probably more oligotrophic than the former. This classification is not the classification of a river into geographical regions which seems to be more satisfactorily accomplished in reference to the life zone arrangement of the second order, that is the faunal change even in the regions of the same ecological structure, but is a classification of a river into ecological types since it is accomplished in reference to the life zone arrangement of the first order, or in short, changes of the ecological structure in the synusia even in the same faunal region.
