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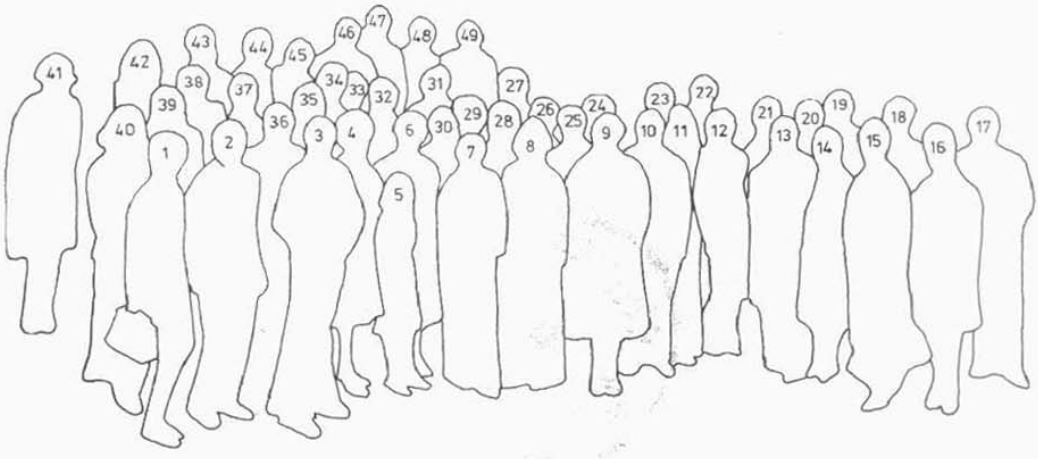

CONFERENCE PHOTOGRAPH

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PREFACE

According to the resolution of the first conference in Tallahassee in 1970 the next international meeting of Ephemeropterologists was to held four years later in the German Federal Republic. However, some time later, after consultations among a group of people, among others Professor PETERS, Dr. MÜLLER-LIEBENAU, and Dr. R. SOWA, Poland was suggested as the venue. Thanks to the approval of the authorities of the Polish Academy of Sciences in Warszawa, in particular to the support of the Secretary of Department II of this Academy, and to financial backing by the Laboratory of Water Biology of the Polish Academy of Sciences in Kraków (from the credits of the Ministry Problem PAN-21), as well as to the goodwill of the Kraków branch, the organization of the conference in Poland became possible. The host institution was the Laboratory of Water Biology in Kraków, whose directors Professor K. PASTERNAK and Professor S. WRÓBEL welcomed the idea of the conference and undertook the task of organizing it.

Preparations were started in autumn 1974, preliminary requests being sent to over 200 persons according to the list proposed by Dr. MÜLLER-LIEBENAU. The data of the conference was finally set as the end of August 1975. Over 60 participants from 19 European and overseas countries attended. The proceedings took place in the Assembly Hall of the Polish Academy of Sciences in Kraków, ul. Sławkowska 17; they began in the morning of Saturday, August 23rd.

The chairman of the Organizing Committee Professor S. WRÓBEL, opened the session and addressed the participants. In his introductory speech he stressed the importance of Carpathian rivers for the whole water economy of Poland. Owing to the montane character of these rivers and, in this connection, to the rapid processes of self-purification, they preserve the natural distribution of the communities of aquatic organisms. This was one of the reasons why Kraków was proposed as the venue of the conference. Professor WRÓBEL also conveyed the best wishes of Professor J. R. VALLENTYNE, the President of SIL, as it was within the framework of the activities of this organization that the conference had been planned.

In the name of the Kraków Branch of the Polish Academy of Sciences Professor M. MIĘSOWICZ welcomed the participants, wishing the successful discussions and a pleasant time in Kraków. He declared that the purpose of the Kraków Branch of the Polish Academy of Sciences was to support and co-ordinate investigations carried out in southern Poland. "We are deeply interested in research in natural sciences", he said, "particularly in biological investigations, because of their important role in the protection of the biosphere and human health. Aquatic animals are sensitive bioindicators and watching them may in due time give warning that efficient action in needed for the preservation of the beauty of rivers and of the whole environment".

The chairman of the morning session was Professor G. F. EDMUNDS, Jr. a member of the Honorary Committee. He paid tribute to the late Dr. Jay R. TRAVER in the following words:

"Since the First International Conference on *Ephemeroptera* in Tallahassee, Florida, the permanent committe has lost an esteemed member and dear friend. Dr. Jay R. TRAVER died in Northhampton, Massachusetts, U.S.A. on September 5, 1974 at the age of 80 years. The monument to Dr. TRAVER'S memory consists of her many excellent papers on the *Ephemeroptera*, principally of North and South America, but extending to the world fauna. Among her contributions was the 501 page Systematic

section of *The Biology of Mayflies* by NEEDHAM, TRAVER, and HSU. An account of her life and a photo have been published by the Fernald (Entomological) Club Yearbook at the University of Massachusetts and in Eatonia No. 20. A list of her publications also appears in Eatonia No. 20. Her graduate students, in entomology, parasitology and medical entomology, owe her a great debt of gratitude. She was the ideal professor for a developing graduate student. Whenever her students presented ideas that were unconventional or contrary to those held by JAY, her response was always a challenge to «prove it». Everyone was encouraged to think independently but to get solid evidence to test the validity of our concepts. I request that the members of the conference stand for a moment in silence in honour of our departed friend".

The morning session was closed by a comprehensive invited paper by Professor J. ILLIES on the ecology of running waters. The afternoon session consisted of 6 reports on the phylogenesis, zoogeography, and faunistics of Mayflies and a short film by Dr. C. R. FREMLING, with comment by Professor PETERS, on the biology of *Hexagenia bilineata* in the River Mississipi. On Sunday the participants went on an excursion in the region of the middle course of the River Dunajec and made a trip on rafts through the picturesque gorge of the river in the Pieniny Mts. On Monday and Tuesday all-day sessions were held, 29 further reports being presented on the systematics, ecology, and biology of Mayflies as well as on their morphology, functional anatomy, and various forms of association, among others of parasitism. The contribution by Dr. A. SAITA was illustrated by an interesting short film. On Tuesday evening the conference was brought to a close with a summing up speech by Professor PETERS.

On the next day the participants went on an excursion in the catchment area of the Raba, a montane river, and a subject of intense hydrobiological investigations. One of the aims of the excursion was to collect materials there. Thursday was a free day for sightseeing in the ancient city of Kraków and its vicinity and for unofficial meetings. These meetings, also held on other days of the symposium, allowed the participants to get to know each other, to establish scientific contacts, and to exchange experiences and opinions. The guests also visited the Laboratory of Water Biology of the Polish Academy of Sciences and the Laboratory of Hydrobiology of the Jagiellonian University. On Friday some of the participants left for West Germany, where among others they visited the hydrobiological centres in Schlitz and Plön. The Max Planck Limnological Institute was the host, while Dr. MÜLLER-LIEBENAU assisted by Dr. J. FITTKAU were the organizers.

The conference was prepared and supervised by an Executive Committee composed of: Dr. ANDRZEJ KOWNACKI, Dr. INGRID MÜLLER-LIEBENAU (vice-chairman), Docent KAZIMIERZ PASTERNAK, FELICJA SKOLIMOWSKA M. A. (technical secretary), Dr. RYSZARD SOWA (vice-chairman), Dr. BRONISŁAW SZCZĘSNY, Docent JAN WŁODEK, Professor STANISŁAW WRÓBEL (chairman), and JANUSZ WILTOWSKI M.A., Director of the Kraków Branch of the Polish Academy of Sciences, as the Organizing Secretary, also took an active part in the initial preparations. In the organization of the social programme in Kraków the Committee was supported by the staff of the Laboratory of Water Biology of the Polish Academy of Sciences and by Dr. MARTA KOWNACKA and MARIA SOLSKA, M. Sci.

The papers contained in the present volume constitute almost the whole scientific output of the conference. The reports have been omitted: the introductory invited paper by J. ILLIES and the report by M. KOWNACKA on the life cycle of *Baetis alpinus* — both at their author's request. The order of the reports accords with their theme and, with some exceptions, is the same as that of their presentation during the conference. From discussions only those fragments are published which were recorded immediately after the presentation of a given report and whose texts were authorized.

RYSZARD SOWA

KAZIMIERZ PASTERNAK

BIOGEOGRAPHY, FAUNISTIC

BIOGEOGRAPHICAL RELATIONSHIPS OF THE ORIENTAL AND ETHIOPIAN MAYFLIES

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Faunal interchanges of *Ephemeroptera* between the Ethiopian realm (Africa and Madagascar) and the Oriental realm generally have been assumed to be primarily through Asia Minor, largely from Oriental to Ethiopian and much less frequently from Ethiopian to Oriental. It appears, however, that several families of *Ephemeroptera* have had their primary evolutionary development on the Gondwanaland supercontinent. Subsequently these southern groups have dispersed to the temperate areas of the northern Hemisphere. In the western hemisphere, at least, when these are tropical groups invading temperate regions they have not become truly adapted to temperate conditions, but the eggs hatch only at "tropical" or "subtropical" temperatures of midsummer, emerging in late August or September. Probably the same invasion mode is common in the Old World.

Gondwanaland forms that have entered the Nearctic from South America are mostly, if not all, congeneric with their South American ancestors. This is consistent with the drift of South America so as to arrive near North America rather late in geological time, South America contacting and forming a land bridge to North America only 5.7 million years ago.

Africa has had various contacts and near contacts with Europe, Asia and the Oriental Region, at various times and with varying climates, therefore, the invasion and exchange pattern is complex. Thus we see various levels of evolutionary divergence between the Ethiopian realm forms and their Holarctic or Oriental relatives. An important transport of *Ephemeroptera* of Gondwanaland origin, especially to the Oriental realm was the detachment of Madagascar and India from Africa at least 100 million years ago and the later splitting off of the Indian plate and its subsequent collision with Asia about 45 million years ago. The leading edge of the Indian plate probably started to form mountains early in its movement. Thus the Indian plate could readily have served to deliver a variety of plants and animals, including *Ephemeroptera*, to Asia where subsequently they could have spread to Southeast Asia and Asia Minor (and possibly to Europe or North Africa). With subsequent changes in climate much of the area would have become uninhabitable for these austral groups. The best habitats for such groups would now be in Ceylon and the highlands of southwestern India and in Southeast Asia, while isolated populations might occur in Asia Minor or North Africa and some might have spread to Europe. There seems to be no biological reason to assume that Borneo or any other part of Southeast Asia was part of Gondwanaland.

The confidence that one can apply in reconstructing the history of groups spreading to Asia from Gondwanaland is highly variable and is greatly handicapped by an inadequate knowledge of the real total distribution and details of relationships of the mayflies involved. As yet the mayflies do not provide phylogenetic sequences of Africa — Madagascar — India distribution to dete rmine whether

or not India and Madagascar remained together after separating from Africa. However, the evidence suggests that this was the case.

The genus *Prosopistoma* (the sole representative of the family *Prosopistomatidae*) appears to have originally had a Gondwanaland distribution in Africa and Madagascar and India. At present there are several species in Africa, one in Madagascar, and another on Comores Archipelago, one in Europe and a series of closely related species stretching from Ceylon east to the Philippine Islands and New Guinea. A careful analysis of the evolutionary pattern of the species relationships is essential to clarify the details, but it appears that India carried the genus *Prosopistoma* to Asia.

It is probable that the family *Oligoneuriidae* evolved in Gondwanaland. *Lachlania* and *Homoeoneuria* are geologically recent immigrants into North America. *Oligoneuriella* apparently entered Eurasia from Africa (probably not via India). The European *Oligoneurisca* is a sister-group of *Homoeoneuria* (distributed from Brazil to central North America). One must presume that *Oligoneurisca* is either undiscovered or extinct in Africa to maintain the hypothesis that *Oligoneurisca* came from Gondwanaland. If the *Oligoneuriidae* evolved primarily in Gondwanaland, then how can one explain the distribution of *Chromarcys* in China and Sumatra? *Chromarcys* has the most generalized adult characters of the *Oligoneuriidae* and in the larvae gill one is in the primitive dorsal position. *Elassoneuria* is also primitive in that the behaviour and general appearance of the larvae are similar to those of *Isonychia*. *Chromarcys* occurs also in Ceylon and Thailand. I hypothesize that the *Oligoneuriidae* occupied primarily tropical South America and Africa and Madagascar and India with the more primitive genera on the eastern edge. Thus *Chromarcys* probably was carried to the Asian continent as suggested by its present occurrence in Ceylon.

The *Tricorythidae* also appear to have evolved primarily in Gondwanaland. All of the subfamilies occur in Africa. The genus *Tricorythus* (sensu lato, including *Neurocaenis*) is found in Madagascar, Ceylon, and Southeast Asia. The distribution pattern is consistent with the transport of the genus by the drift of India to Asia.

The *Euthyplociidae* also seems to have had their major evolution in Gondwanaland with genera in South America (now extending to Central America and Mexico), Africa and Madagascar. The only genus outside the Gondwanaland remnants is *Polyplocia* known from Burma to Borneo. This genus was probably transported to Asia via India, but it is not known to occur now in Ceylon or India. The family relationships have not been studied in detail.

The distribution of the *Palingeniidae* is rather unusual in that the nearest ancestor-like relative of the *Palingeniidae*, *Pentagenia*, is in North America. *Cheirogenesia*, whose larvae I collected in Madagascar appears to be one of the most primitive forms presently assigned to the family. The larvae of *Anagenesia robusta* with similar development of the mandibles occurs in India (GRAVELY, 1920). It is not possible to suggest the distributional history of the *Palingeniidae* from the present knowledge, *Cheirogenesia* and *Anagenesia* are closely related.

From the known distribution of the *Heptageniidae*, it seems most probable that the family evolved in Laurentia and dispersed in the geologically more recent time to Africa. However, Madagascar, which has been separated from Africa for a long period of time, has two genera of *Heptageniidae*. *Thalerosphyrus* is widespread and relatively abundant. This genus could have spread via India to southeast Asia and Asia Minor. It is not reported from Africa. *Compsoneuriella* is found widespread in Africa, in some areas of Madagascar, in Ceylon and Southeast Asia. The geographic history of *Afronurus*, *Thalerosphyrus* and *Compsoneuriella* is very uncertain but it is possible that *Thalerosphyrus* and *Compsoneuriella* owe their presence in Asia to transport by the drift of India.

The *Leptophlebiidae* are in great need of study in the area. In India and Ceylon the genus *Kimminsula* and undescribed related genera are reported (PETERS and EDMUNDS, 1970). In Madagascar there are several genera closely related to the *Kimminsula* complex and unknown elsewhere. The genus *Choroterpides* of India or a very close relative is found also in Madagascar. *Choroterpes* and *Thraulus* are common to Africa, Madagascar, India and Asia but their presence on some islands near Madagascar is suggestive that drifting India may have played a significant role. Species studies here will be critical to proper evaluation.

It is my opinion that the *Baetidae* had their principal evolutionary development in Gondwanaland

with South America as the prime center of evolution, and Africa as a secondary evolutionary center. The fauna of *Baetidae* in Africa, Madagascar, India and Southeast Asia is diverse. There are suggestions from baetid specimens that I have examined, but not carefully studied, of transport from Gondwanaland to Asia via drifting India. The baetids, however are such reduced and simplified forms as adults, and frequently so conservative as large that any evaluation of their biogeographic history in the areas being considered is premature.

Obviously a number of groups of *Ephemeroptera* have moved from the Oriental region to the Ethiopian realm. Almost certainly the *Caenidae* have spread from the Oriental realm to much of the world. Some *Leptophlebiidae*, many *Baetidae*, certain *Ephemeridae* (e.g., *Ephemera*, subgenus *Ephemera* and subgenus *Dicrephemera*), and *Ephoron* have probably dispersed from the Oriental to the Ethiopian.

The main purpose of the present paper is to point out the significance of drifting India to the Oriental fauna and the subsequent spread to other parts of Eurasia. The high concentration of eastern Gondwanian elements surviving in the Oriental realm almost certainly results from the fact that there is a large area of suitable climate in the Oriental region (while many other areas are unsuitable either because of the dry seasons or of cool periods). It is also recognized that the Oriental region serves as a refugium for the subtropical Laurasian fauna and flora that was more widespread during most of the Tertiary period.

A meaningful analysis of the biogeography of Oriental-Ethiopian interchanges at the present time is severely handicapped by gross inadequacies in knowledge of present distribution. In fact, the current, inadequate analysis, is based in large part on unpublished data from my collections in Madagascar, collections by W. L. and J. G. PETERS in India and from largely unstudied collections from Ceylon by a cooperative project with the U. S. Smithsonian Institution. Ecological and life history studies have also been neglected in the region, but are essential to meaningful biogeography.

SUMMARY

Biogeographical relationships of the Oriental and Ethiopian mayflies

Faunal interchanges between the Ethiopian Realm (Africa and Madagascar) and the Oriental Realm have generally been assumed to have been via the Middle East. The drift of the Indian plate from Madagascar must have carried with it a substantial fauna of *Ephemeroptera*. Such faunal elements would have subsequently spread from the Indian plate area, and Southeast Asia is the area where this fauna most likely survived. Among the groups that are most likely to have entered the Oriental Realm by this means is *Prosopistoma*, a palingeniid related to *Cheirogenesia*, *Povilla*, *Tricorythus* (including *Neurocaenis*), *Chromarcys*, probably *Compsoneuriella* (=*Notonurus*), *Thalerosphyrus*, and several genera of *Leptophlebiidae*.

Groups such as the *Caenidae*, *Ephemerellidae* (*Teloganodinae*), most *Baetidae*, some *Leptophlebiidae* and *Ephemera* (*Dicrephemera*) apparently used the route through the Middle East. The most convincing examples of dispersal through the drift of India are the cases where lineages are found in Madagascar, Ceylon and/or South India and Southeast Asia, but not Africa. Lineages in Africa and the Oriental Realm that are absent in Madagascar probably dispersed through the Middle East. Incomplete knowledge of the mayflies of the area makes the interpretation of a complicated problem difficult.

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СРАВНИТЕЛЬНЫЙ ОБЗОР ФАУНЫ ПОДЕНОК (*Ephemeroptera*) СИБИРИ И СОВЕТСКОГО ДАЛЬНЕГО ВОСТОКА

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Специальные довольно полные исследования по фауне поденок Восточной Сибири проведены к настоящему времени только в притоках среднего и верхнего течения р. Енисея (многолетние сборы Ю. И. Запекиной-Дулькейт). Русло же Енисея едва затронуто исследованиями (Грезе, 1957).

В бассейнах Ангары и Витима проводились лишь рекогносцировочные обследования и имеющиеся сведения об этой очень важной группе гидробионтов ограничиваются пока работами И. К. Сукацкене (1962), О. Я. Байковой (1965, по сборам А. А. Томилова) и Р. А. Голышкиной (1967); из водоемов Алтая определены небольшие материалы по поденкам Алтайского заповедника (сборы Ю. И. Запекиной-Дулькейт).

Среди водных насекомых в ряде притоков Енисея и Ангары поденки оказываются доминирующей по численности и биомассе группой и служат основным объектом питания многих рыб.

Изучение поденок бассейнов Енисея, Ангары и Витима, включая и литературные данные, позволяет дать более полный обзор фауны Восточной Сибири. В настоящее время для этих водоемов известно 74 вида поденок. В притоках Енисея и Ангары сформировалась оригинальная фауна поденок, состоящая из общесибирских, восточных и западных видов.

Сопоставление результатов этих исследований показывает, что видовой состав во всех водоемах является почти сходным. Однако в бассейне р. Енисея наблюдается большее видовое разнообразие сем. *Heptageniidae* по сравнению с таковым в бассейне реки Ангары (табл. I). Так, в водоемах Приангарья пока не обнаружены такие восточно-азиатские виды как *Cinygma vernalis* Iman., *Heptagenia tena* sp.n. (=*Heptagenia "nb"* Iman.), *Cinygmula grandifolia* Tshern. и *Rhithrogena baikovae* Sowa, или европейские и сибирские — *Heptagenia fuscogrisea* Retz., *Ecdyonurus peterseni* Tshern. и *Cinygma pellucida* Brodsk.

В целом бассейн р. Енисея отличается наибольшим разнообразием видов, чем бассейн р. Ангары и Витима. Частично это можно объяснить большей его изученностью.

Фауна поденок Восточной Сибири носит резко выраженный восточно-азиатский характер (Байкова, 1972). Из общего числа видов (74), указанных для Восточной Сибири, 60 видов или 81 процент отмечаются также для бассейна Амура, рек Приморья, Камчатки и Сахалина. Из них 18 видов распространены в водоемах северного Китая и Японии. Из остальных 14 видов — 4 относятся к числу голарктических форм, 5 видов широко распространены в Палеарктической области и 5 видов свойственны преимущественно северной части Палеарктики.

В ангарской и енисейской фаунах встречаются виды, распространенные в европейской части СССР (26 видов) и на Алтае (15 видов).

Для дальнейшего изучения фауны Восточной Сибири целесообразно проводить детальное качественное и количественное обследование русловой части рр. Енисея, Ангары и Витима с тем, чтобы выявить все своеобразие фауны поденок этих интересных водоемов.

Первые наиболее полные исследования гидрофауны русла Амура и устьев некоторых его притоков были проведены в 1945—1949 гг. Амурской ихтиологической экспедицией. Собранные материалы позволили О. А. Черновой (1952) составить фаунистическую сводку по поденкам, в которой она приводит для бассейна Амура 65 видов и форм.

Со времени исследования водоемов Приамурья прошло более 20 лет. За этот период накопились обширные материалы по гидрофауне горных и предгорных притоков бассейна Амура и рек Приморья, а также сборы поденок, полученные от различных лиц и организаций из водоемов Приморья, Камчатки, Сахалина и Кунашира (Курильские острова).

В результате изучения собранного материала и литературных данных в фауне поденок бассейна Амура и прилежащих вод в настоящее время известно 134 вида. Среди них массовых видов — 60, редких или единично встречающихся — 74. Из общего числа поденок впервые отмечено 57 видов, из которых 16 — новых для науки. Кроме того, у 25 видов установлена личиночная или имагинальная стадии и дано их описание; выявлена видовая принадлежность и идентичность 8-ми видов (Байкова, 1965, 1972)

1. *Heptagenia flava* Rost. (=*H. arsenjevi* Tshern., 1952).
2. *Rhithrogena lepnevae* Brodsk. (=*R. unicolor* Tshern., 1952).
3. *Paraleptophlebia chocolata* Iman. (=*P. cothurnata* Tshern. 1952).
4. *Ephemerella lepnevae* Brodsk. (=*Ephemerella "nM"* Iman., 1940; *E. longipes* Tshern., 1952).
5. *Ephemerella* (*Ephemerella*) *aurivillii* Bengtss. (= *E. taeniata* Tshern., 1952).
6. *Ephemerella* (*Ephemerella*) *ignita* Poda (= *E. sibirica* Tshern. 1952).
7. *Ephemerella* (*Cincticostella*) *tshernovae* Bajk. (= *Ephemerella* (*Cincticostella*) *imanishii* Allen, 1971); новый синоним.
8. *Ephemerella* (*Cincticostella*) *orientalis* Tshern. (= *Ephemerella "nay"* Iman., 1940; *E. levanidovae* Tshern., 1952; *E.* (*Cincticostella*) *delicata* Allen, 1971); новые синонимы.

Поденки в бассейнах Енисея, Ангары, Витима и Амура распространены всюду — от временных луж до горных потоков с каскадами и порогами, заселяя самые разнообразные экологические ниши. Так, например, опытные работы, проведенные нами на оз. Б. Шарга (нижнее течение Амура), показали, что личинки *Siphlonurus chankae* Tshern. некоторое время могут жить и в осушенной зоне (от 3-х до 6 дней) под влажными, отмершими корнями растительности (старый кочкарник, принесенный течением). При высыхании луж личинки последней стадии вылетают, более молодые — гибнут, но отсаженные в аквариум полностью заканчивали свой метаморфоз.

Активное расселение личинок поденок совершается на всех этапах их жизни. Они мигрируют от берегов к местам обитания и обратно к прибрежьям рек для линьки в субимаго, а также при неблагоприятном газовом режиме или при отсутствии подходящего субстрата. Почти все виды поденок являются частью сносимого бентоса Амура и его горных притоков.

По времени лета различается 5 групп поденок:

I- весенняя. Виды, вылетающие в первых числах мая, середине мая, или в последней его декаде и исчезающие в конце июля — начале августа, редко в середине августа.

II- весенне-летняя. Виды, вылетающие в последних числах мая и исчезающие в конце третьей декады августа.

III- переходная. Эта группа очень близка и предыдущей, но ее виды летают дольше и обычны до середины сентября.

IV- летняя. Виды, вылетающие и исчезающие летом: июнь — начало сентября. Летний период этой довольно обширной группы — 2—3 месяца.

V- летне-осенняя. Виды, вылетающие летом и исчезающие осенью — в конце третьей декады сентября или в первой декаде октября, редко — в середине октября; имеют наибольший период лета — 3—4,5 месяца. Сюда относится большинство видов.