

A C T A Z O O L O G I C A
C R A C O V I E N S I A

Tom XIX

Kraków, 31. I. 1974

Nr 1

Józef RAZOWSKI

Phylogeny and Classification of *Lepidoptera*

[Pp. 1—20 with 1 text-fig.]

Filogeneza i klasyfikacja motyli

Филогенез и классификация бабочек (*Lepidoptera*)

Abstract. A survey of the most important achievements in the field of the systematics and phylogeny of the *Lepidoptera* published hitherto and the author's own interpretation of the evolutionary system of this group of insects are given.

INTRODUCTION

No sooner had LINNAEUS published his *Systema Naturae* (1758), than the work at the improvement of the system of *Lepidoptera* was undertaken. Its historical outline is given, among other writers, by KIRIAKOFF (1960). Far more studies were given to the system of butterflies and moths than to their phylogeny. The authors of those papers based themselves chiefly on the nominalistic and typological principles, and the results achieved by them have recently been criticized severely by the followers of two new trends, that is, those represented by numerical taxonomists (pheneticists) and cladists. The members of the first group were not directly concerned with butterflies and moths, but their opinions on the studies of typologists are of some importance to lepidopterology (RAZOWSKI, 1973). On the other hand, the cladists, thanks to numerous studies published by KIRIAKOFF (mentioned below) and HENNIG,

contributed greatly to this branch of science, even though we cannot agree with a number of their statements. MAYR (1965, 1965a), among other authors, submitted both these trends to a critical examination. The third trend, represented by the school of evolutionary taxonomists, drawing conclusions from all the previous theories, does not reject valuable achievements of any of them (MAYR, 1965; GISIN, 1969; RAZOWSKI, 1973, and others). The interpretation of the evolution of butterflies and moths and their division into systematic categories above families given in the present paper are based, as regards theory, on the achievements of this last group. The author however owes an explanation. In the criticism of cladists carried out by MAYR in the above-mentioned studies and in his discussion of the advantages of evolutionary taxonomy there are some understatements. Consistent interpretation of the strict determination of the branching points in evolutionary lines is in practice impossible, since different groups have come down to us as fossils in different states of preservation and numbers. Butterflies and moths constitute an example of the poor preservation of fossil forms and, in addition, their extant fossils are nearly exclusively the remains of wings, sometimes even too scanty to allow a very general diagnosis. The essential characters cannot even, at least with the present methods of investigation, be utilized in the case of lepidopterans closed in amber. The lack of exact data concerning the points of ramification of lines makes it impossible to determine the rate of evolution of individual groups. Even in the case of relatively well-known animals the accurate determination of these parameters is almost impossible. The gaps in the data concern very large time intervals, often exceeding the periods needed for new lines to arise. Thus, there is no certainty that no links are missing in these groups and we do not know whether the reconstructed lines start at the proper points and also whether the rate of evolution measured on the basis of these data is not, for instance, overestimated. The objection that the cladists assume mean values as the evolution rate and so it is false is justified. None the less, it must be stated that theoretically in MAYR's interpretation the same error cannot be avoided, only that here the mean evolution rate concerns shorter periods. It is not however known if the rate of evolution was not distinctly differentiated in these very periods. It would follow that it is not so much the exact determination of the branching points of the lines and the evolution rate as taking them into consideration as far as possible that is necessary for the presentation of the history of a group studied. As regards the *Lepidoptera*, the reconstruction of phylogeny in MAYR's sense of the word is impossible at the present time. There remains therefore a general treatment of the problem. The lack of fossil remains in the explorations made so far does not augur a dramatic change for better in the future. Thus we have no choice but to take up the indirect way of determining the periods in which individual lines may have branched, the study of similarities and differences between modern forms and the framing of hypotheses, and the evaluation of known characters as well as search for new ones.

SYSTEMATIC POSITION OF THE *LEPIDOPTERA*

HANDLIRSCH (1908) divided the *Pterygota* into several subclasses, one of which was the *Panorpoidea* and embraced 5 orders (*Panorpatae*, *Phryganoidea*, *Lepidoptera*, *Diptera* and *Suctoria*). He traced the ancestry of *Panorpatae* through the *Megasecoptera* back to the *Palaeodicyptera*. According to him, the *Trichoptera*, *Diptera* (together with the *Suctoria*, closely related to them), and *Lepidoptera* evolved directly from the primitive *Panorpatae*. KRAUSE and WOLFF (1919) divided this group into the *Lepidopteroidea* (with the *Trichoptera* and *Lepidoptera*) and *Dipteroidea*, considering the *Megasecopteoidea* (embracing the *Megasecoptera* and *Panorpata*) to be remote from the *Lepidopteroidea*. TILLYARD (1919) included the *Panorpata*, *Trichoptera* and *Lepidoptera* in his "Panorpooid Complex", deriving the *Trichoptera* from the *Paramecoptera* and the *Lepidoptera* from the *Trichoptera*. In TILLYARD'S opinion, the *Paramecoptera* and *Panorpata* come from a common hypothetical ancestor. IMMS (1934) thinks that the *Diptera* and *Aphaniptera* are not related directly to the *Mecoptera*, *Trichoptera* and *Lepidoptera*. KIRIAKOFF (1948) places the *Mecoptera* and the new order *Amphiesmenoptera* composed of three suborders, the *Zeugloptera*, *Trichoptera* and *Lepidoptera*, in the superorder *Panorpaemorphia* (described in 1946), and HENNIG (1969) brings the *Mecoptera* close to the *Diptera* and the *Trichoptera* to the *Lepidoptera*, placing them, respectively, in two sisterly groups, the *Antliophora* and above-mentioned *Amphiesmenoptera*, however without defining the rank of these categories.

The taxon *Amphiesmenoptera*, introduced by KIRIAKOFF and accepted by HENNIG (1953 and 1969), initially included (KIRIAKOFF, 1948) the three suborders named above. KIRIAKOFF (1948) and HINTON (1958) found the differences between the *Micropterygoidea* (*Zeugloptera*) and the rest of *Lepidoptera* to be sufficient for their separation as a taxon of the same rank as the *Trichoptera* and *Lepidoptera* (the remaining groups). This view is not new, since as early as 1917 CHAPMAN recognized the *Micropterygidae* as a separate order, holding an intermediate position between the *Trichoptera* and *Lepidoptera* (he is the one who introduced the name *Zeugloptera*), and COMSTOCK (1918) included them as a suborder in the *Trichoptera*. This opinion was refuted by TILLYARD (1919), who listed a number of characters differing the *Micropterygidae* from the *Trichoptera*. After HENNIG (1953) had published his work in which he included the *Zeugloptera* back in the *Lepidoptera*, KIRIAKOFF (1955) changed his previous opinion and acknowledged them to be a suborder of the *Lepidoptera*. Finally, HENNIG (1969) placed the *Trichoptera* and *Lepidoptera* in the above-mentioned group *Amphiesmenoptera* without determining their rank. The *Amphiesmenoptera* were initially a hypothetical group (KIRIAKOFF, 1948, 1955; HENNIG, 1953), and it was not until 1969 that HENNIG numbered a few species, hitherto regarded as members of the *Trichoptera*, among them. These species are *Cladochorista belmontensis* TILLYARD from the Upper Permian of Australia, *Microptysmodes uralicus* MARTYNOVA from the Upper Permian

of the Ural Mts. and *M. sibiricum* MARTYNOVA from the Lower Permian of the Kuznetsk Basin. HENNIG assumes that they were already evolved in the Upper Permian and regards them as a monophyletic group (in his own interpretation from 1953). As the group of issue for the *Trichoptera* and *Lepidoptera*, the *Amphiesmenoptera* combine the characters of both these orders. The most important of these characters are, according to HENNIG, the lack of the spermatoc pump and the formation of the spermatophore, and also the fact that from among all insects only the female *Trichoptera* and *Lepidoptera* are heterogamous, which has been confirmed by WHITE (1957). So far as the *Amphiesmenoptera* are concerned, these characters are naturally hypothetical. The structure and venation of wings, practically the only characters preserved of fossil members of this group, are consequently very important. The loop-shaped structure of the anal veins in the forewing is the most essential character of the *Trichoptera* and *Lepidoptera*. The crossveins constitute the original connections between the anal veins, which may be atrophied in the peripheral region of the wing (they may end without reaching the margins of the wing). Analysing the position of this loop in the wing, MARTYNOVA (1957) states that the through-like area lying behind it is covered with hairs in the group under discussion. The hairs of the wings, present also in the *Trichoptera* and, in a vestigial form (microtrichia), in the lower groups of *Lepidoptera*, indicates the adaptation of the imagines for a temporary stay in water, since then a supply of air is retained on the hairs. It would follow that the *Amphiesmenoptera* had similar modes of life to those of contemporary *Trichoptera*, and their larvae, having an open respiratory system (HENNIG, 1968), did not need to be associated exclusively with water environment (the larvae of contemporary *Xiphocentronidae* and some *Limnophilidae* live in mosses). Naturally, it is not certain if the species included here by HENNIG actually formed the ancestral group of *Trichoptera* and *Lepidoptera*. It may well have been only a side line of evolution of the primitive *Trichoptera* or perhaps the above-mentioned species should be counted among the caddis-flies, for it is impossible to determine any major differences within this group on the basis of fossil remains (e. g., the *Lepidoptera* can be distinguished from the *Trichoptera* only because they lack the vein m_4 , fused with the vein cu_1 in them). For the same reasons, however, HENNIG'S hypothesis cannot be rejected either. MARTYNOVA (1962) includes the afore-named species among *Trichoptera* and places them in the family *Microptysmatidae* of the suborder *Permotrichoptera*, giving the following characteristics: "veins rs and m with 6 branches each, terminal portions of cuP and $A1$ close to each other and ending half-way along wing, in its hind part". At any rate, we should acknowledge the priority of the *Permotrichoptera* and interpret them as ancestral to *Lepidoptera* and caddis-flies sensu HENNIG, at least until more detailed materials have been acquired. On the other hand, it seems only right that the group from which the *Trichoptera* and *Lepidoptera* descend should be characterized by the traits discussed above, listed by HENNIG (1969), irrespective of the fact whether or not the *Permotrichoptera* (= *Amphiesmenoptera*) are this very group actually.

CHARACTERISTICS OF *TRICHOPTERA* AND *LEPIDOPTERA*

The fossil and contemporary *Trichoptera* and *Lepidoptera* resemble each other very much, so their recognition as suborders (KIRIAKOFF, 1948, 1955; HENNIG, 1953) may be justified. Personally, I continue to regard them as orders, if not for other reasons, in order to be able to handle lower categories within them more easily.

Unlike the *Lepidoptera*, a vast majority of the trichopterous larvae lead aquatic lives. The larvae of butterflies and moths are terrestrial and only in very few cases secondarily associated with water environment, to which they are more or less well-adapted. The tracheal system of *Lepidoptera* is open, the postthoracic trachea is regressive in all of them but the *Micropterygidae* (after HINTON, 1958). In addition, their larvae are not so clearly differentiated into campodeoid and eruciform types as caddis-worms are and only the larvae of *Micropterygidae* show a number of characters of their own. However, lack of detailed data does not allow a close analysis of these lepidopterous larvae. According to a few data (MARTYNOVA, 1957; COMMON, 1970) that we have, the larvae of *Micropterygidae* live in damp places in moss. Their great humidity requirements refer them to the aquatic life of the group of issue and to the transition to the higher *Lepidoptera*, whose larvae show markedly smaller water requirements and need not stay in its vicinity. Nevertheless, similar requirements may be observed even in a number of the remaining lepidopterous families, especially at early larval stages, namely, those feeding in mines, in environment rich in water (yet here a tendency is seen for the larva to remove its excess by the appropriate disposition of frass and, as a result, its quicker evaporation through the epidermis of the leaf). Feeding in other plant tissues (e. g., *Hepialidae* in roots) is also a primitive character in many cases.

As regards pupae, the main difference between the two groups is the occurrence of two tracheal trunks in the wings of *Trichoptera*, whereas in all *Lepidoptera* there are always four such trunks, well-developed even in the *Micropterygidae*. Activity at the pupal stage and morphological adaptations connected with it are more conspicuous and common in the *Trichoptera* (e. g., swimming before emergence) than in *Lepidoptera*.

Unlike the *Trichoptera* the lepidopterous imagines have always two lateral ocelli and they completely lack the middle one. The *Trichoptera* may have three ocelli and only in some *Hydroptilidae* there are exclusively two lateral ones. The mouth-parts of the members of both orders are derived from the biting type, but in the *Trichoptera* they are a specialized type, different in character (the mandibula is often preserved in a vestigial state, the galea and lacina are reduced, the fusion of the lateral lobes of the labium forms the haustellum, and the labrum participates together with the hypopharynx in the formation of the suction canal. In primitive *Lepidoptera* there occur typical biting mouth-parts, which in the *Eriocranioidae* are already partly receded, owing to the loss of functionality as regards the mandibulae. These are comple-

tely reduced in all higher *Lepidoptera* and partly in primitive ones (*Hepialoidea*), and the haustellum is formed of the galea. Primitive *Lepidoptera* (*Micropterygoidea*) feed on flower pollen, the higher ones, on sap and, chiefly, nectar. There are no detailed data concerning the food of *Trichoptera*. They may suck sap and nectar, but the number of observations of their visiting flowers is extremely small.

The thorax of *Lepidoptera* is much better specialized than that of the *Trichoptera*, in which all the annuli are comparatively well developed, although the prothorax is strongly reduced. Their mesonotum bears a more or less reduced longitudinal suture, which in the *Lepidoptera* is preserved only in the *Hepialoidea*. The pronotum of *Micropterygoidea*, *Eriocranioidea* and *Hepialoidea* is stout and broad, that of all the other members being small and narrow. The patagia of these two groups of *Lepidoptera* also show corresponding differences.

The wings of the members of both orders are membraneous, though in the *Trichoptera* the fore-wings are more hardened than the hind ones. The wing venation in the *Lepidoptera* is simplified in comparison with that of *Trichoptera*, the *Homoneura* being the only exception. In addition, in the *Lepidoptera* the thyridium is missing and the vein m_4 fused with cu_2 in the fore-wing. The wings of *Lepidoptera* are covered with scales to a greater extent and the scales are better specialized in them, whereas in the *Trichoptera* the scales, if present at all, are primitive, without well-developed ribs. The members of a number of primitive *Lepidoptera* have microtrichia beside scales. The microtrichia are well developed in the *Homoneura* and in several primitive families of the *Heteroneura* and occupy considerable areas of their wings, whereas in the remaining families their occurrence is limited to small vestigial regions. The microtrichia seem to be a remnant of hairs, which occur commonly in the *Trichoptera*. Hairs on the wings are typical of the insects which, as imagines, come temporarily into contact with water. The butterflies and moths have lost them since they left water to live on land (MARTYNOVA, 1967), but the formation of scales has not been explained up to now. Their development seems to have been an adaptation to flight and they constitute a streamline cover of the membranes. Later, they also took up the cryptic role (location of pigment) and perhaps that of a thermal cover (heating in sunshine, emitting of heat, insulation). The additional character that differs the two orders is, according to Ross (1967) the disappearance of the cerci in female butterflies and moths and the reduction of the lateral limitations of the praescutum. There are remarkable differences in the structure of their genital apparatus.

The above-mentioned characters are more or less visibly reflected in the biology of the two orders and they indirectly indicate the mode in which the two lines have differentiated. The turning point seems to have been the passage from the aquatic environment to the terrestrial one, the development of the competent wing apparatus and mouth-parts which allowed the utilization of the rich resources of liquid food and made these insects dependent upon flowering plants (according to TAKHTADZHAN, 1961, angiosperms were originally

insect-pollinated plants). Imagines of both groups are marked by evening and night activity. Adaptations to the diurnal ways of life have, however, developed in both of them. Only few *Trichoptera* (e. g., some *Leptoceridae*) fly by day, whereas numerous species of *Lepidoptera* (*Papilionoidea*, *Hesperioidea*) are adapted exclusively to the diurnal ways of life and their eyes lack the tapetum, which proves that their passage to diurnal activity occurred a very long time ago. Numerous *Sphingoidea*, *Geometroidea* and *Noctuoidea*, with the nocturnal type of eyes, have also, secondarily, diurnal activity. Some further converging adaptations have developed in both groups. An interesting fact is, e. g., the reduction of the mouth-parts. Most of the *Trichoptera* (RIEK, 1970) are able to drink water, which enables them to live without taking food in the imaginal stage. On the other hand, in the members of quite a number of groups of higher *Lepidoptera* and in the *Hepialoidea* belonging to the lower *Lepidoptera* the mouth-parts are completely reduced, non-functional, and the insects avail themselves of the energy accumulated during their larval stages.

PALAEONTOLOGICAL DATA

The fossil material is very scanty, especially that of the *Lepidoptera*. The remains preserved consist mainly of wings, whose characters are often insufficient for the determination of the order even. The *Trichoptera* first appear in the Jurassic, when they were greatly differentiated. The *Necrotaulidae*, some forms of which were later included in the *Rhyacophilidae* and other contemporary families (ULMER, 1907), come from the Lias. Thus, it was already a well-developed group then and MARTYNOVA (1959) affirms that the Tertiary families occurred as early as the Mesozoic. The earlier data seem to be unreliable. It is worth noting that MARTYNOVA (1962) numbered all the fossil remains of *Trichoptera* from the Trias and Jurassic and the *Cladochoristidae* from the Upper Permian and Trias of Australia in the *Annulipalpia*. HENNIG (1969), however, thinks that their inclusion in the *Annulipalpia* results only from the use of symplesiomorphic characters in the analysis. There are still fewer fossil data considering the *Lepidoptera*. They are lacking completely in the Mesozoic and certain forms regarded previously as lepidopterous appeared to be other insects (*Palaeontinidae* from the Jurassic belong in the *Homoptera*). The position of *Geisfeldiella benkertii* KUHN (1951), described on the basis of one wing from the Lias (from Bamberg in northern Frankonia) remains unexplained and so it cannot be taken into account. TINDALE (1945) described remains (wings, probably a fore and a hind, supposedly belonging to one and the same specimen) from Australia (Mt. Crosby, Queensland) as *Eoses triassica*, which he included in the *Lepidoptera* and for which he erected a separate suborder, *Eoneura*. KIRIAKOFF (1948) doubts its membership in the *Lepidoptera* and BOURGOGNE (1951) considers it to be a pathological specimen from the family *Hepialidae*. HENNIG (1969) was the first to give a keen analysis of this

problem. The lack of the anal area does not allow the unquestionable inclusion of *Eoses triassica* TINDALE in the *Lepidoptera*, the more so since a number of similarities in the arrangement of the other veins (fusion of m_4 and cu_1A) occur also in numerous *Mecoptera* (e. g., in *Choriatidae*, cf. RIEK, 1970), in which it presumably belongs. Some similarities to the *Diptera* may also lead to an error, seeing that only one wing has been found.

The most ancient *Lepidoptera* preserved come from the Tertiary. The *Micropterygidae* are known from the Oligocene (Baltic amber) and Miocene (amber from Burma), and three contemporary genera and an extinct one of the *Eriocraniidae* from the Oligocene. Members of the *Incurvariidae*, *Adelidae*, *Tineidae*, *Tortricidae*, *Hyponomeutidae*, *Oecophoridae*, *Lyonetidae*, *Gelechiidae*, *Pyrallidae* and *Cossidae* are known from the Miocene of the Caucasus Mts. and the *Syntomidae* from the Tertiary of Kazakhstan. However, in considering the relationships among the *Lepidoptera*, and the more so between them and the caddisflies, these data proved insignificant.

Attempts were made to draw some conclusions concerning the time of occurrence of the *Lepidoptera* in an indirect manner. JEANNEL (1949) infers from their distribution that they inhabited Gondwana from the beginning of the Mesozoic and that the line *Frenatae* was represented as early as the Jurassic (the *Castniidae* and primitive lepidopterans related to the present *Cossidae*).

HISTORY OF THE SYSTEM OF LEPIDOPTERA

The first system was the so-called "natural system" worked out by LINNAEUS, in which he divided the *Lepidoptera* on the basis of a number of external characters, like the shape of wings, the manner of their folding, the shape of antennae, etc., into three groups: *Papilio*, *Sphinx* and *Phalaena*, this last group being composed of *Bombyces*, *Noctuae*, *Geometrae*, *Tortrices*, *Pyrallides*, *Tineae* and *Alucitae*. This system was next repeatedly improved and completed.

In addition to the old division of the order (into the *Microlepidoptera* and *Macrolepidoptera*, the separation of the *Rhopalocera* and *Heterocera* from the *Macrolepidoptera*, etc.), a number of other divisions, often containing attempts to establish the phylogeny of the order, were introduced. They were recognized by cladists as typological divisions (HENNIG, 1953). Only divisions into categories higher than family will be included below. The most important ones were introduced by the following authors:

CHAPMAN (1893) divided the *Lepidoptera Heterocera* on the basis of the structure of their pupae into the *Obtectae* (with obsecta type pupae) and *Incompletae* (with incompleta type pupae).

COMSTOCK (1893, 1895) assumed the mode of attachment of the wings as the basis for his division. In the *Jugata* (*Jugatae*, having the jugum) he included

the *Micropterygidae* (sensu lato) and *Hepialidae*, and in the *Frenata* (*Frenatae*, having the frenulum) the remaining *Lepidoptera*.

PACKARD (1895) considered the structure of mouth-parts to be the most important character. His *Lepidoptera Laciniata* (*Protolopidoptera*) contained the *Micropterygidae*, and *Lepidoptera Haustellata*, having the haustellum, were further divided into the *Palaeolepidoptera* (*Eriocraniidae*) and *Neolepidoptera* (other families).

KARSCH (1898) introduced a division, to some extent corresponding to COMSTOCK'S division but based on the type of venation. The *Isoneria*, having the same venation in the fore- and hind-wings, embraced the *Micropterygidae* (s. l.) and *Hepialidae*, and in the *Anisoneria*, with the venation of the fore-wings different from that of the hind-wings, he placed all the other *Lepidoptera*. Later, the same author introduced another division, based on the structure of legs in larvae. In the *Stemmatoncopoda* the circles of hooks on the soles of the abdominal legs are closed and in the *Harmoncopoda* they are only partial and opened.

SPULER (1910) distinguished a group characterized by the presence of spikes on the abdominal annuli of pupae among the *Lepidoptera* and named it *Archilepidoptera*, and BÖRNER (1920) divided the so-called *Microlepidoptera* on the same principle into the *Acanthopleona* (with spikes) and *Lipacanthina* (spikeless).

TILLYARD (1918) replaced the names introduced by KARSCH with new names, i. e., *Isoneria* with *Homoneura* and *Anisoneria* with *Heteroneura*. Although these names were introduced later, they have been generally adopted.

BÖRNER (1925) divided the *Lepidoptera* on the basis of the structure of the female genital organs. His *Monotrysis* are characterized by the presence of one genital opening and *Ditrysis* have two genital openings, one copulatory and the other for laying eggs.

LE MARCHAND (1945) substituted the names *Monostomiogyna* and *Distomiogyna*, respectively, for BÖRNER'S names and AGENJO (1946) separated the *Psychidae* as a distinct group, which he denominated *Heterotrysis*.

HINTON (1946) separated the *Zeugloptera* (including the *Micropterygidae*; cf. p. 3) from the *Lepidoptera*, the rest of which he divided into three suborders: *Dacnonypha* (including *Eriocraniidae*), *Monotrysis* (*Hepialoidea*, *Nepticuloidea* and *Incurvarioidea*) and *Ditrysis* (remaining families).

TURNER (1946) based his classification on the venation of wings and divided the *Lepidoptera* into two suborders corresponding with TILLYARD'S groups. He included the *Micropterygoidea* and *Hepialoidea* in the *Homoneura* and the other families in the *Heteroneura*, these last families being grouped in the divisions *Asthenochorda* (devoid of the chorda, the inner vein of the central cell of the fore-wing, representing the veins r_4+r_5), including the *Rhopalocera* and *Microptila*, and *Sthenochorda* (the chorda present or only exceptionally lacking). In the *Rhopalocera* TURNER placed the *Hesperioidea*, *Papilionoidea* and *Nymphae-*

loidea, treated as superfamilies, and in the *Microptila* the families *Elachistidae*, *Gelachiadae* and *Tortricidae*. The ancestral group of the *Asthenochorda* and *Sthenochorda* are the hypothetical *Protocossidae*.

In lepidopterology the cladists are represented by two investigators named below, though HENNIG (1953) regarded LAMEERE (1936) as the first phylogenist. LAMEERE divided the order discussed into the Jugates and Frenates, and these last into the Adeliformes and the remaining, unnamed, forms. KIRIAKOFF improved the cladist system in his later papers on the system and phylogeny of butterflies and moths (perhaps except the first one of 1946, in which he shares TILLYARD's opinions). In 1948 he separated the *Zeugloptera* as a distinct suborder on a par with the remaining *Lepidoptera* and *Trichoptera* and erected a common group for all the three of them, the order *Amphiesmenoptera*. Further he divided the *Lepidoptera* into the *Hoplostomatoptera* (including *Eriocraniidae*) and *Aplostomatoptera* (with *Hepialidae*), separated the *Nannolepidoptera* (*Nepticulidae*) and named the other lepidopterans the *Eulepidoptera*, which he, in turn, divided into the *Stemmatoncopoda* and *Harmoncopoda*. The first division into groups is based on the structure of mouth-parts, the second on the venation of wings and the third on the structure of the larval prolegs. HENNIG (1953) approved of this division only that he considered the *Zeugloptera* to be a group of the *Lepidoptera* and not a separate suborder standing outside them and the suborders *Trichoptera* and *Lepidoptera* to be sibling groups. He also introduced a different nomenclature. His cladogram is as follows: *Lepidoptera* divided into *Zeugloptera* (with *Micropterygidae*) and *Glossata* (remaining ones), *Glossata* into *Dacnonypha* (*Eriocraniidae* sensu lato) and *Neolepidoptera* (remaining ones), *Neolepidoptera* into *Aplostomatoptera* (*Hepialidae*) and *Frenata* (remaining ones), *Frenata* into *Nannolepidoptera* (*Nepticulidae* sensu lato) and *Eulepidoptera* (remaining ones), finally *Eulepidoptera* into *Incurvariina* and *Ditrysia*, further undivided.

The bases for successive divisions were the following plesiomorphic characters: the presence of functional mandibles, the well-developed lacinia, the regularly structured galea in imagines, the situation of the anterior tentorial pit close to the clypeus, the occurrence of the abdominal legs on all segments, the lack of the adfrontal suture in larvae (first division), the fusion of the adfrontal and frontal sutures and the occurrence of pupae of the libera type (second division), the lack of the frenulum (third division), the development of the jugum (fourth division), the occurrence of microtrichia (fifth division) and the presence of a single genital opening in females.

KIRIAKOFF (1955) introduced similar criteria in his modified system. He divided the *Amphiesmenoptera* into the sibling groups *Trichoptera* and *Lepidoptera*, *Lepidoptera* into *Zeugloptera* and *Glossata* (infraordines), *Glossata* into *Dacnonypha* and *Neolepidoptera* (superlegiones), *Neolepidoptera* into *Aplostomatoptera* and *Frenata* (legiones), *Frenata* into *Nannolepidoptera* and *Eulepidoptera* (sublegiones) and, finally, these last into *Stemmatoncopoda* (*Incurvariidae*) and *Harmoncopoda* (remaining families; supercohortes).

EVALUATION OF THE SIGNIFICANCE AND USEFULNESS OF CHARACTERS

As mentioned in the survey of the systems on p. 8, different authors ascribed essential significance to different characters. As regards butterflies and moths, WARREN (1947) dealt with this problem in a general manner, confining himself chiefly to the diurnal *Lepidoptera*. We owe the theoretical justification of the significance of character mainly to HENNIG (1953, 1969), who gathered and analysed different criteria used to determine it.

So far as the *Lepidoptera* are concerned, the discussion on this subject was actually started in 1946, when KIRIAKOFF stated that only the venation of wings is important to the main division of the order. His paper contains a discussion of the previous systems and characters assumed in them, in the first place, however, the criticism of the views published by BÖRNER (1939) and HINTON (1946). According to KIRIAKOFF, the occurrence of one or two genital openings in females cannot be used as the basis for the division into suborders in BÖRNER'S sense of the word. He also rejects BÖRNER'S interpretation of the secondary formation of the single genital opening (characterising the *Monotrysia*). This character was also erroneously applied by HINTON, since in his division it occurs both in the *Daenonypha* and in the *Monotrysia*. KIRIAKOFF concludes that after eliminating the useless (differently distributed within the order) genital characters, there remain only two characters of remarkable use. One of them is the structure of the abdominal legs in larvae, already assumed by KARSCH (1898) before but rejected by BÖRNER (1939) and HINTON (1946). KIRIAKOFF claims that there is not always a direct relationship between their structure and the ways of life of the larva. The other character is the venation of wings, or more exactly its type (identical or different venations of the fore- and hind-wings), but KIRIAKOFF rejects the old division into the *Homoneura* and *Heteroneura*. He (1948) attaches most importance to the structure of mouth-parts, next to the venation and, finally, to the structure of abdominal legs in larvae. HENNIG (1953), similarly, considers the structure of the mouth-parts of imagines and larvae to be the most important character, followed by the type of wing coupling, the occurrence of microtrichia and, lastly, the presence of one or two genital openings in females. The application and my own interpretation of individual characters are given in the next section.

PROPOSAL OF A NEW PHYLOGENETIC SYSTEM

The proposal of the phylogenetic system of the *Lepidoptera* (Fig. 1) presented below concerns only the higher classification units and the most primitive groups. On the basis of the present state of knowledge it is difficult to substantiate further divisions. The characters assumed by KIRIAKOFF (1948) for the separation of the higher lepidopterous groups are not sufficient and their criticism made by HINTON (1952) seems to be justified.

The evolution of the primaeval *Lepidoptera* undoubtedly led through the transformation of the mouth-parts from the primitive biting type to a more and more specialized one. The earliest tendency was the reduction of the labium in imagines. There was no such reduction in the *Trichoptera* and the well-developed labium occurs in all the contemporary families of this order. Instead, in the *Lepidoptera* it has been reduced to a short sclerite (except for the *Micropterygoidea*, in which its division into parts is preserved), which is however always furnished with the labial palps. The next stage was the transition from the functional biting mouth-parts to the highly specialized sucking ones. The first phase of this stage was marked by the loss of functionality of the mandibles. Out of the contemporary *Lepidoptera* only the *Micropterygoidea* have their mandibles preserved in the original form, which is a plesiomorphic character. These moths use the mandibles to take and partly grind pollen. Their lacinia is well developed and the galea has the shape typical of the biting type of mouth-parts. A further character, non-correlated with the characters mentioned, is the lacinia of typical shape in the mouth-parts of the larva. The anterior tentorial pit of the larva is situated near the clypeus, the adfrontal suture being missing. The appendages occur on all body segments of the larva, but the abdominal ones are shaped differently from those in the larvae of the remaining *Lepidoptera*. Many authors (see p. 10) recognized the foregoing character as sufficient to separate this most primitive group of *Lepidoptera* as a distinct order or suborder. Later KIRIAKOFF and HENNIG used these characters to carry out the "first division", placing the *Micropterygoidea* in opposition to the remaining *Lepidoptera* and treating them as infraordines. It was only HINTON (1952) and COMMON (1970) that, basing themselves on fairly rich material, observed some transitional stages in the structure of mouth-parts between the *Micropterygoidea* and *Eriocranioidea*, and STEKOLNIKOV (1967) found that the types of musculature of the genital apparatus in the *Micropterygoidea* and *Hepialoidea* are very much alike and, consequently, he defied the separation of this first superfamily as the order *Zeugloptera*.

The *Eriocranioidea* are the most primitive group of the remaining *Lepidoptera*. In comparison with the *Micropterygoidea* they are far more specialized and show a large number of transitions to the higher *Lepidoptera*. In the studies referred to above, KIRIAKOFF and HENNIG marked out a clear-cut boundary between these superfamilies arbitrarily, establishing the main line of division just between them. In their opinion, the mandibles of the imaginal *Eriocranioidea* are not functional, the lacinia is vestigial and galea transformed into haustellum, while in the larvae the lacinia is changed, atypically orthopteroideal, the anterior tentorial pit distinctly remote from the clypeus, and the adfrontal suture fused with the frontal one in contradistinction to all the other *Lepidoptera*, in which it is well developed and extends separately. However, the discovery of the species *Agathiphaga queenslandensis* DUMBLETON in Australia necessitated the widening of the diagnosis of the *Eriocraniidae* (KRISTENSEN, 1967, even suggested the erection of a new family, *Agathiphagidae*, for it). It should be

stated now that the *Eriocranioidea* have well-developed muscles of the mandibles, although these last are only exceptionally functional. The lacinia has a tendency to disappear and the galea to become elongate and form a primitive haustellum. These characters mark the transition to the *Micropterygoidea*, the more so, since in some cases (COMMON, 1970) these organs occur in the *Eriocranioidea* in a form resembling that in the *Micropterygoidea*. According to this last author, the adfrontal suture may be missing in the larvae. The character common in both superfamilies discussed so far is the occurrence of pupae of the libera type (in the *Eriocraniidae* they show a hypertrophy of the mandibles), whereas the apodous type of the larval *Eriocranioidea*, more resembling the larvae of the higher *Lepidoptera*, makes a difference. It should however be stated that the studies carried out on the larvae of the primitive *Lepidoptera* till now are insufficient and it is hard to base oneself on the poor data we have at our disposal. The differences between these two superfamilies will perhaps appear to be still smaller than those found at present. STEKOLNIKOV (1967) found remarkable resemblances between them in the structure of the musculature of the male genital apparatus. He thinks that the differences have probably been caused by the decline of the role played by the valves in copulation. The females of both superfamilies have a single genital opening.

In separating the *Hepialoidea* from the bulk of the remaining *Lepidoptera* HENNIG (1953) based himself on the lack of the frenulum. As can be easily seen, the frenulum is variously preserved in different lepidopterous groups and the type of wing-coupling in males sometimes differs from that in females of the same species. In many respects the *Hepialoidea* have reached a higher evolutionary level than the two previous superfamilies. The mouth-parts were transformed from the transitional type (arising from the biting one) in the *Eriocranioidea* into the sucking type to be next almost completely reduced. The haustellum is vestigial or missing. It may be supposed that the mouth-parts of the imaginal *Hepialoidea* never attained as high a level of specialization as that in the higher *Lepidoptera* and they probably resembled, especially as regards the haustellum, the best-developed suction organs of the *Eriocranioidea*. The mandibles have however disappeared completely, and so have other parts characteristic of the biting-type mouth-parts. The musculature of the male genital apparatus is similar to that in the *Micropterygoidea*. The structure of the female genital organs is very instructive. They have two genital openings connected together by a trough-shaped infolding of the membrane of the external part of the abdomen. This infolding may be displaced farther inside and then it makes a primitive duct between the reproductive and copulatory tracts. This type resembles the highly specialized female genital organs of most *Lepidoptera* (so-called *Ditrysia*), but is not identical with them. Its evolution may have proceeded similarly to the evolution of these organs in the higher *Lepidoptera*; at least the same tendency to the separation of the two tracts can be observed. The structure of the larva (mouth-parts, sutures of the head, appendages) is the same as in the higher *Lepidoptera*, the pupa is

of the obtecta type and shows the most primitive form of the incompleta type. The presence of the longitudinal suture of the mesoscutum is a primitive character that has been preserved (its re-formation seems doubtful). This suture has completely disappeared in the two preceding groups, but it is present though strongly reduced in the *Trichoptera*.

All the three superfamilies mentioned have several important characters in common. The prothorax is stout as compared with that in the other *Lepidoptera* and its pronotum is broad. The mesothorax predominates considerably over the metathorax, although the size of the fore-wings does not differ so much from that of the hind wings as in the other *Lepidoptera*. The venation of the fore-wings is identical with the venation of the hind-wings and exhibits a number of primitive characters, absent from the other *Lepidoptera* (e. g., the branching of veins of the radial trunk, the occurrence of fairly numerous cross-veins). These characters should be regarded as sufficient for the combination of the three superfamilies discussed into a suborder opposed to the rest of the *Lepidoptera* on the principle, accepted in evolutionary taxonomy, that the accumulation of genetic changes between these three superfamilies and the other *Lepidoptera* is far more important than the direct relationships between the *Micropterygoidea*, *Eriocranioidea* and *Hepialoidea*. For this suborder I use the generally accepted name *Homoneura*, introduced by TILLYARD (cf. p. 9), and for the remaining ones the name *Heteroneura*. The differentiation of the superfamilies within the *Homoneura* is not uniform. In spite of a large number of primitive characters the *Micropterygoidea* stand closer to the *Eriocranioidea* than these last to the *Hepialoidea*.

The determination of the time when these three evolutionary lines (superfamilies) branches off is impossible in a direct way, because of the lack of fossil evidences mentioned before. If we accept HENNIG'S (1969) interpretation that the *Lepidoptera* descend from the *Amphiesmenoptera* (more precisely from the *Permotrichoptera*), whose remains occur as early as the Upper Permian, the first primaeval *Lepidoptera* may have appeared in the Lower Trias. The lack of their remains may be explained by the hypothesis that they were exclusively mountainous insects and in the mountains sedimentation is too poor to create the conditions necessary for fossilization. Out of the contemporary *Lepidoptera* the *Micropterygoidea* appeared first. Their imagines have lived on pollen till now, so originally they could feed on gymnosperms, even on pteridophytes, and later they became associated with angiosperms. Their keeping to the old sort of food and poor flight caused that the *Micropterygoidea* have survived only slightly changed till the present time. It may be supposed that they appeared at the end of the Trias or at the beginning of the Jurassic. The development of a primitive haustellum in some *Eriocranioidea* made it possible for them to take water and plant sap. The most primitive representatives of this superfamily resemble the *Micropterygoidea* in many respects, at least in respects of mouth-parts. In the mode and purpose of taking liquids they most probably resembled the modern *Trichoptera*. They may therefore have appeared before

the occurrence of angiosperms, at the beginning of the Jurassic, occupying the similar ecological niches to these occupied by them today. The third superfamily of the *Homoneura*, *Hepialoidea*, supposedly appeared at the onset of the expansion of the angiosperms, i. e., at the mid-Jurassic. The haustellum of the extinct forms may have been well developed and long enough for the insects to avail themselves of flower nectar, later however it underwent a reduction as in the members of many families of the higher *Lepidoptera* (tendency towards the atrophy of mouth-parts is encountered in numerous members of the *Heteroneura*).

The evolutionary line of the *Heteroneura*, showing a number of apomorphic characters (opposite to those mentioned for the *Homoneura*), is associated with the evolution of the angiosperms. The *Heteroneura* acquired two essential characters that allowed them to adapt themselves better to new conditions, namely, the sucking mouth-parts with the haustellum varying in length and the efficient organ of flight. The predominance of the fore-wings over the hind-wings and the progressive costalization probably increased the dirigibility and power of flight. The *Heteroneura* had most likely been closely connected with the angiosperms since the very beginning, these plants being originally pollinated by insects (TAKHTADZHIAN, 1961) and similarly to them occurring only in the mountains. It should therefore be supposed that they appeared towards the end of the Jurassic together with these plants (there are some fossil evidences from this period) or as late as the Cretaceous.

It is impossible to reconstruct the phylogeny of the *Heteroneura* at the present state of knowledge, with two exceptions. This group, quantitatively including most of the *Lepidoptera*, is characterized by a tremendous morphological diversity and numerous biological adaptations. The primitive characters disappear gradually and only few families have microtrichia all over the wings or exclusively in some parts of theirs. The single genital opening of females occurs merely in the *Nepticuloidea* and *Incurvarioidea* and the pupa is always the obtecta type, but some families have incomplete pupae. Primitive characters are also the occurrence of spikes on the abdominal segments of pupae and the mobility of these segments. The distribution of the plesiomorphic characters in the venation is hard to interpret in most cases and it is not correlated with the other characters analysed so far. The occurrence of two types of the abdominal legs in larvae, which character KIRIAKOFF (1948) holds to be very important (he divides his *Eulepidoptera* into the *Stemmatoncopoda* and *Harmoncopoda*), does not seem to be a sufficient character to make the basis for the division into categories above the family level. Neither is this character uniformly distributed within the order and e. g., in the members of the *Hepialoidea* there occur complete many-rowed wreaths of spikes on the feet.

Only the separation of the two most primitive superfamilies, i. e., the *Nepticuloidea* and *Incurvarioidea*, from the *Heteroneura* seems possible. The *Nepticuloidea* are characterized by the simplified venation of wings, accompanied by a number of less essential characters (cf. KIRIAKOFF, 1948). The opinion on the

primitiveness of the *Nepticuloidea* was held by some older lepidopterologists, e. g., MEYRICK (1928), and recently by KIRIAKOFF, who in the above-mentioned study introduced the "supercohors" *Nennolepidoptera* for them. He thinks besides that the lack of the haustellum in the *Nepticuloidea* is a primitive character.

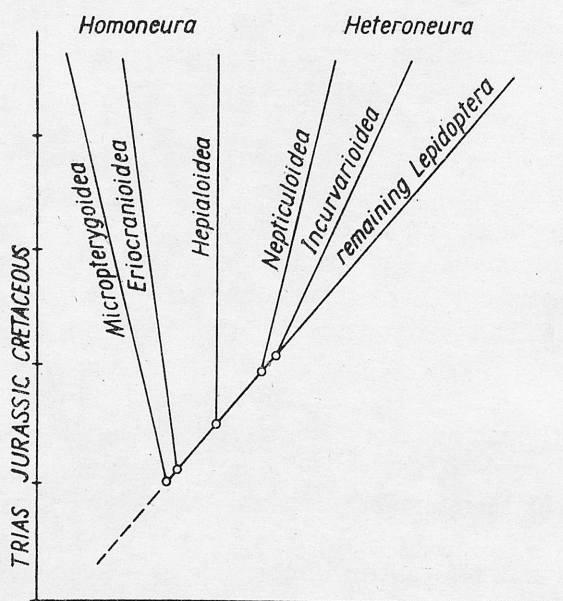


Fig. 1. Phylogenetic tree of *Lepidoptera*

The other moths whose females have a single genital opening are the *Incurvarioidea*, to which all the remaining families marked by the constant presence of two genital openings may be placed in opposition. These last, often, after BÖRNER (1939), called the *Ditrysia*, are out of necessity still divided into families and superfamilies in the traditional typological manner. Attempts to determine and explain the relationships between particular families were made, e. g., by STEKOLNIKOV (1967, 1967a) and KIRIAKOFF (a number of papers from 1946 onwards), but only small groups of families were included in them. It may well be that the characters taken into consideration so far are not sufficient for the comprehension of the phylogeny of the other *Lepidoptera*, hence further studies are necessary. The conclusions that might be drawn on the basis of the characters studied hitherto seem to be too unreliable to be presented here. There are, all the more, no possibilities to determine the time points at which the evolutionary lines of the two superfamilies distinguished in this suborder branched off. I think that the *Nepticuloidea* were the first *Heteroneura* to appear and that they might be dated at the end of the Jurassic or the beginning of the Cretaceous, if there were no other more primitive extinct groups.

REFERENCES

- BÖRNER C. 1939. Die Grundlagen meines Lepidopterensystems. VII. Internation. Kongress Entomol., Berlin: 1372—1424.
- BOURGOGNE J. 1951. Ordre des Lépidoptères [in] P. GRASSÉ: Traité de zoologie, anatomie, systématique, biologie, Paris, **10**, Insectes supérieures et Hémiptéroïdes, fasc. 1, Névroptéroïdes, Mécoptéroïdes Hyménoptéroïdes, (Symphytes et Térébrants): 172—448.
- CHAPMAN A. 1893. On some neglected points in the structure of the pupae of Heterocerous *Lepidoptera*, and their probable value in classification; with some associated observations on larval prolegs. Trans. ent. Soc. London, **1893**: 97—119.
- CHAPMAN T. A. 1917. *Micropteryx* entitled to ordinal rank. Order *Zeugloptera*. Trans. ent. Soc. London, **1917**: 310—314, 12 pls.
- COMMON I. F. B. 1970. *Lepidoptera* (Moths and Butterflies) [in] The Insects of Australia, Melbourne University Press: 765—866.
- COMSTOCK J. H. 1893. Manual for the study of Insects. Evolution and Taxonomy. Ithaca, N. Y. (next edition: 1895).
- COMSTOCK J. H. 1918. The Wings of Insects. Ithaca, N. Y.
- GISIN H. 1969. Principles and concepts of systematic biology, Discussion. Proc. internat. Conference Nat. Acad. Sci., Washington, D. C. **1969**: 61—64.
- HANDLIRSCH A. 1906—1908. Die fossilen Insecten. Leipzig.
- HENNIG W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik, Berlin.
- HENNIG W. 1953. Kritische Bemerkungen zum phylogenetischen System der Insecten. Beitr. Ent., Sonderheft, Berlin, **3**: 1—85.
- HENNIG W. 1969. Die Stammesgeschichte der Insecten. W. KRAMER, Frankfurt am Main.
- HINTON H. E. 1946. On the Homology and Nomenclature of the Setae of Lepidopterous Larvae, with some Notes on the Phylogeny of *Lepidoptera*. Trans. R. ent. Soc. London, **97**, 1—37.
- HINTON H. E. 1952. The structure of the larval prolegs of the *Lepidoptera* and their value in the classification of major groups. Lepid. News, Connecticut, **6**: 1—6.
- HINTON H. E. 1958. The phylogeny of the Panorpoid orders. Ann. Rev. Ent., Palo Alto, **3**: 181—206.
- IMMS A. D. 1934. A general textbook of entomology including the anatomy, physiology, development and classification of Insects (third edition), Methuen and Co., London.
- JEANNEL R. 1949. Les Insectes, classification et phylogénie, les insectes fossiles, évolution et géonémie [in] P. GRASSÉ: Traité de zoologie, anatomie, systématique, biologie, Masson, Paris, **9**: 1—110.
- KARSCH F. 1898. Gibt es ein System der recenten Lepidopteren auf phyletischer Basis? Ent. Nachr. Berlin, **24**: 296—303.
- KIRIAKOFF S. G. 1946. Position systématique des Lépidoptères et les divisions primaires de l'ordre. Lambilliona, Bruxelles, **46** (2—3): 21—26.
- KIRIAKOFF S. G. 1948. A classification of the *Lepidoptera* and related groups with some remarks on taxonomy. Biol. Jaarboek, Antwerpen, **15**: 118—143.
- KIRIAKOFF S. G. 1955. Le Système phylogénétique: Principes et méthodes. Bull. Annls Soc. ent. Belg., Bruxelles, **91**: 147—158.
- KRAUSE A., WOLFF M. 1919. Eine Übersicht über die bisher aufgestellten fossilen und rezenten Insectenordnungen. Arch. Naturgesch. Berlin, Leipzig, **85**, A, **3**: 151—171.
- KUŹNICKI L., URBANEK A. 1967. Zasady nauki o ewolucji. PWN Warszawa, **1**: 1970, vol. 2.
- LAMEERE A. 1936. Evolution des Lépidoptères. Bull. Annls Soc. ent. Belg. Bruxelles, **76** (12): 407—413.
- MARTYNOVA O. M. 1957. Filogenija otriadov nasekomykh s polnym prevashcheniem. III Soveschenie vsesoyuznogo Entomolog. obshchestva Tbilisi. Tezisy dokladov, Leningrad, **1**: 113—114.

- MARTYNOVA O. M. 1959. Filogeneticheskie vzaimootnosheniya nasjekomykh mekopteroidalnogo kompleksa. Trudy Inst. morfol. Zhiwotnykh im. SEVERTSOVA, Moskva—Leningrad, **27**: 221—229.
- MARTYNOVA O. M. 1962. Otryad *Trichoptera*. Ruchaĭniki [in] B. B. RODENDORF, Osnovy paleontologii, Moskva: 294—302.
- MAYR E. 1965. Numerical Phenetics and Taxonomic Theory. Syst. Zool. Lawrence, Kans., **14**: 73—97.
- MAYR E. 1965a. Classification and Phylogeny. Am. Zoologist, **5**: 165—174.
- MEYRICK E. 1927. A Revised Handbook of British *Lepidoptera*. London.
- PACKARD A. S. 1895. On a new Classification of the *Lepidoptera*. Am. Nat., **1895**: 636—647, 788—803.
- RAZOWSKI J. 1973. Uwagi o filogenezie motyli. Przegl. zool., Wrocław, **17**: 21—32.
- RENSCH B. 1960. Evolution above the species level. Columbia Univ. Press, New York.
- RIEK E. F. 1970. *Trichoptera* (Caddis-flies, caddies) [in] The Insects of Australia, Melbourne Univ. Press: 741—764.
- ROSS H. H. 1967. The evolution and past dispersal of the *Trichoptera*. Ann. Rev. Ent., Palo Alto, **12**: 169—203.
- SIMPSON G. G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York.
- SNEATH P. H. A. 1961. Recent developments in theoretical and quantitative Taxonomy. Syst. Zool. Lawrence. Kans., **10**: 118—139.
- STEKOLNIKOV A. A. 1967. Filogeneticheskie svazy vnutri *Rhopalocera* na osnove funkcyonalnoj morfologii genitalnogo apparata. Ent. Obozr., Moskva, Leningrad, **46**: 3—24.
- STEKOLNIKOV A. A. 1967a. Funkcyonalnaja morfologija kopulativnogo apparata arkhajnykh cheshujekrylnykh i obshchije napravleniya evolucii genitalij Lepidoptera. Ent. Obozr., Moskva, Leningrad, **46**: 670—698.
- TAKHTADZAN A. L. 1961. Proiskhozhdenie pokrytosemnykh rastenii, **1**: 513—543.
- TILLAYARD R. J. 1918. The Panorpoid Complex. Part I. The wing-coupling apparatus with special reference to the *Lepidoptera*. Proc. Linn. Soc. N. S. Wales. Sydney, **43**: 286.
- TILLAYARD R. J. 1919. The Panorpoid Complex. Part II. On the morphology and systematic position of the family *Micropterygidae* (sens. lat.). Proc. Linn. Soc. N. S. Wales. Sydney, **44**: 95—136, pl. III.
- TINDALE N. B. 1945. Triassic insects of Queensland I. *Eoses*, a probable Lepidopterous insect from the Triassic beds of Mt. Crosby, Queensland. Proc. R. Soc. Queensland, Brisbane, **56**: 132—153.
- TURNER A. J. 1947. A review of the phylogeny and classification of the *Lepidoptera*. Proc. Linn. Soc. N. S. Wales. Sydney, **71**: 303—338.
- WARREN B. C. S. 1947. Some principles of classification in *Lepidoptera*, with special reference to the butterflies. Entomologist, London, **80**: 208—217.
- WHITE M. J. D. 1957. Cytogenetics and systematic entomology. Ann. Rev. Ent., Palo Alto, **2**: 71—90.

STRESZCZENIE

Praca zawiera przegląd dotychczasowych najważniejszych osiągnięć z zakresu systemu i filogenezy motyli oraz własną interpretację układu ewolucyjnego tej grupy owadów.

РЕЗЮМЕ

Статья содержит просмотр наиболее важных достижений в области систематики и филогенеза бабочек, а также собственное объяснение эволюционной системы этой группы насекомых.

Redaktor zeszytu: dr A. Szeptycki

PAŃSTWOWE WYDAWNICTWO NAUKOWE — ODDZIAŁ W KRAKOWIE — 1974

Nakład egz. 700+90. Ark. wyd. 2. Ark. druk. $1\frac{1}{16}$ + 1 wkładka. Papier ilustr. kl. III, 70×100, 80 g
Zam. 864/73

Cena zł 12,—

DRUKARNIA UNIWERSYTETU JAGIELLOŃSKIEGO W KRAKOWIE