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Coordinating the Traditional and Modern Approaches in the Systematics of Insects

S. Yu. Sinev

Zoological Institute, Russian Academy of Sciences, 199034 St. Petersburg, Russia

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Abstract—The problem of coordinating the traditional and modern approaches to systematics is ever-lasting due to the continuous development and enrichment of our knowledge of biodiversity, means of analysis, and concepts. Comparative morphology was and still is the cornerstone of studies of insect taxonomy. It gives the most extensive and diverse information on the organisms studied, particularly when it is supported by the data on embryology and functional morphology as well as by analysis of adaptive significance of morphological characters. The limitations of this approach are often related to the presence of homoplasies, reversions, etc. Comparative paleontology is the only approach providing direct evidence of the historical succession of taxa and their characters. However, this approach is fully applicable only to some groups due to the specific features of their morphology and taphonomy. All the modern approaches (molecular, cytogenetic, etc.) are very informative but also have their own limitations; they should not be contrasted with the traditional approaches and certainly should not replace them. The traditional approaches do not become obsolete; it is only their comparative importance in the set of taxonomic tools that may be reevaluated. No single approach can be considered universal for an unambiguous reconstruction of phylogeny and substantiation of the natural system of taxa. Each approach has its own advantages and limitations, and only combined use of different approaches allows a broader range of the problems to be solved. Different approaches may prevail in the studies of different groups of insects and at different levels of taxonomic hierarchy. The intuition of the taxonomist, which is so often criticized by the followers of “objective” systematics, is based on taxonomic experience and scope of knowledge of a particular taxon. It does not imply a subjective bias, but allows the taxonomist to choose the instruments adequate to a particular case.

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For many years, taxonomy has been the subject of heated discussions. In the first half of the XX century, the advocates and opponents of typologism and evolutionism had furious debates. Departure from the typological tradition was in many ways conducive to the growth of the prestige of taxonomy as one of the unifying branches of biological science and not as some craft totally dependent on the empirically acquired skill of a certain researcher. The second half of the XX century passed under the banner of two leading scientific schools: an extremely popular school of “phylogenetic taxonomy” of W. Hennig (1950, 1966), which dominated among the western researchers, and the school of “evolutionary taxonomy” which took root in Russia. The main postulates of the latter school were summarized by E. Mayr (1942, 1947, 1971; Mayr et al., 1956) and G. Simpson (1961); its merits and some drawbacks were later considered by Yu.A. Pesenko (1989) and A.P. Rasnitsyn (1996, 2002). The present century started with a new round of confrontation, this time between the so-called “tradi-

tionists” and quite active, and sometimes even aggressive molecular taxonomists who arrived en masse on the wave of another fashion related to the use of recent computer technologies.

Despite the heated debates between the advocates of different scientific schools, the main directions in the development of taxonomy should not be treated as mutually exclusive since each of them contains many rational elements. Strict contradistinction is appropriate only in historical and philosophical aspects but cannot be justified by the logic of development of scientific knowledge. The decisive advantage of evolutionary taxonomy lies in its balanced dialectical approach to the studied phenomena, which allows its theoretical basis to be continuously improved by accumulation of all the most valuable ideas, wherever and by whoever they may be suggested. It is not accidental that one of the most significant events in the recent evolutionary taxonomy has been establishment of strict rules of phylogenetic analysis based on the hypothetico-deductive method (Popper, 1959, 1983),

even though it took place mostly beyond the scope of evolutionary taxonomy proper. The exact procedure was for the first time clearly formulated by the adherents of cladism; the indisputable merit of W. Hennig (1966) was also the development of standardized, terse, and clear terminology which provided a universal language of communication between the adherents of different views.

In their controversial ardor, and sometimes because of their inability to think dialectically, the representatives of different scientific schools often defend their own point of view which they deem to be the only correct one. Quite a few lances are also broken about the merits and drawbacks of different methods of research: which of them is better; which of them is more or less informative, etc. In many cases, this unnecessary polemics could be avoided if the disputants asked themselves simple questions: in which cases are they better? In which taxon are they more informative? Under which conditions are they more reliable? What are the limitations of this or that method? Sometimes it is very disappointing that the researchers limit themselves to one method and each of them fights tooth and nail for their method of choice without seeing the golden mean. Taxonomy evidently does have problems but these problems are often not in the methods but in the heads of the researchers.

Since the formulation of the classical method of triple parallelism or "Haeckel's triad" (Haeckel, 1902, 1908), according to which phylogeny should be based on the combination of data obtained by comparative anatomy, comparative embryology, and paleontology, the methodology of taxonomy has been considerably expanded. The problem of the relation between the classical and the most recent methods of research deserves special consideration.

The Classical Methods

The comparative morphological method has always been and still remains the cornerstone of research in the field of insect taxonomy. It is this method which yields the most abundant and versatile information on the organisms and provides great number of various characters for analysis; recently, this method is often supplemented with data on functional morphology and analysis of the adaptive significance of characters. It can be used to compare recent forms and resolve their relationship. At the same time, the comparative morphological method has a number of limi-

tations associated with the fast evolution of many insect groups and their extraordinary diversity both in the past and at present. Fast divergence, the absence of evident dichotomy, and a powerful adaptive radiation do not facilitate the task of reconstruction of insect phylogeny. Extension and deepening of research reveal many cases of homoplasy, heterobathmy, reversion, etc., practically in each of the main phylogenetic branches of insects, and such phenomena blur the general picture of their historical development.

The comparative embryological method is rather promising since it allows the historical sequence of forms to be reconstructed indirectly, based on "the law of embryonic similarity" and ontogenetic recapitulation of characters. This method, however, is not favored by entomologists because it is very labor-consuming, in particular due to a very small size of insects. Usually, only few species from some groups are studied in this respect, which limits the possibility of analysis. In addition, the complex nature of insect metamorphosis, especially in Holometabola, leaves open the question of the upper boundary of embryonic development.

The paleontological method is based on the study of fossil forms, most of which have already become extinct. Since this method actually deals with comparative morphological data, its value as an independent tool of phylogenetic reconstruction is doubted by some researchers, who suggest instead that the characters of fossil organisms should be analyzed alongside with those of recent forms (Kluge, 2000). Nevertheless paleontology not only provides data on morphology of the already extinct organisms but also gives direct evidence of the historical sequence and the absolute age of taxa. However, this method is not to the full extent applicable to all the groups, due to both the specific morphological traits, such as the presence or absence of sclerotized structures, and the taphonomic conditions, in particular, association with specific biotopes. A very uneven representation of some insect groups in the fossil record, an almost complete absence of larval forms in it, the vagueness of important taxonomic characters in many imprints and inclusions, and, finally, purely taphonomic reasons may create an impression of complete continuum of forms or, on the contrary, leave huge hiatuses which are very difficult to analyze.

The Recent Methods

Recently, molecular and molecular cytogenetic methods of research have gained great popularity in

taxonomy. At the dawn of their appearance at the end of the XX century, these methods were used to analyze only a few terminal taxa and only small fragments of nucleic acids containing hundreds of base pairs, mainly of the ribosomal RNA. The use of a single gene and few selected taxa often resulted in serious contradiction with the concepts based on morphology, after which the conclusions based on such data were naturally rejected by traditional taxonomists. A wider and more thought-out application of the recent methods resulted in considerable and sometimes revolutionary changes in the insect taxonomy. Now such studies have covered hundreds of taxa and included large sets of genes tens of thousand base pairs long, owing to considerable improvement of laboratory hardware and techniques. The so-called phylogenomic approach is successfully used in studying basal phylogeny of the principal insect groups (Simon et al., 2009) and arthropods as a whole (Meusemann et al., 2010). Analysis of nuclear and mitochondrial genes, studies of transformations in the mitochondrial chromosome, and discovery of different types of molecular organization of telomeres have contributed to serious progress in understanding the relationship between high-ranked taxa (Lukhtanov and Kuznetsova, 2010). In view of this, we can now consider not the triad but the modern tetrad of methods of phylogenetic reconstruction.

On the Concept of a "Taxonomic Character"

All the above methods yield factual data for subsequent phylogenetic analysis whose first stage is examination of taxonomic characters. In this connection it is important to decide what we do call a taxonomic character. Here one could agree with the definition of E. Mayr (1942), according to which any attribute of the organism by which it could be compared with other organisms in terms of similarity and relationship should be considered a taxonomic character. Such a general definition allows the entire set of features of the study object to be included in taxonomic analysis, without any artificial limitations. Yet, for a long time the concept of "character" had an almost purely morphological sense, which brought about doubts of its appropriateness at the level of study higher than a merely diagnostic one (Yudin, 1974). This fact was also reflected in the common Hennigian terminology, in which many new terms ended with *-morphic*. This trend was also preserved to some extent in the tradition of classifying characters by their phylogenetic

significance into the principal, or conclusive ones (morphological) and auxiliary ones (ecological and geographic) (Emeljanov, 1980). Such discrimination may be valid if done *a posteriori* for a particular taxon. However, *a priori* these characters should be treated as equal; only phylogenetic analysis itself can determine which of them are more important, or "weighty."

The broad concept of a taxonomic character implies classification of characters by their nature (Mayr et al., 1956); for instance, characters may be subdivided into morphological (including molecular and molecular cytogenetic ones), physiological, ecological, ethological, geographic, etc. The principle of integrated phylogenetic research demands the use of all these categories if possible. In this connection one cannot help mentioning the suggestion of Wolfgang Hennig in the posthumous edition of his father's book (Hennig, 1979) that the term *plesiomorphic* should be replaced by *plesiotypic*, *apomorphic* by *apotypic*, etc.

Significance of Ecological and Ethological Characters

As practice of taxonomic research shows, different characters may prove to be conclusive in phylogenetic analysis at different levels of taxonomic hierarchy and in different groups. A set of morphological (anatomical) characters is usually sufficient for reconstruction of the phylogeny of high-ranked taxa. However, many insect groups, for instance, Lepidoptera, show a very complicated pattern of morphological evolution, manifested in different tempos of development and mosaic distribution of homologous characters, and also parallel formation of some most important structures, including those determining the level of organization in the given group (Sinev, 1988). Therefore attempts at reconstructing phylogeny using only morphological characters face serious difficulties, especially when working with small phytophagous forms usually characterized by intensive adaptive radiation and strictly canalized morphological evolution. A high evolutionary potential and the resulting extreme abundance of phytophagous insects in practically all the landscape-climatic zones is primarily determined by variability of their ecological "microniches" and forms of behavior. Divergence in phytophagous insects at the species and even genus level often seems to occur mostly with respect to ecological and ethological characters (Gilyarov, 1974; Starobogatov, 1977, 1985; Sinev, 1989).

The study of ecological and ethological characters faces evident difficulties. First of all, such characters are not always easy to describe in the formal way suitable for phylogenetic analysis. It may also be difficult to obtain representative material on the ecology and ethology of members of all the key taxa for some little studied group. However, this is no reason at all to give up using such characters in phylogenetic reconstructions. An evidently adaptive nature of many ecological characters should not confuse researchers either, since it does not always imply the inevitable and very high variability of such characters in the direction of the acting selection vector.

The Principle of Integral Research

The basic requirement of evolutionary taxonomy immediately associated with its dialectical nature is the complexity of any phylogenetic study. This principle effectively counterbalances various manifestations of reductionism, which are rather common in taxonomy. The principle implies the following requirements:

(1) The study of the maximum number of different taxa, both within the group in question and within the group of a higher rank including it. For instance, the classification of a family adequate to its phylogeny is difficult or in some cases impossible to achieve without revealing the evolutionary trends and relationships within the respective superfamily or infraorder. The task of studying as many taxa as possible requires work at the scale of the world fauna. Phylogenetic schemes and the corresponding classification systems based on the regional material not only suffer from incompleteness but may also contain serious errors due to insufficient sampling.

(2) A clear understanding of the fact that the evolutionary process involves the entire ontogeny of the organism and not individual characters, organs, systems, or phases of its life cycle. Regrettably, this self-evident idea convincingly demonstrated by I.I. Schmalhausen in his book *The Organism as a Whole in Individual and Historical Development* (1942) is very often completely ignored. Transition from evolution of whole organisms to evolution of individual characters or systems of characters should be regarded as one of the most typical manifestations of reductionism in taxonomy. Separation of characters from real organisms is admissible only at the early stages of phylogenetic analysis as a useful assumption.

Given the usual scarcity of the fossil record, the researcher is simply forced to consider phylogeny actualistically, proceeding from reconstruction of evolutionary changes in individual characters and assuming that these changes are adequate to the historical development of the taxon as a whole (Severtsov, 1981). However, transformation series of characters, or semogeneses (Pavlinov, 2005), always provide only approximate reflections of the phylogenetic process. Therefore it very essential, especially when studying insects with a complex life cycle, not to limit the research to individual phases of this cycle, however important they might seem for the particular task.

(3) Analysis of the largest possible number of various characters, without limiting oneself to the commonly used morphological ones. An attempt at building natural classifications (i.e., those reflecting phylogeny) on the basis of studying one or several characters is almost certainly doomed to failure, for quite obvious reasons. Any taxon of a high rank is a real monophyletic group or “a bunch of lines” (Pesenko, 1989) and has a certain integrity based on a large set of quite different characters. Some of them are interdependent and correlated, whereas others can develop relatively independently and even in different directions. A complete match between “phylogeny” of a character and phylogeny of its bearer seems to be a fairly rare phenomenon. In view of this, a more objective assessment of the phylogenetic significance of the observed similarities and differences and, therefore, understanding of the true ways of evolution of any natural group requires a parallel study of comparative morphological series of many structures taken together, i.e., a complex of characters.

The Procedure of Phylogenetic Analysis

The comparative morphological part of the empirico-intuitive approach typical of E. Haeckel's phylogenetics, i.e., the process of obtaining the necessary data (characters), has always possessed a more or less strict scientific basis; by contrast, the very process of phylogenetic reconstruction looked rather more like art. One of the most important events in the development of taxonomy was establishment by W. Hennig of the strict procedure of phylogenetic analysis, based on the hypothetico-deductive method, which allowed this field to comply with stricter scientific criteria. At present, intuitive phylogenies are practically never to be found in their pure state but are almost always sup-

plemented with the Hennigian terminology and methodology of character analysis.

The so-called “cladistic” analysis (Neff, 1986), i.e., the process of revealing relationships within the group in question, is the next level of phylogenetic research after analysis of characters. It consists in a multistep process of suggesting and testing phylogenetic hypotheses. Without dwelling upon the detailed criticism of the strictly cladistic approach, it is worth noting that acceptance of a cladogram based on selected analyzed characters as the final goal of phylogenetic research means that organisms are regarded as mere “carriers” of certain characters. The so-called “phylogenetic taxonomy” typically considers the optimal cladograms obtained by a parsimony-based search procedure to be self-sufficient; this often results in abstract schemes having no rational explanation within the framework of the evolutionary theory and incapable of standing even elementary test for the adequate reflection of natural processes.

Modern statistical approaches, based on the maximum likelihood method or the Bayesian method as its more advanced variant, allow one to overcome such evident limitations of cladism as admission of only strictly dichotomic evolution patterns and only holophyletic taxa, and exclusion of plesiomorphic characters. These approaches work for any homologous characters, both apomorphic and plesiomorphic, whereas the evolutionary lineages do not have to be interpreted as monophyletic or paraphyletic taxa (Lukhtanov, 2010).

Interpretation of the results of the entire phylogenetic analysis is a kind of summit of the taxonomist’s work; its goal is to understand organisms as integral subjects of the evolutionary process. This can be realized in terms of the “evolutionary scenario” of the group in question.

Evolutionary Scenarios

In the past, evolutionary scenarios, or historical narratives as they are sometimes called, constituted all but the only method of phylogenetic reconstructions despite their inevitable speculative nature. With elaboration of a stricter procedure of phylogenetic analysis, this method was pushed aside or even fell completely into oblivion, especially in the works of the adherents of cladism. At the same time, any historical narrative may be considered as an evolutionary explanation of the cladogram from the viewpoint of close association

between phylogeny and the conditions under which it was realized. Creation of an evolutionary scenario logically concludes phylogenetic analysis proper and includes such essential elements as reconstruction of the hypothetical common ancestor (archetype) of the group, revealing the probable specific biological features of the ancestral forms and the main ways of their further adaptation, and also analysis of the driving forces of the main evolutionary transformations which resulted in the current diversity of taxa of various ranks.

The evolutionary scenario is the synthesis of the results of phylogenetic analysis and the data obtained by many other scientific disciplines (paleoecology, paleoclimatology, paleogeography, etc.). In the process of its creation, the conclusions drawn are matched against the sum total of natural-scientific knowledge available. The evolutionary scenario thus becomes an important tool for testing the proposed phylogenetic hypotheses (Pesenko, 1989) and as such, should be an integral part of an adequate taxonomic research.

System and Phylogeny

Phylogeneticists often follow the motto: let us reconstruct phylogenies without attaching too much importance to their taxonomic interpretations, since such interpretations are always subjective and have only an applied meaning (Felsenstein, 2004). This is not at all surprising since it is at such attempts to pass over from cladistic phylogeny to the cladistic system that the most serious problems arise. Strict correspondence between the branching points of the phylogenetic tree and individual divergence events, and also between the limits of taxa and those of the distribution of some characters or groups of characters considered to be the most essential by a particular author is bound to introduce a considerable bias into the whole construction. With such an approach, subsequent reconsideration of the value of a single character may result in radical changes in the entire phylogeny, which determines the instability of the resulting classification.

Construction of phylogeny should not be considered as a self-sufficient task since the goal of taxonomy as a science is description of the recent and past biodiversity and systematization of the accumulated knowledge in an easily accessible form. Another important task to be solved by any taxonomist is interpretation of the revealed evolutionary lines as taxa, i.e., the construction of a system.

It is often assumed that the best system of the group should almost perfectly reflect its phylogeny. This trend has evident negative consequences: a desire to name each clade, introduction of a great number of intermediate taxonomic ranks, and endless shuffling of names of higher taxa under the pretext of achieving the maximum adequacy, which are capable of misleading even an experienced researcher. In fact, however, the goals of reconstructing phylogeny and building a system are fairly different. The system cannot and should not fully correspond to phylogeny; it simply should not contradict it. Any classification should be not only maximally predictive but also convenient in use, a demand which often contradicts the exact branching pattern of the phylogenetic tree.

In this connection, the problem of taxonomic ranks and the nomenclature cannot be considered idle or lying beyond the scope of "strict" science. The goal of nomenclature is not only to catalogue living organisms but also to provide a universal language of communication which may be used to discuss different problems of biodiversity with the most general audience. In order to meet these demands the nomenclature should be "descriptive," easy to memorize, and certainly as stable as possible.

On the Correlation of Research Methods

In spite of considerable progress achieved by taxonomic entomology during recent years, serious problems in the field of the system of insects as a whole and some of their large groups remain unsolved.

Traditional morphology is not always capable of solving these problems. Reliable data on many insect groups are still insufficient (Kristensen, 1981, 1999; Whiting, 2000); therefore one of the main tasks of further studies should be to obtain more representative morphological matrices with a complete set of characters, well documented for all the taxa in question. This task requires not only intensive accumulation of new data and revision of previous ones but also precise description of characters, evaluation of their quality, reduction of gaps, perfection of data processing methods, etc. The scarcity of data is even more evident in paleontology. Many taxa are very poorly represented in the fossil record, whereas some characters, highly essential for detection of relationship between extinct and recent forms, are very badly preserved in fossils.

The use of modern technologies, allowing new characters to be used in analysis, is important for both comparative morphological and paleontological stud-

ies. Recently, such investigations have been based not only on the traditional dissection technique; innovative morphological approaches have been worked out, such as computer-assisted 3D reconstruction which may be coupled with multilayer image analysis, confocal laser scanning microscopy, micro X-ray computed tomography, and other methods.

Euphoria caused by the first results of molecular genetic studies is also gradually passing. It is now obvious that the study of nucleic acid sequences, which has become an integral part of taxonomy and an important tool of biodiversity analysis, should not be considered as an alternative to classical morphology for resolving the relations between organisms (Wheeler, 2004; Will and Rubinoff, 2004).

In general, one should not expect fast and unambiguous solutions of the problems facing insect taxonomy, either when using only "old" morphological, or exclusively "new" molecular data. It is important to realize that each method of research has its advantages and drawbacks and only their combined use allows one to obtain convincing answers to the most complicated questions. Such a broad (total evidence) approach is increasingly applied to phylogenetic research (Wheeler et al., 2001; Beutel and Pohl, 2006; Grimaldi, 2010). The new bioinformation technique of supertree analysis (Yeates et al., 2003), inferring phylogenetic reconstructions from dissimilar data matrices (with partly non-overlapping sets of taxa and/or characters), may also prove useful for studying such diverse and complex taxa as insects.

The need of performing integrated phylogenetic analysis of particular taxa requires unification and coordination of the efforts of research teams working in the fields of classical morphology and molecular genetics. This step would allow us to hope that in the near future effective collaboration of classical taxonomists, morphologists, embryologists, paleontologists, and molecular taxonomists will lead to development of a well grounded phylogenetic hypothesis and a consistent and entirely natural system of insects. To achieve this, the traditional "morphological" taxonomists should overcome a certain bias against the novel molecular concepts, whereas molecular taxonomists should not forget that in the long run, they study living organisms rather than abstract molecules and genes.

CONCLUSIONS

(1) The problem of correlation between the traditional and new methods of taxonomic work is always

in existence due to the continuous development and enrichment of knowledge of biodiversity and methods of analysis and structuring of this knowledge.

(2) The comparative morphological method has been and still remains the cornerstone of insect taxonomy. It is this method which can yield extensive and versatile information on the organisms, especially when supplemented with data on functional morphology, embryology, and analysis of the adaptive significance of characters. The limitations of this method are first of all related to cases of evolutionary parallelisms, reversions, and other phenomena making the restoration of phylogeny more difficult.

(3) The comparative paleontological method is the only one producing direct evidence of the historical sequence of taxa and their characters. However, this method is not fully applicable in all the groups, due to specific traits of their morphology or taphonomy.

(4) The recent methods (cytogenetic, molecular genetic, and others) are fairly informative but also have limitations of their own; they should not be contrasted with the classical ones and certainly should not replace them. The traditional approaches do not become obsolete, though their relative importance in the set of taxonomic tools may change. None of the methods can be considered universal for an unambiguous reconstruction of phylogeny and substantiation of the natural system of taxa. Each method has its advantages and drawbacks, and only combined use of different approaches expands the range of problems which may be solved.

(5) Different approaches may prevail in the studies of different groups of insects and at different levels of taxonomic hierarchy. The intuition of the taxonomist, which is so often criticized by the followers of the so-called “objective” methods, is not at all a synonym of subjectivity; it allows the scientist to select the set of research instruments in view of his experience and scope of knowledge.

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