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Conceptual issues in phylogeny, taxonomy, and nomenclature

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Abstract

Phylogenetic hypotheses are designed and tested (usually in implicit form) on the basis of a set of presumptions, that is, of statements describing a certain order of things in nature. These statements are to be accepted as such, no matter whatever evidence for them exists, but only in the absence of reasonably sound evidence pleading against them. A set of the most current phylogenetic presumptions is discussed, and a factual example of a practical realization of the approach is presented.

A comparison is made of the three main taxonomic approaches hitherto developed, viz., phenetics, cladistics, and phylistics (= evolutionary systematics). The latter term denotes an approach that tries explicitly to represent the basic features of traditional taxonomy and particularly its use of evidence derived from both a similarity and the relatedness of the taxa involved. The phylistic approach has certain advantages in the answering of the basic aims of taxonomy.

Taxonomic nomenclature is found to rely ultimately on a few basic principles. Nine of these principles are formulated explicitly: six of them are taxonomically independent, and three are taxonomically dependent, that is, they are only compatible with particular taxonomic concepts. Judging from current taxonomic practice, a taxon is neither a class nor an individual, but a continuum (a notion combining some features of both the class and the individual) of subtaxa that is delimited by a gap separating it from other such continua. The type concept is found to be the best available tool to operate within the concept of the taxon-continuum.

Résumé

Les hypothèses phylogénétiques sont élaborées et vérifiées (normalement de manière implicite) sur la base d'une série de présomptions – en d'autres mots, d'assertions décrivant un certain ordre de choses dans la nature. Ces assertions doivent être acceptées comme telles, indépendamment des preuves à leur appui, mais seulement en l'absence de preuves assez solides contre leur validité. On discute une série de présomptions phylogénétiques des plus usuelles, et on présente un exemple concret de réalisation en pratique de cette manière d'aborder le problème.

On compare les trois approches taxonomiques principales développées jusqu'à présent, à savoir la phénétique, la cladistique et la phylistique (= systématique évolutionnaire). Ce dernier terme s'applique à une approche qui essaie de manière explicite à représenter les traits fondamentaux de la taxonomie traditionnelle et en particulier son usage de preuves ayant leur source en même temps dans la similitude et dans les relations de parenté des taxons en question. L'approche phylistique présente certains avantages dans la recherche de réponses aux problèmes fondamentaux de la taxonomie.

L'auteur considère que la nomenclature taxonomique s'appuie, au fond, sur plusieurs principes de base. Neuf tels principes sont explicitement formulés, dont six sont taxonomiquement indépendants, les trois autres étant taxonomiquement dépendants (donc compatibles seulement avec certains concepts taxonomiques). La pratique taxonomique courante montre qu'un taxon n'est ni une classe, ni un individu, mais bien un continuum (notion combinant des traits distinctifs de la classe et de l'individu) de subtaxons, continuum séparé d'autres continua par une lacune. On considère que le concept du type est le meilleur instrument à notre disposition s'il s'agit de travailler avec le concept taxon-continuum.

Introduction

Frequently, scientists do not take much notice of the methodological grounds of their work. However, when the standard means and methods of the work time after time fail to yield satisfactory results, one is tempted to raise a kind of scientific revolution (Kuhn, 1970), i.e., to abandon those traditional means and methods along with the underlying methodology and to replace them with something different. Revolutions, even scientific ones, rarely pass bloodless, in that they usually result in rejecting certain approaches that are in fact workable, albeit in a somewhat different domain, while the data obtained by means of these approaches may still be meaningful and worthy of being reassessed rather than rejected. That is why it seems preferable to examine the methodological background of a scientific approach prior to abandoning it, in the hope to recognize and improve its methodological deficiency and thus to safeguard the approach and the results of its application. This is the objective of the present publication.

Two separate issues forced me to approach the methodological problems of descriptive biology. One was the long-lasting crisis of taxonomy that resulted in the continual conflicts between "traditional" taxonomy and the rival approaches – the phenetic and, later, the cladistic ones. Because of an intuitive feeling of a superiority of traditional taxonomy, I was involved in this controversy, although without much success (Ponomarenko & Rasnitsyn, 1971; Rasnitsyn, 1972, 1983a, 1987a, 1988b, 1992a; Rasnitsyn & Dlussky, 1988). Results of my attempts to develop my arguments are presented below in the chapters devoted to phylogeny and taxonomy.

As regards nomenclature, the cause is different in that it is rooted in my paleontological experience. Despite the long history of taxonomy and nomenclature, I believe the basic principles of nomenclature are only partly understood and formulated as such. Some of these principles are so simple and self-evident that their existence and application is perceptible only in peripheral areas of taxonomy. When one has to classify difficult objects deficient in taxonomically important characters (or even lacking them), one is often forced to break the rules of nomenclature. This is common practice in paleontology, in the study of immature parasitic worms, or of asexual stages of fungi, where a student cannot escape violating normal taxonomic practice and breaking the rules of nomenclature. An experience of this sort gives little satisfaction until the student begins to discern more deep-seated reasons why he has not followed the generally accepted rules. The reason why is that the underlying principles of nomenclature are incompatible with the taxonomically deficient material that nevertheless must be classified. This controversy renders these basic principles discernible, thus permitting their identification and study (Rasnitsyn, 1986; 1992b).

Phylogeny

Each step in cognition, while knowledge is acquired, in my opinion proceeds through four successive stages. First, we start seeking for known elements in an essentially unknown (i.e., not yet understood) pattern. On the basis of previous experience and/or the results of a preliminary confrontation with the pattern, we then sort these known elements as either important (i.e., relevant to the goal set), or as unimportant. In this context, the known elements of an essentially unknown pattern are considered important when we suppose that our knowledge of it permits us to discern (i.e., is correlated with, or otherwise reflects in one way or another) important features of the pattern. In turn, the important features are those that have a more profound influence on, or are correlated with, or otherwise permit us to appreciate and foresee, the structure of the pattern and its behaviour under various circumstances. For example, when an entomologist wishes to instate an in his opinion entirely new group as a separate taxon, he must also deal with the classificatory aspects of his proposal (I mean only the internal classification, not the general taxonomic position of that taxon). In this treatment he will disregard features, how significant per se, that discriminate males and females, or adults and larvae (except when it comes to subdivide the taxon in question and to classify each subgroup separately and eventually to compare the results with other data). In addition he will tend to give preference to morphological similarities over such features as colour patterns.

The second stage of cognition begins here. One creates a hypothesis concerning the particular similarity between the patterns under examination and a class of patterns that previously had been studied already but seemed to be dissimilar to the patterns in question. The supposition ought to be predictive, i.e., it should propose the existence of a particular mechanism that is responsible for the similarity, or it must clarify why there is also a similarity in many other characters. This subsequently allows us to hypothesize that the similarity can predict the behaviour of the pattern in question in various environments and conditions. To continue with the above example, the taxonomist will possibly pose that the similarity in morphological characters could indicate a higher (say, generic) level of the overall similarity, while the similar colour pattern concerns a lower one (say, the species level). In other words, the taxonomist would hypothesize that the inferred tentative classification is more natural, e.g., less burdened with homoplasies, than the alternative one that gives more weight to the colour pattern.

The two above-mentioned stages of cognition depend much on the personal experience and intuition of the investigator, whose formal cognitive nature is still obscure, and I shall not discuss these stages in detail here.

The third stage is to test the proposed assumptions. To reach that end we should propose the longest and most diverse chain of implications, in order to have a better opportunity to compare them with the results of our observations and experiments (for details see below).

The fourth and last step of cognition is to make a decision concerning the availability of each proposed hypothesis: whether any supposition can be retained for further testing, or must be rejected. Examples and a discussion follow.

The third step of cognition has been well studied by Karl Popper (1959), who clarified the fact that there is no way to verify a hypothesis definitively. Moreover, it is not possible to falsify a hypothesis completely, since this would mean the verification of an alternative hypothesis, viz. that the falsifying result arises neither by chance nor is due to neglected external influences (circumstances) (cf. Farris, 1983). Indeed, if you claim that all swans are white and yet encounter a black swan, prior to abandoning your claim you should reject the possibilities that (1) your black swan is not a swan (e.g., it is a convergently modified goose, or a skilful mystification, or something like that), and (2) your black swan is not naturally black (e.g., artificially stained black). I believe that these possibilities are always a matter of setting a likelihood and not just of giving a yes-or-no reply. It is for this reason that the fourth stage of cognition appears necessary when we consider competing hypotheses and assess relevant falsifying evidence in order to reach a decision.

Since both an ultimate verification and falsification are impossible, we can never be certain of any of our observations and considerations concerning the nature of things. If so, how can we live and work in a world which offers nothing definite to us and thus seems so unreliable? This is possible because I suppose we are skilful enough at making correct decisions with insufficient information (when information is sufficient and everything seems to be plain sailing, we act almost automatically and do not admit that we are making a decision). We do make mistakes, but they are (or, rather, were until now) not bad nor numerous enough to lead mankind to extinction.

The explanation of how we make such decisions has existed for a long time (Rasnitsyn, 1988b; Rasnitsyn & Dlussky, 1988). It has been found in courts of justice where information is often insufficient but where the “correct” decision is vital, given that the time needed for seeking a necessary “generalization” has been sufficient. This “generalization” is termed a presumption. This means that for a particular class of problems there exists a decision (or a class of decisions) that is considered to be generally the most likely or otherwise the safest. The decision is consequently to be accepted no matter what tangible evidence for it exists, but only in the absence of reasonably sound tangible evidence against it. Otherwise the alternative decision is to be accepted. The well-known presumption of innocence is based on the observation that for the health of our society it is more dangerous to punish the innocent than to leave a criminal unpunished. That is why a suspect is not generally considered to be a criminal unless the accusation is proved, no matter how strong the suspicion may be.

We can use the above conclusions to understand how we study phylogeny. Phylogeny is commonly interpreted as the history of a particular group of living organisms, their history being described in terms of a diminishing genealogical relatedness between its subgroups. In addition, it is commonly agreed that evolution proceeds too slow for immediate perception, so that phylogeny is perceptible only from its ultimate results, not from the process itself. These results consist of traits of form and function of organisms, including morphological, physiological, and behavioural characters, those concerning attitude of organism to biotic and abiotic factors, their distribution in space and time, and the like.

The first and central presumption in phylogenetic analysis is the postulation of "knowability" of phylogeny. It claims: *any similarity should be considered as inherited unless and until the reverse is reasonably proved.* Hennig (1966) calls this statement "the auxiliary principle", but it is far from being auxiliary. The central dictum of phylogenetic analysis is the claim that phylogeny is generally knowable. Indeed, "if homoplasy [independently gained similarity] is universal, the characters imply nothing about the genealogy" (Farris, 1983: 14).

This is not evident at once. A man does engender a man, and not an ape, under any conditions, but water can be equally obtained by either burning hydrogen or by oxidizing lipids inside organisms. The difference between the two cases evidently lies in the different level of complexity of chemicals vs. living beings. That is why living beings change in close dependence on their history, while changes in chemicals are essentially governed by circumstances and simple rules (not by their history).

Living beings are of different complexity. It has been suggested that in procaryotes the amount of independently acquired similarity is so vast that traditional methods are often of little help in discerning procaryote phylogeny (Zavarzin, 1987). Observations of this sort quite evidently impose restrictions on the domain of phylogenetic analysis.

There is another restriction. Generally speaking, the divergence of taxa of a lower order takes place in a less remote past than that of higher taxa. Hence it should leave clearer evidence of how such a divergence has proceeded. Nevertheless, we often feel that the genealogical relationships of species, especially those in larger genera, are much less manifest and more difficult to sort out than relationships of, say, families or subfamilies (cf. Saether, 1986). I am aware of the explanation of this phenomenon, viz., the hypothesis that homoplasy is a much more common event than students often think. This particularly concerns groups of closely related and thus highly similar forms whose almost identical organization enables them to react in a similar fashion to similar environmental changes. The problem certainly deserves close examination, which, however, lies beyond the scope of the present article.

When a group is meticulously studied, both with regard to paleontological as well as contemporary material, it is evident that extensive parallel evolution resulting in an abundance of homoplasies, is often characteristic of both higher taxonomic levels and species. Vertebrates may serve as an example, for they show numerous cases of parallel transition from the level of organization (grade) of fishes to that of amphibians (i.e., independent acquiring by groups of the characters generally characteristic of amphibians) and further to the level of organization of reptiles and mammals (or birds). In the last two decades this old theme has been under close examination by Russian students of evolution (Tatarinov, 1976, 1987; Shishkin, 1987; Vorobyeva, 1992). Under the old term aristogenesis (Osborn, 1934), this pattern is discussed by Rautian (1988).

Parallel evolution in closely related groups is commonly described as a manifestation of particular evolutionary tendencies intrinsic to a group. The tendencies can be understood as an epiphenomenon of the underlying synapomorphy (Saether, 1979, 1986; Sluys, 1989; a term of similar albeit not identical meaning is key apomorphy, proposed by Iordansky, 1977, 1979). The notion of underlying synapomorphy implies an apomorphy (any change in structure or function) that has been gained by the common ancestor of the group and that is present in some or many members of the group, probably because the genetic capacity to develop the feature is not expressed in every member of the group (cf. Sluys, 1989). For instance, the acquisition of the resilient longitudinal "string" (the chord and its successor, the backbone) that permits to accumulate the mechanic energy of the body bending, has been the common base for various chordate animals to obtain independently the fish-like general appearance whenever they become a strong swimmer (whales, dugongs, ichthyosaurs, tadpoles, etc.). Another case is the costal breathing, being a remote cause of the independent development of homoiothermy, as discussed by Iordansky (1977, 1979). Unlike these examples, however, we are rarely aware of the concrete causes that are responsible for the repeated acquisition of a particular feature by a particular group of organisms. Nevertheless, I believe that a real common cause, albeit yet unknown (but see Sluys, 1989, for suggestions) underlies the majority of cases of massive parallel evolution. This cause results in a tendency to develop the apomorphic character – hence the term "underlying synapomorphy".

Wide distribution of parallel evolution does not permit us to think of taxa as simple products of divergence of their common ancestor. Parallel adaptation of closely related forms to similar niches could contribute as well, especially if it is combined with a reduction of the "archaic diversity" (term proposed by Mamkaev, 1968). The process of parallel evolution as a whole can be described as taxon maturation, i.e., the accumulation of similar changes combined with the elimination of unbalanced (inadaptive in the sense of Rasnitsyn, 1987b) intermediate groups. This approach leads back to the old and well-known hypothesis of Darwin (1859) that gaps between extant taxa are in part (probably to a large extent) due to extinction of intermediate forms. This maturation often takes quite a long time. That is why higher taxa at later stages of their evolution are often more clear-cut and seem to have a more easily discernible phylogeny as compared to lower taxa, or even to themselves at an earlier stage in their history.

The hypotheses involved in explaining the pattern of extinction of intermediates are proposed elsewhere (Rasnitsyn, 1987b). Here it is important to note that the pattern described above seems to cause less difficulties for the phylogenetic study of eucaryotes than in the case of procaryotes. Anyhow, we are still able to construe a phylogenetic tree, although an assessment of its general validity is restricted. We can never be quite certain about the tree and particularly about its details, so that it becomes pointless to speak of an ancestral species of say, for example a family[1]. In quite a few cases, a thorough and sophisticated research has failed to identify even the ordinal position of the common ancestor of a class. And this may be true even if the real ancestor has already been collected and described, albeit not yet recognized among other fossils (Vorobyeva, 1992). In short, parallelisms affect cladograms by filling them with unresolved (polytomous as opposed to dichotomous) clades, but otherwise the above considerations change but little in the actual practice of phylogenetic study.

Further phylogenetic presumptions can be arranged in two gross classes according to whether the respective phylogenetic methods are directed toward the analysis of history of either groups or characters[2].

Group analysis

The main method of group analysis is the paleontological one, which has been recently redefined as stratophenetics (Gingerich, 1979, 1990). It is based on the presumption that *among two apparently closely related groups the one appearing earlier in the fossil record should be considered ancestral unless and until sound contradictory evidence is presented.* We shall call it the paleontological presumption for groups. The paleontological method is not universal in application because the fossil record is known to be incomplete. However, this incompleteness is neither vast nor due to chance, but rather regular. There is a special paleontological discipline called taphonomy that deals with the patterns of burial and fossilization of organisms, and it has already gathered a considerable amount of data relevant to those patterns (see e.g., Briggs & Crowther, 1990). In many cases, it is already known what kinds of organisms have a good chance of becoming buried and fossilized and stand a good chance to be excavated later and which do not, and what kinds of fossil environments stand a better chance to contain fossils than other ones. Additionally, deposits vary greatly in their degree of information. Using this information, it is often possible to infer with reasonable certainty whether a particular case of absence of a group from a particular section of the fossil record is due to a true non-existence or not.

For instance, fossil insects are found mostly in lacustrine and, especially in the Paleozoic, in shallow marine deposits (other sources of paleoentomological information became important only in relatively late stages of the group's history). That is why most fossil insects seem to be either flying or aquatic/semiaquatic, shore-dwelling forms. The bristle-tailed insects (Thysanura s.l.) are wingless, terrestrial, and not especially common along sea and lake shores. The Thysanura entered the fossil record later than the Pterygota [that is, at Westphalian vs. Namurian time; older findings described by Shear et al. (1984) and Labandeira et al. (1988) are based on fossils that are too fragmentary to be identified with sufficient certainty]. Absence of bristletails from the Lower Carboniferous (Mississipian) fossil record cannot be seriously taken as evidence that they could not be the Pterygote ancestors. On the other hand, hymenopterous insects are good fliers, and their absence from the pre-Triassic record should figure in any analysis using the above presumption; that is, until we have strong evidence, we should avoid hypotheses that require searching for a hymenopteran ancestor among groups that died out before the Triassic[3].

There exist other phylogenetic methods that rely on group analysis, first of all, the biogeographical method. Indeed, the aim of the method is to restore the history of a group in terms of its distribution. Groups are evolving on their distributional routes. Thus the distributional history of a group could correlate in a way with its genealogy, so that phylogeny may benefit from biogeography. There are problems, however.

The classic, dispersalist biogeography considers distribution of a group as a result of its individual dispersal through various barriers. Major factors of distribution are thus supposed to be (1) the geographic structure of the space, (2) the dispersal potential of the group, and (3) chance. Similar distribution patterns of two groups could imply their similar history, including genealogy, depending on similarity of the three above factors. However, it seems not particularly likely that all three factors will be essentially similar, so we should suppose that the pattern similarity is often due to chance. Therefore, under the classic concept of biogeography, the biogeographical method appears to be of doubtful value for phylogenetic analyses.

In contrast, the cladistic concept of biogeography (the treatment here based mostly on the summary by Humphries & Parenti, 1986) considers the distribution of plants and animals as a result, both phylogenetic and geographic, of barriers imposed by various physical agents (primarily connected with continental drift, but also of a climatic nature, etc.) on a continuous ancestral distribution. The approach ignores unique events and relies solely on the pattern that repeats in various groups that frequented the areas under investigation. The congruent area cladograms (the cladograms with the animal/plant names replaced by the names of their populated areas) are interpreted there as the evidence of the respective area-dependent genealogy of all groups concerned.

A cladistic biogeography seems to fit ideally the objectives of the phylogenetic analysis of groups. In seeking a particular repeating pattern of area cladograms, we then should simply hypothesize isomorphic cladograms for each group involved. The matter is not so easy, however. Dispersion of organisms is known to be a common event and, depending on an existing system of barriers and on the dispersal potential of a group (which does vary but not in a disorderly way), is not necessarily so chaotic as to be easily sorted out as producing unique area cladograms. Regular dispersal events may produce repeating patterns of area cladograms that could be easily but deceivingly interpreted in terms of cladistic biogeography. Unless research could demonstrate a subordinate role for dispersion in the origin of the area cladogram patterns, I would refrain from using the biogeographical method in restoring genealogy.

There is another serious reason to be cautious as regards the prospects of the biogeographical method as a phylogenetic tool. Both classic (dispersalist) and cladistic biogeography pay little attention to extinction events. And yet they are not only very common but often consistent enough to concern the entire biota. The area cladograms affected by extinction can produce a pattern easily but wrongly interpretable by the cladistic method. For example, there are numerous cladistic reconstructions of austral ("Gondwanian") distribution patterns (for a review, see Humphries & Parenti, 1986). I suspect that most of them are of no use, because the fossil record, if it exists, quite often shows that at some time in the past presumed austral groups occurred in northern continents and became extinct there (for details, see Eskov, 1987, 1992). Austral paleontology is often less complete than the boreal one, and yet there are finds of austral fossils known for groups that now seem to have a strictly boreal distribution (same references). Similarly, extinction could be indeed responsible for the amphitropical (bipolar) distribution of many taxa. These amphitropical distributions, instead of being a heritage of a hypothetical Pacifica continent (Humphries & Parenti, 1986), are more likely to be remnants of past world-wide distributions that have become separated by the tropical biota that originated in the equatorial zone probably during the Eocene (Razumovsky, 1971; Zherikhin, 1978, 1993). Unfortunately, tropical paleontology is more poorly developed than the austral one. Nevertheless, it is of importance that there are no sound indications of equatorial Late-Cretaceous non-marine biota comparable with the tropical ones of the present (Meyen, 1987). The only known relevant and comparatively rich fossil arthropod assemblage (ca. 200 specimens buried in the Late Cretaceous or earlier Paleogene amber from Burma), now under my investigation, has revealed no characteristically tropical forms. Instead, among the fossils already identified, there are several groups very common in assemblages from the Late-Cretaceous fossil resins of North Siberia and Canada, e.g., the hymenopteran genera *Serphites* Brues, 1937 and *Palaeomymar* Meunier, 1901 (Rasnitsyn, 1980; the latter genus is extant and at present at least predominantly extratropical and bipolar). Additionally, there are fossil groups that have survived with either a northern (snakeflies, insect order Raphidiida), or a bipolar (*Phryssonotus* Scudder, 1885, a millipede) extratropical distribution (Condé, 1954). *Phryssonotus* is now known from the Mediterranean, South Africa (Cape Province), South Australia (New South Wales), Uruguay, Chili, and Cuba (the Cuban record is equivocal zonally, because the lowlands of the island are tropical and the more elevated territories subtropical). In contrast, in the Late Eocene, as the Baltic amber specimens witness, *Phryssonotus* extended far into the northern extratropical zone.

There is some even stronger evidence that the past Burmese forest that has yielded the fossiliferous amber differed fundamentally from the tropical rain forest as we know it. Unlike the tropical assemblages from the later Paleogene Mexican and Dominican ambers, as well as those from the Miocene of Sicily and northern Apennines (Zherikhin, 1993), the Burmese assemblage is completely devoid of the isopteran family Termitidae, and of social bees, and higher social ants. As was demonstrated by Zherikhin (1978, 1993), these are the three animal groups that play key roles in the functioning of tropical rain forests, and possible functional analogues are not known nowadays, nor did they occur in the past.

It follows that the repeated pattern of area cladograms is still meaningless unless it is substantiated by a reasonably complete fossil record. That is why I believe that we still have much to do before it will be possible to formulate a workable set of biogeographical presumptions for the analysis of taxonomic groups.

The same holds true for other apparently relevant methods, e.g., the parasitological approach, which suggests the use of the cladogram of the host as a model for that of the specialized parasite, or vice versa, depending on which cladogram looks more promising (see Brooks & McLennan, 1991, for an overview).

Character analysis

Character analysis is used either to polarize the transformation series (morphocline), or to falsify suppositions of a unique origin of similarity

Polarizing transformation series. – There are several methods for polarizing transformation series: (1) The paleontological method is similar to that described above as a method for group analysis (stratophenetics). These two applications are independent of one another, however. Homoplasies are paleontologically shown to be not only fairly common, but also often to have a similar direction in various contemporary groups. The cases of mammalization of the theromorph reptiles (Tatarinov, 1976, 1985) and angiospermization of the gymnospermous plants (Krassilov, 1991) are good examples. That is why in many cases we can use the presumption that *a transformation series should be* *polarized according to the succession of the respective character states in the fossil record, unless and until sound contrary data are presented.* This presumption will be particularly useful in groups that are well represented in the paleontological record with an inconclusive morphology (either by being simple and thus poor in characters, or teeming with homoplasies).

(2) Another and very similar method is the ontogenetical one. It is based on the biogenetic presumption: *Transformation series should be polarized in agreement with the ontogenetic succession of the respective character states, unless and until there are serious reasons to decide otherwise.* In fact, this presumption just rewords the famous Von Baer's (1828) "law" of the differentiation through ontogeny, claiming that *"Aus dem Allgemeinsten der Formverhältnisse bildet sich das weniger allgemeine und so fort, bis endlich das Speciellste auftritt"* (p. 224; Von Baer's italics). Or, in translation: "From the most general relationships [that is, beginning from synapomorphies of the most inclusive taxa – AR], develop the less special ones [synapomorphies of the less inclusive taxa], and so on, until the most special relationships [synapomorphies of the terminal taxa] appear".

There is a widespread belief that the "biogenetic law" has extraordinary importance (as a "direct argument") in phylogenetics (e.g., Nelson, 1978; Bonde, 1984). I do not believe this. Ontogenesis is flexible, any of its stages can be possibly modified secondarily or it may get lost due to paedomorphosis, pre-adult adaptation (caenogenesis), or in the process of rationalization (streamlining) of the developmental path. As a result, the biogenetic method, while highly effective in deciphering the phylogenesis of some groups, can often be misleading. It has no a priori advantage in comparison with other methods, and does not work as a hard rule but only as a presumption. Indeed, the ontogenetic succession of developmental stages is a result of direct observation. The same holds true for the stratigraphic succession of fossils and their traits, as well as for the pattern of character states over the system of organisms. Each of these three sets of data leaves some traces and thus reflects, in one way or another, the process of descent of living beings. Each of them deserves to be used as material for phylogenetic inferences, and the results should be evaluated according to their own merits, not after an a priori principle. Bonde's (1984) example of human paedomorphosis is instructive: we infer that the human skull is paedomorphic solely because we know the topology of the anthropoid cladogram from other sources (primarily from taxonomic patterns of various character states, particularly from the structure of DNA, see below). Otherwise, basing ourselves on ontogeny per se, we could infer that the human skull features are symplesiomorphic with respect to the gibbons and monkeys, while those of the great apes could be synapomorphic.

(3) The next important method and presumption are the method and presumption of analogy: *If a transformation series is polarized in a group, the results should be considered as valid for another group, unless and until sound contrary data are adduced.* Indeed, if we are reasonably sure that the bat wing is a modified leg, we can legitimately believe it to be an example of what prevailed during the evolution of pterosaur and bird wings as well. However, to pose a similar hypothesis concerning insect wings is less evident because of great differences between the groups and the important dissimilarity of their wings. Nevertheless, it is not completely absurd. Kukalova-Peck (1978) argues (not without reason: cf. Rasnitsyn, 1981) that the insect leg and the insect wing are both modified parts of a biramous ancestral leg, but Bitsch (1994) disagrees. Likewise, we know that most mammalian lineages evolved in the direction of increasing body size ("law of phylogenetic growth", Cope, 1904). Therefore we should infer this direction of evolution everywhere in mammals where no sound contrary evidence is found. The same holds true for many other so-called empirical laws of evolution.

(4) The well-known polarizing method using functional efficiency can be formalized as based on the presumption of functional efficiency: *Of two character states the one corresponding to a more efficient adaptation should be considered apomorphic, until and unless there is reliable contradicting evidence.* For example, viviparity is generally considered as apomorphic in comparison to oviparity because it secures the safety of progeny better than the latter (it permits viviparous animals to sur-

vive despite a lower mean number of offspring).

(5) Subordinate to the above presumption is that of complexity: a more complex device is more wasteful of resources and thus originates only if it is more efficient. That is why *complex structure should be considered as apomorphic in relation to a more simple one, unless and until we have strong reason to decide otherwise.* Indeed, complex structures often tend to become simpler and more efficient in the course of evolution (compare e.g., the primitive therian paw and the horse's hoof).

(6) Such secondarily simplified structures commonly display rudiments or other signs of their lost complexity, indicating one more polarizing presumption, viz., the presumption of vestiges: *The character state showing any signs of being modified from another state is apomorphic over the latter, unless and until there is strong contrary evidence* (e.g., until it is found that what we took for the vestige is in fact an *Anlage*).

(7) The last and most popular polarizing method is the outgroup comparison. It is a probabilistic test for conformity of a cladogram with our basic phylogenetic model (evolution is generally divergent, and homoplasies are not so abundant as to make similarity say nothing about genealogy: cf. the first presumption of knowability of phylogeny, p. 6). In this model, a character state acquired by a more remote ancestor has a chance to persist in a wider range of descendants than that which appeared later in the same group. When we can see a character state represented both within a group and beyond its limits, and another one which is found only within that group, we should infer (unless there are strong contrary arguments) that the first character state is plesiomorphic, and the second apomorphic. This is because, when doing so, we could infer only one evolutionary change that took place at the origin of a subclade of the group in question. Otherwise, hypothesizing the first character state apomorphic and the second plesiomorphic, we should imply at least two identical evolutionary changes – one within the group, and another beyond its limits. If we agree that the inherited similarity is more likely (more common) than the independently acquired one, then, all other things being equal, we should conclude that the second hypothesis is less likely (or less parsimonious; see below). Keratin scales are known in all amniotes, hair only in mammals (and in some related reptiles: Tatarinov, 1976; the homology of the pterosaurian hairs described by Sharov, 1971, is still to be proved). Similarly, feathers are known only in birds (and again in some related reptiles, cf. Kurzanov, 1987). These cases are typically subjected to application of the outgroup presumption, which claims: *A character state found only within a group should be considered apomorphic in respect of that distributed both within and outside the group, unless and until strong contrary evidence appears.* The application of this presumption to the above transformation series should result in the hypotheses that both hairs and feathers are apomorphic and scales plesiomorphic.

Similarity analysis. – The similarity analysis was characterized above as pursuing discrimination between inherited similarity and homoplasy. If we consider our first presumption ("similarity is inherited unless and until...") as valid, the similarity analysis is not necessary until the "unless and until" applies. It is only when we encounter similarities that are distributed in a contradictory way that we ought to analyse them. The distribution is contradictory when the similarities cannot be all considered as inherited: if we accept the similarity of whales to other mammals in their homoiothermy as inherited, we must treat their swimming adaptations as acquired independently of fishes, and vice versa.

There are two main methods to detect homoplasy: (a) The presumption of parsimony, which is in turn one more implication of our first presumption. Indeed, if similarity is usually inherited and only less commonly appears as a homoplasy, then "homoplasy ought not to be postulated beyond necessity" (Farris, 1983: 8), and *the most likely cladogram is that implicating the least number of homoplasies, unless and until there are sound reasons indicating another cladogram as the most likely.*[4] But why again "unless and until?" Why is parsimony only a presumption and not a hard rule, or even a law as many students believe? It is so because characters are not equal. If we consider similarity between mimicking butterflies and count each similar element in their colour pattern separately, and then we count similarities of each mimicking species to its relative, I am not sure that the result will always be pleading in favour of true relatedness. Similarities do vary in how reliably they indicate relatedness, depending on what kind of character state is involved. We generally assess similarity in the type of symmetry or in the gross structure of basic organs as more important phylogenetically than, say, a colour pattern or details of the surface structure. However, exceptions exist even here, for all mammals are similar in absence of blue pigments from their hairs, not to mention the importance of differences in pigment sets for procaryote and plant taxonomy. Nevertheless, a colour pattern is generally considered as only of subsidiary phylogenetic importance.

The above observations indicate that the phylogenetic importance of one and the same sort of similarity varies greatly depending on what taxa are compared and what characters are involved. Therefore, I believe, we should operate by use of weighted characters when discriminating homoplasy. Hard rules seem to be impossible to describe the situation, at least for the present. That is why we have to rely on one more presumption: (b) the presumption of weighted similarity. In fact there are quite a number of such presumptions, and some of them have already been discussed elsewhere (Rasnitsyn, 1988b; Rasnitsyn & Dlussky, 1988). However, many more efforts are needed to clarify the problem in detail, so I can only safely propose here a generalized definition: *In the case of conflicting similarities* (when not all similarities can be accepted as inherited) *those which should be considered as inherited are known to be more reliable in other cases (especially in closely related groups), unless and until strong contra-arguments appear.*

Examples

How we can use the above presumptions is better illustrated with examples. I think that the early evolution of the hymenopterous insects, and particularly the problem of the phylogenetic position of the sawfly family Xyelidae, seems appropriate, since it is a difficult case and the subject of long-lasting disagreement. Unless stated otherwise, the discussion below is based on my previous relevant papers (Rasnitsyn, 1969, 1980, 1983b, 1988a & c, 1990; and references therein).

The hymenopterous insects (order Vespida; the reasons for using this name instead of Hymenoptera are given in Rasnitsyn, 1982, 1988a, 1989) first appear in the fossil record in the second half of the Triassic period. These Triassic species have been found in both Australia (one species) and Central Asia (two dozen species). These all belong to the family Xyelidae, as indicated by their characteristic wing venation and antennal structure (Fig. 1). The family survives in the northern Hemisphere as a relict group comprising 5 genera and about three dozen species, but not until the mid-Cretaceous did it become one of the leading hymenopterous groups – at least in more temperate climates.

Other hymenopterous groups appeared later than the Xyelidae and are not recorded before the Early Jurassic. This makes it possible to apply the paleontological presumption for groups and to propose a hypothesis that Xyelidae could be ancestral to all other hymenopterous insects. This hypothesis is in agreement with most of the other observations that show this family to be the most plesiomorphic within the order as regards all its characters, with the only exception discussed below. Indeed, the xyelid wing venation is the richest, having the highest number (the most complete set) of veins and cells, and resembles that of other insects most: the fore wing with its RS diverging into two branches in a way similar to that of various primitive insects and with supernumerary SC veinlets in some fossil species, and the hind wing with free Cu base. The same holds true as regards the body morphology and supposed groundplan bionomic features. Particularly relevant is the suggestion that their development inside gymnosperm staminate cones was possibly retained from the earliest holometabolic insects (Rasnitsyn, 1980). Plesiomorphies are cladistically unimportant, however, so that we have to scrutinize the nature of the xyelid antenna, the only character not easily to be disregarded as the autapomorphy of the family.[5]

The xyelid antenna (Figs. 2, 3a) is evidently apomorphic in respect to a normal insect antenna,

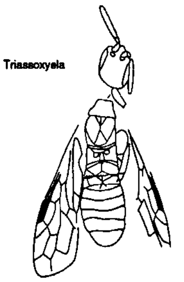

Fig. 1. Triassoxyela foveolata Rasnitsyn, 1964 (Vespida, Xyelidae); Middle or Late Triassic of Kirghizia (after Rasnitsyn, 1969).

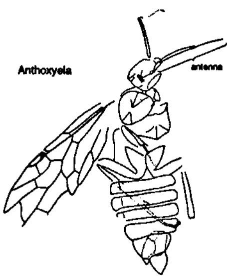

Fig. 2. Anthoxyela turgensis Rasnitsyn, 1990 (Xyelidae); Lower Cretaceous of Transbaikalia (after Rasnitsyn, 1990).

with several basiflagellar segments fused into a long and thick compound “third” antennal segment. The latter is mounted apically with a thread of normal (thin and short) flagellar segments. The apomorphic nature of such an antenna is supported by the application of a number of the above presumptions. The paleontological presumption for groups is relevant because the closest and oldest non-hymenopteran group (the extinct order Palaeomanteida = Miomoptera, Fig. 4) had normal antennae. The respective presumption for characters is also applicable, because all known pre-Triassic insect antennae do not display xyelid apomorphy. The same holds true for the biogenetic presumption, because at the earlier developmental stage (Fig. 3a) the antennal segmentation is more homonomous than in the adult insect. Equally important is the presumption of analogy, because the similarly inflated (though not evidently compound) 3rd antennal segment of flies (Fig. 3f) is certainly apomorphic. The outgroup presumption suggests the same conclusion, for the xyelid antenna type is found only within the Vespida while the normal one is common both within and outside this order.

Some of the above presumptions seem to yield the same result when also applied intraordinally. It seems to be especially true in outgroup comparison, because the normal antenna type is widespread within the order, and this is not the case with the xyeloid one. This inference is probably erroneous, however. Indeed, although among the living insects the xyeloid antenna in its full appearance occurs only in that family, also the antennae of some lower hymenopterous insects (sawflies and horntails) can be described as variously modified xyeloid antennae. The least modified of them are the antennae of the tenthredinoid families Blasticotomidae and Argidae. Both of them have the “third” segment even hypertrophied as compared to that of the Xyelidae themselves, but the following segments are reduced to a single one (in some Blasticotomidae), or became completely lost (Figs. 3b–c).

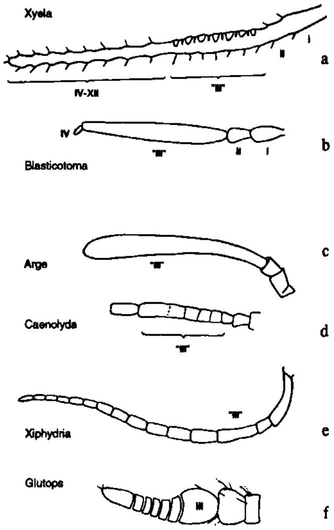

Fig. 3. Antennae of various sawflies, horntails, and flies (unless stated otherwise, of imago): a, *Xyela julii* Brébisson, 1818 (Xyelidae, pupa); b, *Blasticotoma filiceti pacifica* Malaise, 1931 (Blasticotomidae); c, *Arge ustulata* (Linnaeus, 1758) (Argidae); d, *Caenolyda reticulata* (Linnaeus, 1767) (Pamphiliidae); e, *Xiphydria camelus* (Linnaeus, 1767) (Xiphydriidae); f, primitive fly *Glutops semiformis* Nagatomi & Saigusa, 1970 (Rhagionidae) (a–e, after Rasnitsyn, 1968; f, after Nagatomi, 1982). I–XII = segments of antenna, “III” = compound “third” antennal segment.

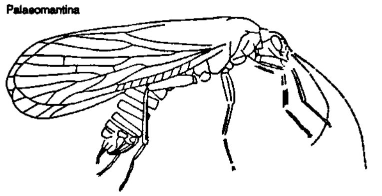

Fig. 4. Palaeomantina pentamera Rasnitsyn, 1977 (Palaeomantiscidae, order Palaeomanteida); Lower Permian of Ural (after Rasnitsyn, 1977).

Another source of evidence is provided by the living pamphiliid sawflies and siricoid horntails. Pamphiliidae (except some species of *Pamphilius*) have the "third" segment subdivided but it is comparatively small, several times longer than the fourth and of subequal width (Fig. 3d). Less known, though no less important, is the antenna of the primitive horntail genus *Brachyxiphus* Philippi, 1871 (Siricoidea, Xiphydriidae) that has a rather thick and long "third" segment (subequal in length to three more distal segments combined), and additionally subdivided into 4 primary segments in males of *B. grandis* Philippi, 1871 (specimens were studied in the collection of the Smithsonian Institution, Washington, D.C.). Most if not all other Xiphydriidae also have this segment somewhat enlarged (Fig. 3e), so this character state is possibly a part of the family ground plan.

The above distribution of the compound 3rd antennal segment can be explained by its independent development in five different groups. That number doubles, however, when we consider data reported by Van Achterberg & Van Aartsen (1986: tables 1, 2, fig. 366) and suppose that the composite structure of the segment was never lost (cf. Fig. 11).

The cases of an independent acquisition of the compound segment become even more numerous if we take fossils into consideration. The fossil collections of the Paleontological Institute, Russian Academy of Sciences, Moscow, are particularly demonstrative in this respect. These collections contain an overwhelmingly large number of Jurassic and Lower Cretaceous hymenopterous insects collected all over the world, though mostly hailing from Kazakhstan, Siberia, and Mongolia. Among them, 515 specimens of the above age belong to sawflies and horntails (lower hymenopterous insects comprising the suborder Siricina). Of these, 120 display their antennal structure clearly enough to render the identification of the antennal type possible. In turn, 65 of these specimens belong to the Xyelidae and have the corresponding antennal type. Among the remaining 55 fossils, 23 also have xyeloid antennae, including those with the "third" segment not so large as in the Xyelidae but still clearly thicker and much longer than the distal segments. The remaining 32 fossils have antennae that are of the normal type or nearly so.

Among the non-xyelid fossils displaying the xyeloid antenna type there are, firstly, four genera that share several important putative synapomorphies with living Tenthredinoidea (Fig. 5). These genera have the fore wing with 2r-rs meeting RS distally of 2r-m, and 1mcu cell enlarged so that the first abscissa of RS is short or got lost. Most genera also have the SC stock fused, albeit only distally, with R, so that its fore branch, when present, forms an intercostal cross-vein (*Pseudoxyela* Rasnitsyn, 1968 is exceptional in retaining the free SC and thus probably forms the sister group of the rest of the tenthredinoid clade). The four genera also share synapomorphies with the Tenthredinoidea as regards their antennal flagellum, which is thick with a reduced number of segments (supposing that the antenna is secondarily multisegmented in Diprionidae and some Pterygophoridae). I consider *Xyelotoma* Rasnitsyn, 1968, *Xyelocerus* Rasnitsyn, 1968, *Dahurotoma* Rasnitsyn, 1990 and *Pseudoxyela* as forming an extinct family Xyelotomidae. No autapomorphies are recorded for the family, which implies its ancestral position in respect of the other Tenthredinoidea.

The next five extinct genera with the xyeloid type of antenna (Fig. 6) show the important synapomorphy of the superfamily Pamphilioidea, viz., the reduced claw-like ovipositor of a characteristic general form and position in the body. The general appearance and wing venation are also similar to that of the living pamphilioids. Among these fossils, *Xyelyda* Rasnitsyn, 1968, *Prolyda* Rasnitsyn, 1968, and *Mesolyda* Rasnitsyn, 1963 are assigned to the extinct family Xyelydidae which lacks autapomorphies and hence is supposed to be ancestral to the other Pamphilioidea. *Praesirex* Rasnitsyn,

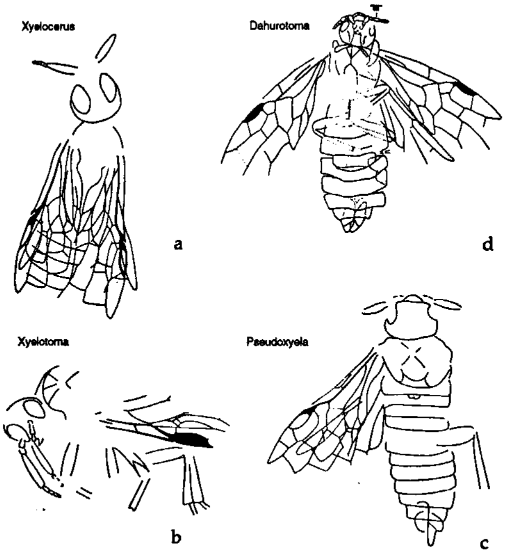

Fig. 5. Representatives of the sawfly family Xyelotomidae: a, *Xyelocerus admirandus* Rasnitsyn, 1968; b, *Xyelotoma nigricornis* Rasnitsyn, 1968; c, *Pseudoxyela heteroclita* Rasnitsyn, 1968 (all from the Upper Jurassic of South Kazakhstan); d, *Dahurotoma robusta* Rasnitsyn, 1990, Lower Cretaceous of Transbaikalia (a–b after Rasnitsyn, 1969; c, based on Rasnitsyn, 1969, fig. 82, and specimen PIN 2997/650; d, after Rasnitsyn, 1990).

1968 and *Turgidontes* Rasnitsyn, 1990 are synapomorphic with the living family Megalodontidae in having wings without SC. They are assigned to the extinct family Praesiricidae which was probably ancestral to the Megalodontidae.

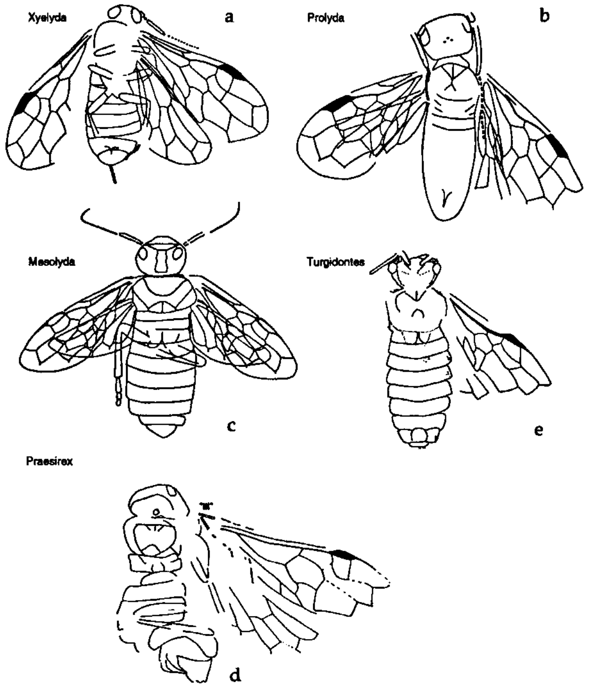

Fig. 6. Representatives of the sawfly families Xyelydidae (a–c) and Praesiricidae (d–e): a, *Xyelyda excellens* Rasnitsyn, 1968; b, *Prolyda karatavica* Rasnitsyn, 1968; c, *Mesolyda depressa* Rasnitsyn, 1968 (all from the Upper Jurassic of South Kazakhstan); d, *Praesirex hirtus* Rasnitsyn, 1968; e, *Turgidontes magnus* Rasnitsyn, 1990 (both from the Lower Cretaceous of Transbaikalia) (a, b, d, after Rasnitsyn, 1983b; c, original, based on holotype; e, after Rasnitsyn, 1990).

One more group marked by xyeloid antennae comprises several genera (Fig. 7) which are now assigned to the extinct family Sepulcidae (Rasnitsyn, 1993). The Sepulcidae are placed in the superfamily Cephoidea because of their synapomorphy with the living Cephidae (Rasnitsyn, 1988c). Both families have their fore wings with the costal space moderately narrow and band-like (secondarily very narrow or basally lost), with the SC fused with R (except sometimes only basally), and lacking the apical SC branch crossing the costal space. The Sepulcidae lack the characteristic venational synapomorphies of the living Cephidae and were probably the cephid ancestors. As to the Cephidae themselves, the observation of their most ancient (Early Cretaceous) genus *Mesocephus* Rasnitsyn, 1968, as having xyeloid antennae (Rasnitsyn, 1988c) has been found to be erroneous.

The last group with a xyeloid antenna is rather loosely constructed. I include here *Protosirex* Rasnitsyn, 1969 (Fig. 8) which seems to belong to the horntails (Siricoidea) because of its general appearance and some siricoid plesiomorphies (e.g., the presence of a free SC). Alternatively, it may represent a group ancestral to both siricoids and cephoids. Along with a few other Jurassic fossils, *Protosirex* represents the extinct family Gigasiricidae. Other siricoids with a xyeloid antenna are *Syntexyela media* Rasnitsyn, 1968, and *S. inversa* Rasnitsyn, 1968 (Fig. 9a–b). They surely belong to the Siricoidea, as witnessed by their characteristic synapomorphy (a strong, needle-like ovipositor). In particular they represent the predominantly Mesozoic family Anaxyelidae (with a single living

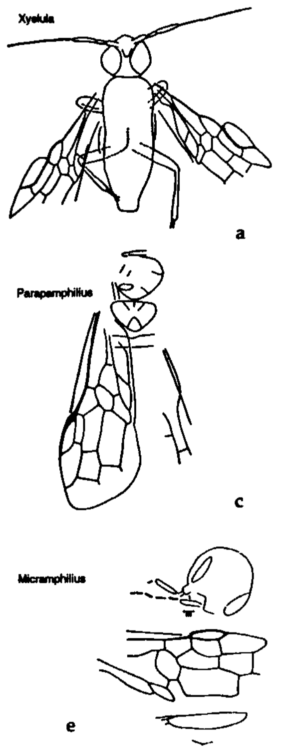

Fig. 7. Representatives of the sawfly family Sepulcidae: a, *Xyelula hybrida* Rasnitsyn, 1969; b, *Onokhoius aculeatus* Rasnitsyn, 1993; c, *Parapamphilius confusus* Rasnitsyn, 1968; d, *Pamparaphilius mongolensis* Rasnitsyn, 1993; e, *Micramphilius minutus* Rasnitsyn, 1993; from the Upper Jurassic of South Kazakhstan (a, c) and Lower Cretaceous of Mongolia (b) and Transbaikalia (d) (all after Rasnitsyn, 1993).

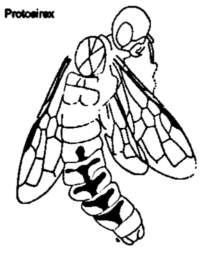

Fig. 8. The primitive horntail *Protosirex xyelopterus* Rasnitsyn, 1969 (Gigasiricidae) from the Upper Jurassic of South Kazakhastan (after Rasnitsyn, 1969).

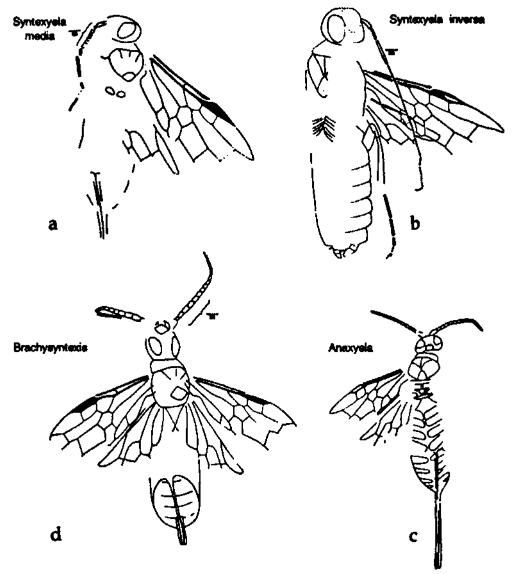

Fig. 9. Representatives of the horntail family Anaxyelidae: a, *Syntexyela media* (Rasnitsyn, 1963); b, *S. inversa* Rasnitsyn, 1968; c, *Anaxyela gracilis* Martynov, 1925; d, *Brachysyntexis micrura* Rasnitsyn, 1969; all from the Upper Jurassic of South Kazakhstan (a, c, d, after Rasnitsyn, 1969; b, original, based on holotype).

species), as confirmed by the synapomorphic reduction of the SC stock and of the 2r-m cross-vein in the fore wing and of 1r-m in the hind wing. It is important that these two species have the 3rd segment slightly modified in comparison to the Xyelidae, and modified in two different ways: it seems simply diminished but seemingly entire in *S. inversa*, while it is large but clearly subdivided into primary segments in *S. media*. Closely related anaxyelid genera display antennae that are either normal or with the 3rd segment only slightly enlarged (Fig. 9c–d; for details see Rasnitsyn, 1969).

Now we can take all the above data into consideration for assessing the meaning of the xyeloid antenna with regard to the early evolution of hymenopterous insects. In fact, we encounter here the conflicting putative synapomorphies. The above-mentioned genera are supposedly synapomorphic with the Xyelidae in their antennal structure, while their various other characters seem to be apomorphies shared with some other sawflies and horntails. These hypotheses cannot all be correct, i.e., the above similarities cannot *all* be synapomorphies. Therefore our next task is to decide which of the conflicting putative synapomorphies can be falsified (reassessed as symplesiomorphies or homoplasies) to arrive at the most likely and consistent cladogram. Four different hypotheses can be considered here: (1) similarity in the xyeloid antenna is a synapomorphy while the alternative sets of similarities of the listed genera are symplesiomorphies, (2) as above, but the alternative similarities being homoplasies, (3) the alternative sets of similarities are synapomorphies (the above groups of genera are monophyletic with the respective non-xyelid superfamilies and families) while the xyeloid antenna has been acquired independently (as a homoplasy), and (4) as above, but the similarity lies in having the xyeloid antenna as a hymenopterous symplesiomorphy.

The first two hypotheses (1, 2) mean that all the genera in question are monophyletic with the Xyelidae (i.e., cladistically belong to the family), while their similarity to other groups is either (a) inherited from some remote ancestor or (b) of independent origin. Hypothesis 1, when applied to all those similarities, seems the least likely because it implies that the direction of evolution of the respective characters is opposite to that which is generally accepted as normal (i.e., most common and thus satisfying the relevant presumptions). This seems possible in some cases but hardly so in other ones. For instance, it is difficult to believe that the specifically reduced and modified pamphilioid ovipositor or the strong needle-like siricoid one are plesiomorphic in respect of the saw-like ovipositor of the Xyelidae and Tenthredinoidea. Indeed, several presumptions suggest the reverse direction of evolution. In the majority of the non-hymenopterous winged insects, and particularly so among the Paleozoic ones (including Palaeomanteida, an order supposedly ancestral to the hymenopterous insects; Rasnitsyn, 1980), the ovipositor, unless reduced, is a flat leaf- or saw-like structure (Fig. 4). Other (non-hymenopterous) examples of the needle-like ovipositor, e.g., in some members of the oldest hemipteran family Archescytinidae, or in crickets, are clearly of an apomorphic nature. This involves both the paleontological presumptions, the outgroup one, and the presumption of analogy, which all support the plesiomorphic nature of the serrate ovipositor of the sawflies. The same judgement of apomorphy holds true for the reduced anaxyelid wing venation, which is hardly acceptable as ancestral to the more complete xyelid and pamphiliid venation, because again many presumptions confirm that in the Hymenoptera a more complete wing venation is plesiomorphic.

Unlike the next three hypotheses, I cannot illustrate the one just discussed with a relevant cladogram. This is because this hypothesis infers incompatible polarization presumptions, as can be seen from the case of the ovipositor (see above).

The second hypothesis (2), suggesting the homoplastic nature of the similarities between the genera discussed and the respective non-xyelid groups, presents fewer difficulties. However, it does imply a vast amount of homoplasy, because the above-listed putative synapomorphies with other members of the respective superfamilies and families would have to be considered as having originated independently (Fig. 10, italics[6]). This seems unlikely since these traits have been accepted by generations of taxonomists as sound diagnostic characters for families and superfamilies. These characters were observed as not especially prone to a homoplastic development in related groups and therefore agree with the presumption of weighted similarity.

One more reason to consider either of the above hypotheses as unacceptable is the incidence of intermediate antennal types described above for two species of *Syntexyela*. Indeed, the antennal structure of *S. media* is easily interpretable as an intermediate stage of transformation of a normal antenna into a xyeloid one. In contrast, in *S. inversa* (and in several other congeners) the basiflagellar segment, which is rather large but seemingly entire, is either a reduced xyeloid segment (which is impossible under the above hypothesis), or otherwise has nothing in common with that of *S. media*. In both cases, the two species cannot be close relatives, and all their similarity should be homoplastic.

So we now move on to the last two alternative hypotheses (3, 4). Both of these claim that the similarity of the above-listed genera (those possessing the xyeloid antennae) to the respective non-xyelid groups is synapomorphic. These hypotheses differ from each other in proposing that the similarity of possessing the xyeloid antennal structure is either homoplastic or symplesiomorphic in nature. The

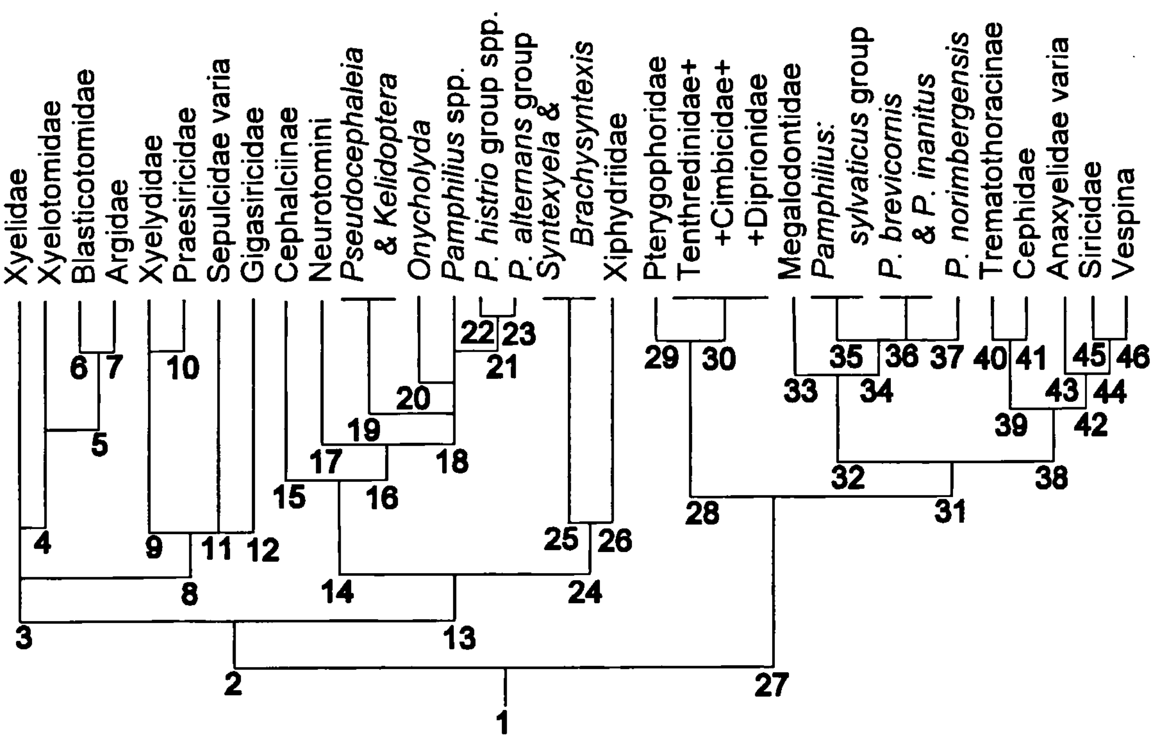

Fig. 10. Cladogram of the lower hymenopterous insects (suborder Siricina) constructed consistent with the hypothesis [(2) in the text] that similarity in the xyeloid antenna is synapomorphic, and the alternative similarities are homoplastic. Figures under the lines of descent refer to the sets of synapomorphies of respective clades (or terminal taxa), as follows (based on Rasnitsyn, 1988a, and, for Pamphiliidae, on Van Achterberg & Van Aartsen, 1986; homoplasies are marked by italics):

1 – Synapomorphies of the order Vespida (wing venation specialized, flight dipterous, haplo-diploidy, etc.: see Rasnitsyn, 1988a, for details);

2 – 3rd antennal (basiflagellar) segment compound;

3 – basiflagellar segment much enlarged (antenna xyeloid);

4 – *antennal flagellum short (up to 5 segments beyond basiflagellar segment), rather thick; fore wing with 2r-rs connecting pterostigmal apex and RS far beyond 2r-m, with 1st abscissa of RS short, and with 1mcu cell large;*

5 – single flagellomere beyond composite one; *pronotum short medially; fore wing with SC lost except crossvein-like fore branch,* and *with RS2 lost* (for further possible synapomorphies, see Rasnitsyn, 1988a: 120, *items 2-3, 3*);

6 – fore wing with RS lost between submarginal cells; larva boring fern stem, with caudal structures modified;

7 – flagellum lost beyond composite segment; *fore wing lacking 2r-rs; male genitalia rotated 180°; larva with eye and antenna distant, with antenna 1-segmented, with mandible lacking incisive molar flange, and with suprapedal and subspiracular lobes merged;* for numerous further synapomorphies, see Rasnitsyn, 1988a: 120, items 5, 6, 8, 9);

8 – *propleurae contiguous ventromesally; tentorium issuing anterior arms from below tentorial bridge; fore wing with RS2 lost;*

9 – *ovipositor small, claw-like modified;*

10 – *both wings lacking SC, pseudosternum extending over all* or almost all *length of mesothoracic venter;*

11 – fore wing with SC short, appressed to R, *lacking fore branch;*

12 – *fore wing with costal space narrow; ovipositor needle-like* (not known with full certainty);

13 – *propleurae contiguous ventromesally; fore wing with RS2 lost; male gonostylus with gonomacula subapically;* etc. as described in Rasnitsyn (1988a: 121, item 13);

14 – *lower tentorial bridge intervening between hypostomae; mandible of cutting type (with cutting edge twisted into moving plane); fore wing with M+Cu angulate; ovipositor small, claw-like; larva exophytic, silk-protected, with appendages setiform, antenna distant from eye;*

15 – tibial spurs with soft tips; inner tooth of tarsal claws reduced; hypopygial depression large;

16 – *membrane of fore wing more or less folded apically; larva on Angiospermae;*

17 – *fore wing with SC lacking fore branch;* femora widened; hypopygial depression medium-sized;

18 – *vertex with grooves deep and subparallel anteriorly; tarsal claws with two long bristles medially;*

19 – fore wing with 1st abscissa of RS very short, with 1r-rs very short and thin, and with conspicuous dark patches;

20 – malar space with differentiated setose depression; tarsal claws with acute basal lobe;

21 – *ovipositor sheath with large stylus* [possibly secondarily

first (3, Fig. 11) means that the genera in question have acquired the compound “third” segment independently, while the second hypothesis (4, Fig. 12) supposes that this character has been uniquely acquired by a common ancestor, and later has been lost independently in groups with normal antennae. Both hypotheses seem more likely in comparison with the first pair of hypotheses, because they propose little more than numerous homoplasies in a single character (either in acquisition or in loss of

lost in *Pamphilius betulae* (Linnaeus, 1758) and *P. festivus* Pesarini & Pesarini, 1984];

22 – female fore wing with distal third of costal cell glabrous;

23 – *female with inner tooth of hind claw shorter than apical tooth;*

24 – *fore wing with costal space narrow; ovipositor needle-like;*

25 – *fore wing and hind wing with single cross-vein r-m each;*

26 – *head capsule with hypostomae contiguous* and with postgenae subcontiguous *between oral cavity and occipital foramen;* pronotum short medially, dorsally; propleurae neck-like elongate; *mesoscutum bearing transscutal suture* and incipient adlateral lines; *prepectus concealed under postero-lateral edge of pronotum; fore tibia with hind (outer) spur rudimentary (or lost); mesofurca with fore arms long, fused for some distance; fore wing with SC lost except crossvein-like fore branch; male gonostylus with gonomacula subapical; larva feeding on dead angiosperm wood conditioned by symbiotic fungi, with abdominal sterna lacking prolegs and longitudinal and oblique sulci; larval salivary gland covered by common envelope, with ductus quadrangular in section (for further details, see Rasnitsyn, 1988a: 122, items 19 & 22,* other possible synapomorphies listed there at item 21–22);

27 – *fore wing with RS2 lost;*

28 – *pronotum short medially; fore wing with 2r-rs connecting pterostigmal apex and R-RS far beyond 2r-m, with 1st abscissa of RS short, and with 1mcu cell large); male genitalia rotated 180°; larva with eye and antenna distant, with mandible lacking incisive molar flange; also numerous synapomorphies as described in Rasnitsyn (1988a: 120, items 2–3, 3, 5);*

29 – *fore wing lacking 2r-rs,* hind wing lacking m-cu cross-vein; *larva with antenna 1-segmented, and with suprapedal and subspiracular lobes merged;*

30 – pseudosternal sulci lost; preapical tibial spurs lost; male with sternum 8 hardly visible, strongly excised apically; larva with prolegs 2-segmented, with subanal appendages lost, and with salivary gland ductus margined with 2 rows of glandular cells;

31 – *head capsule with hypostomae contiguous between oral cavity and occipital foramen; tentorium issuing anterior arms from below tentorial bridge; propleurae contiguous ventromesally; male gonostylus with gonomacula subapical; larva with abdominal sterna lacking prolegs and longitudinal and oblique sulci,* with subanal appendages segmented, shifted basally toward base of anal slit; *larval salivary gland covered by common envelope, with ductus quadrangular in section;*

32 – *ovipositor small, claw-like modified; larva exophytic, silk-protected, with appendages setiform, antenna distant from eye;*

33 – *both wings lacking SC, and pseudosternum extending over all length of mesothoracic venter;* antenna pectinate; fore wing with basal sections of RS and M forming entire straight line, and with A2+3 straight, running behind area aspera; larva feeding on herbaceous angiosperm plants;

34 – *vertex with grooves deep and subparallel anteriorly; lower tentorial bridge intervening between hypostomae; mandible of cutting type (with cutting edge twisted into moving plane); tarsal claws with two long bristles medially; female with inner tooth of hind claw shorter than apical tooth; fore wing with M+Cu angulate; ovipositor small, claw-like; larva exophytic on Angiospermae, silk-protected, with appendages setiform, antenna distant from eye; membrane of fore wing more or less folded apically;*

35 – *ovipositor sheath with large stylus* [possibly secondarily lost in *P. nemorum* (Gmelin, 1790)];

36 – frons with pair of swellings; ovipositor sheath with stylus glabrous; larva makes specialized leafroll;

37 – ovipositor sheath with stylus large, glabrous;

38 – *fore tibia with hind (outer) spur rudimentary (or lost); mesofurca with fore arms long, fused for some distance; fore wing with costal space narrow; larva xylophagous* on living plants, *modified as described by Rasnitsyn (1988a: 122, item 19);*

39 – *fore wing with SC lost* and with Cu straight within 1mcu cell;

40 – mesonotum membranous except laterally; fore wing with costal space very narrow in basal third or half; ovipositor long extending;

41 – metanotum with cenchri lost; *fore wing with 1st abscissa of RS very short and with cell 1mcu large,* with cross-vein 1r-rs long, with A2 straight, and with area aspera lost; abdomen compressed; larva boring in angiosperm plants;

42 – *ovipositor needle-like; larva feeding on dead wood conditioned by symbiotic fungi, modified as explained in Rasnitsyn (1988a: 122, item 22);*

43 – *fore wing and hind wing with single cross-vein r-m each;*

44 – *head capsule with postgenae contiguous; mesoscutum bearing transscutal suture, prepectus concealed under postero-lateral edge of pronotum;*

45 – mesoscutum with transscutal suture bent cephalad laterally; fore wing with basal abscissa of RS subvertical;

46 – tentorial bridge narrow stripe-like, n-like bent; mesonotum with adlateral lines; fore wing with SC lost; 1st abdominal tergum modified into mesosomal propodeum; larva parasitic; etc., as listed in Rasnitsyn (1988a: 123, item 28).

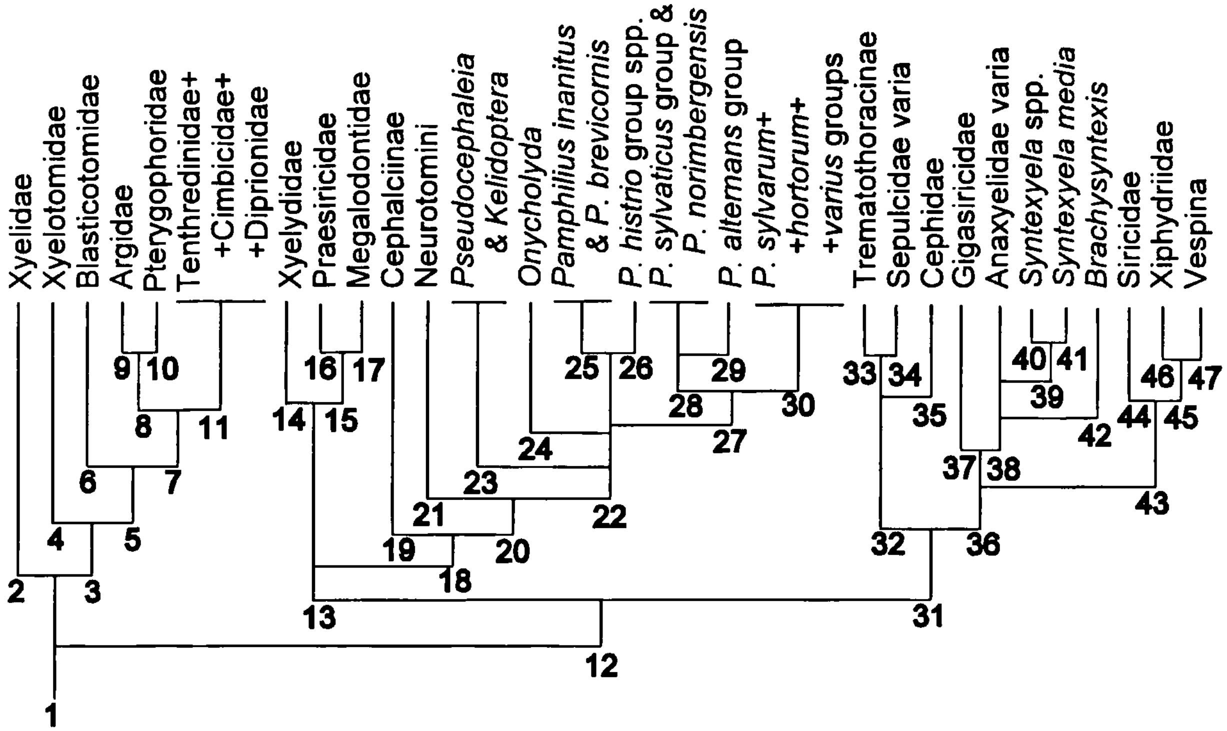

Fig. 11. Cladogram of the lower hymenopterous insects (suborder Siricina) constructed consistent with the hypothesis [(3) in the text] that similarity in the xyeloid antenna is homoplastic, and the alternative similarities are synapomorphic. Otherwise as in Fig. 10, with the following synapomorphies inferred:

1 – Same as in Fig. 10;

2 – *basiflagellar (3rd antennal) segment compound and very large;*

3 – fore wing with 2r-rs connecting pterostigmal apex and RS far beyond 2r-m, *with 1st abscissa of RS short, and with 1mcu cell large* (for further possible synapomorphies see Rasnitsyn, 1988a: 120, item 2–3);

4 – *basiflagellar (3rd antennal) segment compound and very large;* flagellum short (up to 5 segments), rather thick;

5 – pronotum short medially; *fore wing with SC lost except crossvein-like fore branch;*

6 – single flagellomere beyond composite one; fore wing with RS lost between submarginal cells; larva boring fern stem, with caudal structures modified;

7 – male genitalia rotated 180°;

8 – fore wing lacking 2r-rs; larva with eye and antenna distant, with antenna 1-segmented, with mandible lacking incisive molar flange, and with suprapedal and subspiracular lobes merged; for numerous further synapomorphies see Rasnitsyn, 1988a: 120, items 5, 6, 8);

9 – *basiflagellar (3rd antennal) segment compound and very large;* flagellum lost beyond composite segment; larval leg secondarily 2-clawed with 2nd claw modified;

10 – hind wing lacking m-cu cross-vein;

11 – pseudosternal sulci lost; preapical tibial spurs lost; male with sternum 8 hardly visible, strongly excised apically; larva with prolegs 2-segmented, with subanal appendages lost, and with salivary gland ductus margined with 2 rows of glandular cells;

12 – head capsule with hypostomae contiguous between oral cavity and occipital foramen; tentorium issuing anterior arms from below tentorial bridge; propleurae contiguous ventromesally; male gonostylus with gonomacula subapical; larva with abdominal sterna lacking prolegs and longitudinal and oblique sulci, with subanal appendages segmented, shifted basally toward base of anal slit; larval salivary gland covered by common envelope, with ductus quadrangular in section;

13 – ovipositor small, claw-like modified; larva exophytic, silk-protected, with appendages setiform, antenna distant from eye;

14 – *basiflagellar (3rd antennal) segment compound and very large;*

15 – both wings lacking SC; pseudosternum extending over all or almost all length of mesothoracic venter;

16 – *basiflagellar (3rd antennal) segment compound and very large;*

17 – antenna pectinate; fore wing with basal sections of RS and M forming entire straight line, and with A2+3 straight, running behind area aspera; larva feeding on herbaceous angiosperm plants;

18 – lower tentorial bridge intervening between hypostomae; mandible of cutting type (with cutting edge twisted into moving plane); fore wing with M+Cu angulate;

the hypertrophied "third" segment) and do not imply any falsification of the existing and apparently well-based ideas regarding the evolutionary pathways of other characters.

The two last hypotheses are not equivalent in terms of being the best founded. Hypothesis 3, of a homoplastic origin of the xyeloid antenna from a homonomously segmented one, results in more abundant cases of homoplasy as compared with the alternative hypothesis (4) of a homoplastic loss of the character state (cf. italics in the captions to Figs. 11 and 12). This makes it possible to apply the presumption of parsimony, which will confirm the multiple loss hypothesis. However, applying the presumption of weighted similarity seems to give still more clear results.

Complex structures are generally considered to originate with great difficulty; thus such structures are less likely to have multiple origins as compared to their multiple loss. Equally it seems logical to assume that for a structure of enigmatic function, a unique origin and subsequent multiple reduction is generally more likely to have occurred than a multiple origin. The compound antennal segment is an organ with a rather complex structure and of obscure function. This makes its multiple and widely asynchronous homoplastic origin difficult to explain. The hypothesis of a repeated loss of the compound antennal segment needs only a single and quite remote event of acquisition of the enigmatic structure, and thus it seems superior compared to the hypothesis of a repeated gain of the obscure adaptation. This is especially so if one takes into consideration the above-mentioned case of *Syn-*

19 – *basiflagellar segment compound, enlarged;* tibial spurs with soft tips; inner tooth of tarsal claws reduced; hypopygial depression large;
20 – fore wing membrane more or less folded apically; larva on Angiospermae;
21 – *basiflagellar segment compound, enlarged; fore wing with SC lacking fore branch;* femora widened; hypopygial depression medium-sized;
22 – vertex with grooves deep and subparallel anteriorly; tarsal claws with two long bristles medially;
23 – *basiflagellar segment compound, enlarged;* fore wing with 1st abscissa of RS very short, with 1r-rs very short and thin, and with conspicuous dark patches;
24 – *basiflagellar segment enlarged;* malar space with differentiated setose depression; tarsal claws with acute basal lobe;
25 – frons with pair of swellings; *female with inner tooth of hind claw shorter than apical tooth;* ovipositor sheath with stylus glabrous; *larva makes specialized leafroll;*
26 – *basiflagellar segment enlarged;* fore wing of female with distal third of costal cell glabrous;
27 – *female with inner tooth of hind claw shorter than apical tooth;*
28 – ovipositor sheath with large stylus (possibly secondarily lost in *P. nemorum* (Gmelin); *larva makes specialized leafroll;*
29 – *basiflagellar segment enlarged;*
30 – *basiflagellar segment enlarged;*
31 – fore tibia with hind (outer) spur rudimentary (or lost); mesofurca with fore arms long, fused for some distance; larva xylophagous on living plants, modified as described by Rasnitsyn (1988a: 122, item 19);
32 – fore wing with SC short, appressed to R, lacking fore branch;
33 – mesonotum membranous except laterally; fore wing with costal space very narrow in basal third or half; ovipositor long extending;
34 – *basiflagellar (3rd antennal) segment compound and very large;*
35 – metanotum with cenchri lost; *fore wing with costal space narrow, with SC lost, with 1st abscissa of RS very short and cell 1mcu large,* with cross-vein 1r-rs long, with Cu straight before 1m-cu, with A2 straight, and with area aspera lost; abdomen compressed; larva boring in angiosperm plants;
36 – *fore wing with costal space narrow;* ovipositor needle-like; larva feeding on dead wood conditioned by symbiotic fungi, modified as explained in Rasnitsyn (1988a: 122, item 22);
37 – *basiflagellar (3rd antennal) segment compound and very large;*
38 – fore wing and hind wing with single cross-vein r-m each;
39 – scutellum rounded basally;
40 – *basiflagellar segment enlarged though entire externally;*
41 – *basiflagellar segment compound, enlarged;*
42 – several basal flagellar segments enlarged about to form *compound, enlarged basiflagellar segment;* ovipositor scarcely extending;
43 – head capsule with postgenae subcontiguous; mesoscutum bearing transscutal suture; prepectus concealed under posterolateral edge of pronotum;
44 – *head capsule with postgenae contiguous;* mesoscutum with transscutal suture bent cephalad laterally; fore wing with basal abscissa of RS subvertical;
45 – mesoscutum with incipient adlateral lines; *fore wing with SC lost except crossvein-like fore branch;*
46 – *basiflagellar segment compound, slightly enlarged;* pronotum short medially, dorsally; propleurae neck-like elongate; larva feeding on angiosperm wood;
47 – *head capsule with postgenae contiguous;* tentorial bridge narrow stripe-like, n-like bent; mesonotum with adlateral lines well developed; fore wing with SC lost; 1st abdominal tergum modified into mesosomal propodeum; larva parasitic; etc., as listed in Rasnitsyn (1988a: 123, item 28).

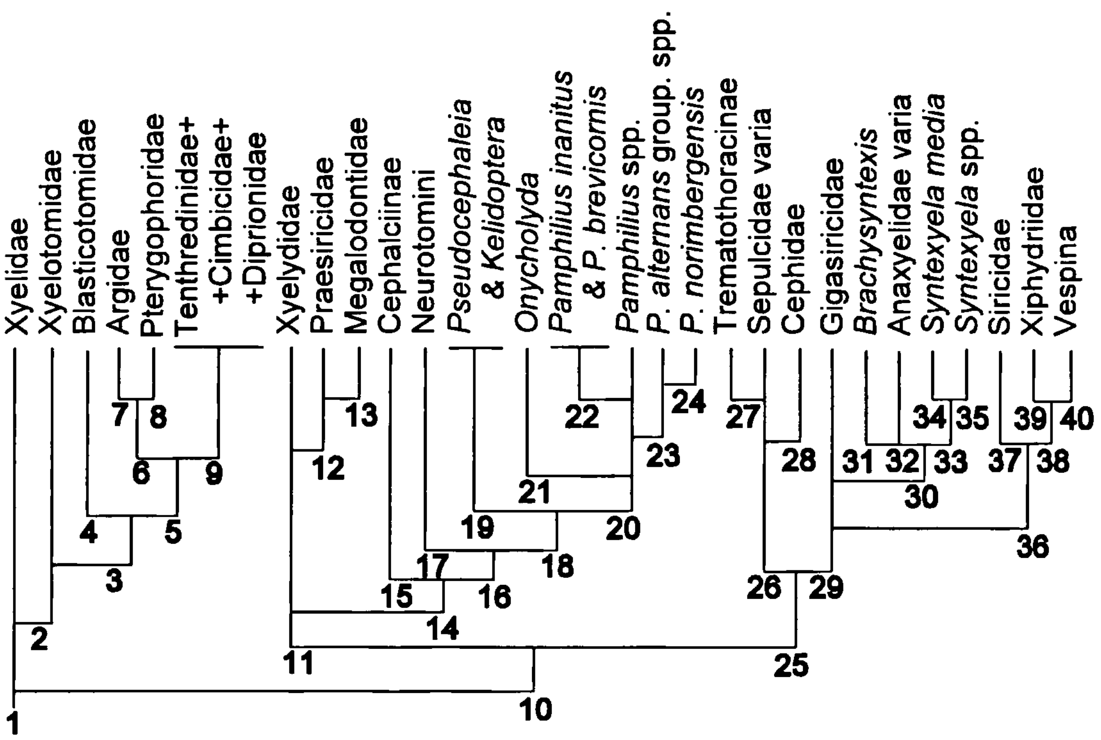

Fig. 12. Cladogram of the lower hymenopterous insects (suborder Siricina) constructed consistent with the hypothesis [(4) in the text] that similarity in the xyeloid antenna is symplesiomorphic, and the alternative similarities are synapomorphic. Otherwise as in Figs. 10–11, with the following synapomorphies inferred:

1 – Same as in Figs. 10–11, and additionally, basiflagellar (3rd antennal) segment compound and very large;

2 – antennal flagellum short (up to 6 segments beyond basiflagellar segment); fore wing with 2r-rs connecting pterostigmal apex and RS far beyond 2r-m, *with 1st abscissa of RS short, and with 1mcu cell large* (for further possible synapomorphies, see Rasnitsyn, 1988a: 120, item 2–3);

3 – pronotum short medially; *fore wing with SC lost except crossvein-like fore branch;*

4 – single flagellomere beyond composite one; fore wing with RS lost between submarginal cells; larva boring fern stem, with caudal structures modified;

5 – male genitalia rotated 180°;

6 – fore wing lacking 2r-rs; larva with eye and antenna distant, with antenna 1-segmented, with mandible lacking incisive molar flange, and with suprapedal and subspiracular lobes merged; for numerous further synapomorphies see Rasnitsyn, 1988a: 120, items 5, 6, 8);

7 – flagellum lost beyond composite segment; larval leg secondarily 2-clawed with 2nd claw modified;

8 – *basiflagellar segment seemingly ordinary;* hind wing lacking m-cu cross-vein;

9 – *basiflagellar segment seemingly ordinary;* pseudosternal sulci lost; preapical tibial spurs lost; male with sternum 8 hardly visible, strongly excised apically; larva with prolegs 2-segmented, with subanal appendages lost, and with salivary gland ductus margined with 2 rows of glandular cells;

10 – head capsule with hypostomae contiguous between oral cavity and occipital foramen; tentorium issuing anterior arms from below tentorial bridge; propleurae contiguous ventromesally; male gonostylus with gonomacula subapical; larva with abdominal sterna lacking prolegs and longitudinal and oblique sulci, and with subanal appendages segmented, shifted basally toward base of anal slit; larval salivary gland covered by common envelope, with ductus quadrangular in section;

11 – ovipositor small, claw-like modified; larva exophytic, silk-protected, with appendages setiform, antenna distant from eye;

12 – both wings lacking SC; pseudosternum extending over all or almost all length of mesothoracic venter;

13 – antenna pectinate, with *basiflagellar segment seemingly ordinary;* fore wing with basal sections of RS and M forming entire straight line, and with A2+3 straight, running behind area aspera; larva feeding on herbaceous angiosperm plants;

14 – *basiflagellar segment subdivided into primary segments and diminished in size (subequal in width to, though much longer than, following segments);*

15 – tibial spurs with soft tips; inner tooth of tarsal claws reduced; hypopygial depression large;

16 – membrane of fore wing more or less folded apically; larva on Angiospermae;

texyela. It forces us to make a choice between the different hypotheses that claim that the enigmatic structure evolved either by reduction or by a multiple origin. The option again seems to be clearly in favour of the repeated loss hypothesis.

The comparison of hypotheses is still not complete, for we have omitted one relevant presumption. Indeed, the above considerations are mostly rather obvious, especially those concerning the hypothesis on the monophyly of all groups possessing xyeloid antennae. As far as I know, they have never been proposed before, and an attempt to analyse them looks a bit like creating a straw man. I need them, however, to complete the picture. The other two hypotheses actually have been hotly debated. The one considering the xyeloid antenna as homoplastic can be found in Ross (1937) and, in a more explicit form, in Königsmann (1976). The hypothesis proposing a multiple loss of the xyeloid antenna within the order Vespida is mine (Rasnitsyn, 1968, 1969, 1980, 1988a).

As portrayed here, the last hypothesis evidently looks preferable, but the opinions of Ross and Königsmann are not at all weak. The shortage of knowledge about (Ross) or of respect for (Königsmann) the fossil record provides only a partial insight. The point of view of Ross and Königsmann is additionally based on the presumption of the irreversibility of evolution. We often treat irreversibility as a rule or even as a law, but exceptions are known to be so numerous that it is hardly more than just another presumption. In the framework of our approach it is just one more particular case of the presumption of analogy. Indeed, it is generally agreed that within a particular transformation series, directions of evolutionary changes are

17 – *fore wing with SC lacking fore branch;* femora widened; hypopygial depression medium-sized;
18 – vertex with grooves deep and subparallel anteriorly; tarsal claws with two long bristles medially;
19 – fore wing with 1st abscissa of RS very short, with 1r-rs very short and thin, and with conspicuous dark patches;
20 – basiflagellar segment seemingly entire, thin (though still disproportionally long);
21 – malar space with differentiated setose depression; tarsal claws with acute basal lobe;
22 – *basiflagellar segment seemingly ordinary;*
23 – ovipositor sheath with large stylus;
24 – *basiflagellar segment seemingly ordinary;*
25 – fore tibia with hind (outer) spur rudimentary (or lost); mesofurca with fore arms long, fused for some distance; larva xylophagous on living plants, modified as described by Rasnitsyn (1988a: 122, item 19);
26 – fore wing with SC short, appressed to R, lacking fore branch;
27 – *basiflagellar segment seemingly ordinary;* mesonotum membranous except laterally; fore wing with costal space very narrow in basal third or half; ovipositor long extending;
28 – *basiflagellar segment seemingly ordinary;* metanotum with cenchri lost; *fore wing with costal space narrow,* with 1st abscissa of RS very short, *with cross-vein 1r-rs long and cell 1mcu large,* with Cu straight before 1m-cu, with A2 straight, and with area aspera lost; abdomen compressed; larva boring in angiosperm plants;
29 – *fore wing with costal space narrow;* probably (unless appearing later as a synapomorphy of all remaining Siricoidea and Vespina) ovipositor needle-like; larva feeding on dead wood conditioned by symbiotic fungi, modified as explained in Rasnitsyn (1988a: 122, item 22);
30 – basiflagellar segment somewhat diminished in size; fore wing and hind wing with single cross-vein r-m each;
31 – basiflagellar segment dissociated into primary flagellar segments (still widened); ovipositor scarcely extending;
32 – *basiflagellar segment seemingly ordinary* (unknown to be either diminished in size as a whole, or to dissociate into primarily segments of ordinary size);
33 – scutellar base rounded;
34 – *basiflagellar segment subdivided into primary flagellar segments;*
35 – basiflagellar segment reduced in size as a whole (still disproportionally large);
36 – *basiflagellar segment diminished in size (subequal in width to, though much longer than, following segments);* head capsule with postgenae subcontiguous; mesoscutum bearing transscutal suture; prepectus concealed under posterolateral edge of pronotum;
37 – *basiflagellar segment seemingly ordinary; head capsule with postgenae contiguous;* mesoscutum with transscutal suture bent cephalad laterally; fore wing with basal abscissa of RS subvertical;
38 – mesoscutum with incipient adlateral lines; *fore wing with SC lost except crossvein-like fore branch;*
39 – pronotum short medially, dorsally; propleurae neck-like elongate; larva feeding on angiosperm wood;
40 – *basiflagellar segment seemingly ordinary;* head capsule with postgenae contiguous; tentorial bridge narrow stripe-like, n-like bent; mesonotum with adlateral lines well developed; fore wing with SC lost; 1st abdominal tergum modified into mesosomal propodeum; larva parasitic; etc., as listed in Rasnitsyn (1988a: 123, item 28).

commonly asymmetrical, with one direction appearing to be realized more often than alternative ones. Therefore, *when one can note unidirectional changes as definitely realized, one ought to prefer the cladogram supposing no changes in the opposite direction, or the least of their number, unless and until there is strong contrary evidence.*

Indeed, contrary evidence does exist, as I have tried to show above, so that the final decision depends on what we consider to be the stronger and sounder arguments. I argue in favour of the higher probability of the multiple loss vs. a gain of the complex structure of enigmatic function when more than one mode of change occurred, and against the irreversibility of evolution. I hope that the example selected, per se convincing or not, does permit us to assess the proposed approach to cladogram reconstructions.

The system of phylogenetic presumptions is outlined in Table I.

Taxonomy

We need a taxonomic classification of living beings to arrange the biological diversity in such a way that it facilitates our activity concerning that diversity. There are many kinds of classifications[7] created to fulfil particular functions and to meet requirements of particular kinds of users (e.g., a system of pests according to the type of harm they cause). They present only a little problem to biological taxonomy, so that I shall concentrate on the system, whose very purpose of existence is to be universally accepted as a common (interdisciplinary) reference system for all users.

To meet the above conditions, the system must provide taxa that are meaningful for as many users as possible. For example: "bird" is a definite notion for a taxonomist, and also for a hunter, a cook, and an artist. And to be so, the system must present its taxa as within-group as homogeneous and as between-group as heterogeneous as possible. In other words, it must have the majority of all possible characters similar within taxa and different between them. This property allows the system to fulfil two more functions of no lesser importance. One of them is to store the information in the most concise and available form. Each of us knows much about, say, a sparrow (of course including knowledge of higher taxa of birds). Another function is to predict properties of taxa not yet studied in full detail. Indeed, a very few insect species (in relation to their full number) have ever been studied bionomically, cytologically, and genetically. And yet we can be sure that any insect consists of cells of a normal eucaryote structure and function, with chromosomes, mitosis and meiosis, mitochondria, DNA, particular kinds of RNA, etc. We can predict with equally reasonable confidence where a particular fossil insect or a contemporary one known from a single museum specimen lived and what it feeded on. The above considerations are rather commonplace. I need to mention them only to make the background clearer for further considerations.

There are three main trends in the taxonomy of the last decades – pheneticism, cladism, and the third, once called with a misleading name "evolutionary systematics" to distinguish it from "phylogenetic systematics", an original and equally misleading name for what most people call cladistics (indeed, what is the difference between the terms "evolutionary" and "phylogenetic" relevant to the present context?) There are more names proposed for the third alternative: "eclectic", "synthetic", "syncretistic" systematics, etc. (Farris, 1979: 497, 518). These are, however, not just terms but euphemisms (replacing "bad taxonomy") to qualify the approach. This version of taxonomy tries to reveal and make explicit the principles of traditional taxonomy. It is not a full equivalent of the latter, however, and thus it deserves a distinct name. Once I called it tradistics (Rasnitsyn, 1992b), which is evidently an awkward name. Phylistics seems a more adequate qualification.

Phenetics

Of the three competing approaches, phenetics seems to be the most straightforward in its goals and means. Its claim is that the system must be explicitly constructed in terms of similarity, and this way permits one to avoid subjectivity in the similarity calculation. The methods of calculation are

Table I. Phylogenetic presumptions.

Scope	Term	Statement
General	"Knowability" of phylogeny	Any similarity should be considered as inherited, unless and until the reverse is reasonably proven
Group analysis	Paleontological	Among two apparently closely related groups, the one entering the fossil record earlier should be considered ancestral, unless and until sound contrary evidence is presented
Character analysis		
Dissimilarity analysis (polarizing transformation series)		
	Paleontological	Transformation series should be polarized according to the succession of the respective character states in the fossil record, unless and until sound contrary data are presented
	Biogenetic	Transformation series should be polarized in agreement with the ontogenetic succession of the respective character states, unless and until there are serious reasons to decide otherwise
	Of analogy	If a transformation series is polarized in a group, the results should be considered as valid for another group, unless and until sound contrary data are presented
	Of irreversibility	When we can see one direction of changes as definitely realized, we should prefer the cladogram supposing no changes to the opposite direction, or the least their number, unless and until we have strong contrary evidence
	Of functional efficiency	Of two character states the one corresponding to a more efficient adaptation should be considered apomorphic, unless and until reliable contradicting evidence occurs
	Of complexity	A complex structure should be considered as apomorphic in relation to a more simple one, unless and until we have strong reason to decide otherwise
	Of vestiges	The character state showing any signs of being modified from another state is apomorphic over the latter, unless and until strong contrary evidence exists
	Outgroup	A character state found only within a group should be considered apomorphic in respect to that distributed both within and outside this group, unless and until strong contrary evidence appears
Similarity analysis (identifying homoplasies in case of conflicting similarities)		
	Of parsimony	The most likely cladogram is that implicating the least number of homoplasies, unless and until there are sound reasons indicating another cladogram as the most likely
	Of weighted similarity	Of conflicting similarities, that which should be considered as inherited is that known to be more reliable in other cases (especially in closely related groups), unless and until strong contra-arguments appear

called collectively "taxometry" or, more commonly though less adequate, "numerical taxonomy". Unfortunately, the methods have never been developed to the proclaimed level. In my opinion, this was not because the level has been proved to be unattainable but because phenetics has been forced back by cladistics before it had proceeded far enough in its useful work. Indeed, methods of taxometry are numerous and diverse, and a determination of the most adequate strategy is not easy and cannot be made in a sufficiently objective manner yet. However, this is a problem adherent to any approach (including cladistics: see e.g., Mickevich, 1978), and it evidently needs hard labour to evaluate what is the natural domain of a particular method and which are its strong and weak sides. Phenetics proceeded far in this way before it was "consumed" by the more vigorous discipline of cladistics, but not far enough to render a conscious rather than a chance determination of an adequate clustering method possible.

The above failure does not seem to be the most important weak point of phenetics, however. Probably more important is that the similarity studied by phenetics is not precisely the same as what the system needs. Pheneticists were dealing with similarity of the characters studied, which must be reasonably numerous but not more than that. On the contrary, the quest for similarity which qualifies the system is of another sort. It is a kind of balance between all characters and properties that are shared and not shared by the taxa compared, including the characters not yet studied (and maybe never to be investigated). This kind of similarity is a rather abstract thing, not directly available but important enough to justify attempts to evaluate it in any possible indirect way. This is precisely what both cladistics and phylistics try to do.

Cladistics

The meaning of cladistics differs depending on the appreciation of different students (cf. e.g., Hennig, 1966; Platnick, 1979) so significantly, that De Queiroz & Donoghue (1990a) apparently proposed to re-instate the original term "phylogenetic systematics" to denote Hennig's version, and to apply the term "cladistics" only to its transformed version (the proposal has not gained general acceptance yet, so that I shall continue using the latter term for the entire field). Despite this splitting, there exists a stable and, by inference, central cladistic statement: "Phenetic classifications are constructed by grouping according to raw similarity, while phylogenetic ones are recognized by grouping according to putative synapomorphy" (Farris, 1979: 487). It is the original and most widely accepted explanation by Hennig (1966) that the taxa marked with apomorphies make the system isomorphic to phylogeny and thus the most effective. That is why the system was termed phylogenetic. There is an alternative point of view, however. First, nature is ordered in a single specifiable pattern which can be represented by a branching diagram or hierarchical classification. Second, the pattern can be estimated by sampling characters and finding replicated, internested sets of synapomorphies. Third, our knowledge of evolutionary history, like our classifications, is derived from the hierarchic pattern thus hypothesized (Platnick, 1979: 538). The pattern is hence claimed to be primary and phylogeny secondary. This approach raises a question: what sets the pattern into nature? or, in other words, what could be the generating process of the pattern if not the phylogenetic process? Being unanswered, the question leaves no way to analyse the proposal independently of classic cladistics, so that I shall be concerned only with the latter.

The first question to be raised is what the central cladistic claim (taxon legitimized solely by synapomorphy) means. Synapomorphy is commonly defined as a character state acquired by the stem species of a group and thus characteristic of all and only members of that group. This definition is not correct, however, because any acquired character state can be lost, while an apomorphy is universally treated as unloosable. (Snakes have lost their legs but not their "legness" as a tetrapod synapomorphy.) This means that *an apomorphy is not a character state but the fact that the particular character state ever has been acquired* (a fact of history of a group).

The above considerations are still inadequate to explain the cladistic approach, because there exists a problem with groups lacking apomorphies. Technically such groups are termed *paraphyletic* or *polyphyletic* depending on whether they are defined by symplesiomorphy or homoplasy, respectively. The general cladistic policy in that respect is to split groups of both sorts into subgroups marked by apomorphies (that is monophyletic or, rather, holophyletic, see note 9 below). This policy meets a problem in *metataxa*, paraphyletic taxa resisting the above procedure, i.e., those which cannot be split so as to give subgroups that are all demonstrable as holophyletic (De Queiroz & Donoghue, 1990b). Many fossil hymenopterous groups attested to above (pp. 14–16) as ancestral in respect of other Hymenoptera may serve as examples. Most cases of this kind could be settled by supposing the difficulties as only temporary as a result of our incomplete knowledge (this is especially tempting in the case of fossils). The refuge of ignorance is not secure, however, because parallel evolution, as we made sure above, is prohibitive to a cladogram being deciphered in all necessary details. Besides, obligatory splitting of non-holophyletic taxa inescapably leads us from the stem group to the stem species which cannot be split any further in this way (De Queiroz & Donoghue, 1990a).

Some students again take refuge in ignorance here by claiming that the stem species can never be verified as such (Nelson, 1973a). Thanks to Popper it became clear that no scientific hypothesis can be finally verified at all. Moreover, we are aware of no biological factors preventing a species from surviving in some of its populations after giving birth to another species, and then to do the same again and again. Such species are identified in number in some more detailed paleontological researches.[8] This is not at all a surprise, because the total number of ancestral species that ever existed is precisely equal to the number of terminal species (minus one), because every holophyletic clade must have its own ancestral species.

A species ancestral to more than a single taxon seems to impose insuperable theoretical problems for cladistics unless it makes the central cladistic statement (taxa definable only by apomorphy) less rigid. This necessary step has been already made by Hennig himself. He considered apomorphy as legitimizing a taxon not by definition but only by implication of another, more solid (basic, central) statement that is an isomorphy between the system and phylogeny. "The temporal duration of a species is determined by two processes of speciation: the one to which it owes its origin as an independent reproductive community, and the one that divides it into two or more reproductive communities" (Hennig, 1966: 66). This way of reasoning makes divergence itself the only process that generates taxa, while apomorphy becomes just a marker of divergence and, by inference, of a taxon. Another implication of this point of view is that the ancestral species is to be considered as having disappeared after each divergence event. Even if one of the products of a divergence event does not show the slightest difference from its ancestor (no apomorphy acquired), it must be considered as a different species (but see Sluys, 1984, for a different view of what Hennig himself actually meant by his deviation rule). This proposal seems to me a little strange, but it is at least consistent. It gives the system a double advantage. Firstly, it becomes clearly monistic, as it is usually opposed to the claimed syncretistic nature of phylistics (but see below). Secondly, the system appears as objective and as well grounded as the respective cladogram, though not more than that.

The last observation is important. If some (possibly many) species do not differ from their ancestors, we do not even have any theoretical possibility to identify cladogram topology correctly. Instead, we can expect only to arrive at some limited degree of approximation. This makes advantages of the cladistic approach less evident in comparison with alternatives. Indeed, contrary to the claim above, it seems possible to invert the proposition and to consider the cladistic system as ultimately definable through sequenced apomorphies, with the divergence events used only as a tool of the sequencing. The approach has been already used by Brothers (1975) in his classical study of the phylogeny and taxonomy of aculeate wasps. A similar position apparently allowed Nelson (1989: 280–281) to say that "descent without modification, however, is insufficient explanation of taxa".

Since a divergence event is not necessarily coupled with a gain of apomorphy, that gain can easily proceed unaccompanied by a divergence. This results in a complete knowledge of a fully sequenced array of apomorphies being unattainable even in theory. That is why the two approaches are at least comparable in their value for phylogenetic study. This is not to say that they are precisely of equal value, but the advantages and deficiencies of either seem to deserve special study. For example, besides the impossibility of being fully placed in a sequence, apomorphies are hardly available just for counting in the framework of Brothers' approach. They cannot be usually hypothesized as appearing in one step (during a single speciation event) in their full form, for most apomorphies are phylogenetically complex, not unitary. This causes problems for the identification of the system of internested taxa created by successive steps in acquisition of a complex apomorphy. As has been discussed above as regards phenetics, we are as yet not able to do this for cladistics in a fully objective manner, so that the approach adds more uncertainty to classification. On the other hand, Brothers' version seems richer in information content as compared to that of Hennig, for it takes into consideration both relatedness and the amount of change acquired (but see below).

Together with its undoubtable advantages, cladistics (in both its versions) also has shortcomings. They will be considered later on in comparison with that of phylistics.

Phylistics

Phylistics tries to combine advantages of both phenetic and cladistic approaches in its attempts to take directly into consideration both similarity and relatedness. To reach this result, the phylistic taxon is to be phenetically within-group homogeneous and between-group heterogeneous and at the same time it must be monophyletic. This kind of taxon has been termed a *monophyletic continuum* (Ponomarenko & Rasnitsyn, 1971). Monophyly is used there as explained in note 9. Continuum means: a continuous chain (branching or not) of subordinate taxa with each of them being phenetically more similar to any of its direct neighbours than to members of any other continua. The definition seems clear and close to the traditional understanding of the term "taxon". It looks eclectic, however, in combining independent criteria of similarity and relatedness.

An eclectic approach is a bad one because it uses independent criteria to define one and the same notion. Eventually we shall find the criteria as conflicting and thus impossible to use. So we should inquire into such cases to make it clear whether the eclecticism is real or only apparent. We have seen above that cladistics is also seemingly eclectic, and that we are able to escape this eclecticism in two ways that result in two alternative versions of cladistics.

The eclecticism of phylistics is also escapable. Indeed, the phylistic criteria are in conflict when a continuum is polyphyletic. When we encounter such a result, we should try to falsify it, as we usually do when encountering conflicting data. Some cases of polyphyly will show similarity by failing to resist more sophisticated testing. That was the case with the insect order Neuroptera, which has long been used to comprise groups which later have been found to be only remotely related. For instance, Sharp (1895–1899) still comprised under this name, apart from the Neuropteroidea in the current sense, also the Embioptera, Isoptera, Psocoptera, Mallophaga, Odonata, Plecoptera, Ephemeroptera, Panorpata (= Mecoptera), and Trichoptera. Similarly, the mammal order Pachydermata was long in use during the 18th and 19th centuries to cover the elephants, tapirs, rhinos, hippos, and pigs, until eventually it has been discarded in favour of more natural (monophyletic) orders. In other cases, the hypothesis of polyphyly will be falsified, as in the case of the hares and their relatives. They were once established as the separate order Lagomorpha, only convergently similar to the true rodents (Gidley, 1912), but nevertheless all of them are now considered to form the monophyletic taxon Glires (Wilson, 1989). In theory, it is quite possible also to find cases where both hypotheses will appear equally likely. In practice, there is no real danger there, for the possibility to deepen our knowledge in both the similarity level and phylogenetic relations of the taxa studied are not exhaustible. We can never be fully certain of either aspect of the system, and thus we rely more on probabilistic and intuitive criteria. That is why in case of contradiction we can easily reassess our results and escape the conflict.

There are examples, however, when traditional taxonomy retains taxa in spite of their undisputable polyphyly, namely when they cannot be replaced by monophyletic ones without a significant loss in usefulness. I refer to various kinds of parataxa in fields such as paleontology, parasitology, mycology, as well as many procaryote taxa (see the next section for details). I consider this as evidence that the traditional approach relies ultimately on similarity, while relatedness (monophyly) is used as an indirect clue to allow us to assess similarity in the total array of characters including those yet unknown. The relatedness is used here similarly to show how apomorphy is used in Hennigian cladistics and divergence events in the Brothersian one.

As a result, all three are equally consistent (monistic, not eclectic): Hennigian cladistics relies ultimately on succession of the divergence events, and uses apomorphies to mark and identify them. Brothersian cladistics relies ultimately on the succession of events of acquiring apomorphy, and uses the divergence events to sequence the apomorphies. Phylistics relies ultimately on similarity (in the most complete array of characters) and uses relatedness (as indicated by apomorphies) to improve results of study of incomplete sets of characters. To make the list complete, remember phenetics: it is monistic and straightforward in relying both proximately and ultimately on similarity alone.

Now we can return to the question of comparative advantages and disadvantages of cladistics and phylistics. In my opinion, the most important phylistic advantage is that it relies ultimately on similarity, that is, on characters as such. It may be satisfied with raw similarity alone when no phylogenetic data of any reasonable reliability exist. In this case, it will be as empiric as phenetics is (in fact it will be just like phenetics in this respect). It will use any reliable phylogenetic data when they exist, and because it uses only the more evident ones, it is possible that the resulting system is not exceedingly hypothetical. Opposite to this, the cladistic system relies both primarily and ultimately on the relatedness that is knowable solely from character interpretation. It is based on inferences concerning the evolutionary succession of character states. As a result, the cladistic system contains inference of a lower level of hypothesizing in comparison to phylistics.

Another side of the above result is that phylistics is nearly "omnivorous" while cladistics is highly "stenophagous", that is, cladistics has requirements for characters that are much more restrictive. That is why it has to consider as parataxa ("plesions") many groups whose characteristics are less complete than those available for their relatives. One is forced to do so, despite the fact that the respective groups are characterized well enough to be considered as orthotaxa (normal taxa) in the phylistic system. This makes the domain of cladistics narrow.

Other putative advantages of phylistics seem to be less important or less evident. It can be claimed that phylistics records both similarity and relatedness and, therefore, stores more information. Farris (1979) objects to this in that the cladistic system in its fullest form specifies origin of all characters available and is thus more informative than phenetics (and, by inference, phylistics) is. This claim is disputable, however, because the fullest form is not attainable. The more information we acquire about polarization of the transformation series available, the more new characters we find with the series not yet polarized. As a result, we are never able to polarize the whole transformation series that is available, so that cladistics has to operate with an incomplete set of characters. Phylistics, however, is able to incorporate into its system the total amount of information available for cladistics, and to add the information about similarity of the taxa involved, which is connected with the nonpolarized characters. That is why the phylistic system is potentially richer in its information content.

There is another side to the problem of information content of a hierarchic system. The above discussion concerns in fact the information that is not stored in the system per se but in its description or, rather, in its background. As to the system as such, it contains information solely on the topology of the respective dendrogram and in the length of the dendrogram internodes. As a result, the total information content of the system per se is that contained in the geometry of the respective dendrogram, and as such it is limited. For instance, a symmetrical dichotomous dendrogram with 4 terminal taxa contains 3 bits of information and not a bit more, unless rank information is added. Unless ranking is involved, and beyond that the amount of correlated similarity and relatedness, we can introduce into the system an additional amount of cladistic information only at the expense of any phenetic information, and vice versa.

Additional information can be added only by using a ranking system, especially a highly divided one. That is why the most informative arrangement is the original Hennigian system with its incredible number of ranks that is supposed to reflect the succession in time of divergence events. However, such a practice was found impractical, and now it is virtually abandoned in favour of traditional Linnean ranking (Wiley, 1979). This form of ranking contains little cladistic information, being used as it is in a completely arbitrary way, and thus it transforms post-Hennigian cladistics into an eclectic concept. Artificial conventions like Nelson's phyletic sequencing (Nelson, 1973b; Cracraft, 1974) are of little help. We can accept a convention that a comb-like cladogram should be transformed in a group of taxa of one and the same rank listed in a sequence with the taxon diverged most early listed the first, and the pair diverged most lately listed the last (in an arbitrary order). However, we cannot distinguish this list from the one, which is sequenced arbitrarily by being derived from a cladogram either more complex in form than a simple comb, or representing an unresolved polytomy.

Another and still more striking deviation from the basic cladistic claim is the popular concept of *crown group* (equivalent of the **taxon* by Hennig) and *stem group* (*taxon* minus **taxon* sensu Hennig). Indeed, the stem group (see e.g., Ax, 1985) is by definition a paraphyletic taxon which is explicitly prohibited in cladistics.

It has been claimed that phenetics and phylistics, in contrast to cladistics, use taxa characterized only by an absence of characters (Platnick, 1979), that is, paraphyletic taxa characterized by the absence of apomorphy. However, it is shown above (p. 26) that apomorphy is neither a character nor a character state but rather a hypothesis concerning the history of the taxon. Absence of an apomorphy does not mean absence of a character. Lizards lack the apomorphy of snakes: they have legs instead.

The problem of symbiotic and hybrid taxa must also be discussed here. The problem is important, because both kinds of taxa are common enough not to be disregarded as something exotic. The first category is represented by no less than the entire taxon Eucaryota (their cell organelles being derived from originally free-living organisms), while the latter is very characteristic, for example, of higher plants. As reviewed by Tzvelev (1993), in the grass family (Poaceae), the Tribe Triticeae consists of 500 species, 300 of which are caryotypically certain to be intergeneric hybrids, and the largest genera in the tribe consist of hybrid species. A similar pattern is claimed to hold true for many other higher plant taxa.

The symbiotic and hybrid taxa are polyphyletic, because their lower boundary is crossed by more than a single line of ancestry. At the same time, they can satisfy the definition of a holophyletic taxon: a nearest common ancestor of all terminal subtaxa, and all descendants of that ancestor, may easily be included in that taxon, which thus becomes defined by the synapomorphy(ies) gained as a direct result of the hybridization or symbiosis. Hence, polyphyly and holophyly are not mutually exclusive. This is no surprise, for they refer to different aspects of the history of taxa (either to their past, or to their future, respectively), which are not mutually exclusive. As a result, we have to choose between these aspects to rely on them ultimately as criteria of availability of a group as a taxon. I vote in favour of the future: if we accept a taxon which is either strictly holophyletic (as a cladistic taxon), or holo- or paraphyletic (as a phylistic taxon), and if we exclude those which are neither of the two, we shall avoid polyphyletic taxa in the traditional sense, and not so in the sense of hybrid and symbiotic taxa.

Nevertheless, hybrid and symbiotic taxa do pose a problem for taxonomy. This problem does not affect these taxa themselves but their ancestral taxa (the complete chain between both parent species and their common ancestor!) that are paraphyletic by definition. However, this problem concerns only cladistics, not phylistics, nor, of course, phenetics.

Other considerations relevant to the comparison of the three leading taxonomic concepts certainly exist. Nevertheless, the result already obtained seems sufficient to conclude that each system has its own advantages and disadvantages. The balance between them does not seem equal, however. In my opinion, phenetics and cladistics demonstrate deficiencies important enough to consider the two to be inferior to phylistics. These weak points are: the shortsightedness of phenetics, which fails to use the prognostic power of phylogeny, and the fastidiousness of cladistics, which rejects too large a fraction of available characters and also produces taxonomic constructions with a high hypothetical content. I believe this makes the whole construction somewhat more shaky than the phylistic system. Therefore, I expect that phylistics will appear the winner of the contest.

Nomenclature

Nomenclature is a collection of conventions on how to create and use the names of taxa. It is commonly felt to be a field of sophisticated details and simple basic principles. This is not exactly the case, for the principles are not all appreciated and explicitly formulated. Some of them are mentioned in the Codes (e.g., ICBN, 1994; ICZN, 1985) but not as basic principles. In addition, some of these basic principles are not true conventions by being only a reflection of a particular taxonomic concept, or obtained by inference of a particular evolutionary theory. Indeed, the Linnean principle of binominal nomenclature is fully conventional and easily coupled with any kind of taxonomy accepting a hierarchy formed by genus and species. In contrast, the type principle, as is discussed below, is essentially different. The distinction between the two kinds of principles seems useful, so that they deserve their own names and will be further referred to as taxonomy-independent and taxonomy-dependent ones, respectively.

Because of my personal experience, the following considerations are based on the rules of zoological nomenclature. This seems to make little difference, for various Codes differ largely in details, not in underlying principles.

Taxonomy-independent principles

These are often plain and need but little comment, if at all, and they are discussed here first.

1. "The Code refrains from infringing upon taxonomic judgment, which must not be made subject to regulation or restraint" (ICZN: xiii). This statement is not fully correct because of the existence of taxonomy-dependent principles that validate only particular cases in taxonomy. The statement should probably be completed with the words "beyond restrictions explicitly imposed by the present Code".

2. In zoology, the area of principles of nomenclature is restricted to suprapopulational level groups from subspecies up to superfamily (for details see ICZN Article 1). Exclusion of higher taxa from the scope of the Code seems to me a mistake, though it is a subject for another discussion (see Rasnitsyn, 1982, 1986, 1989, 1991).

3. Identical names of different taxa must not be used as valid names (ICZN Article 52). The scope of the principle of homonymy is arbitrarily restricted so as not to concern (i) the species group names belonging to different genera, (ii) homonymy with (and between) higher taxa and (iii) homonymy between taxa belonging to animals and to plants.

4. Selection of the proper name among competing ones, either synonyms or homonyms, must be made in favour of that proposed earlier (ICZN Article 23). This is the principle of priority.

5. Principle of a standardized and rank-indicating form of the taxon name. It presents a base for the long array of rules on the language, grammar and syntax of the taxon name, including the principle of binominal nomenclature (ICZN Articles 4–6, 11, 25–34).

6. The last among the taxonomy-independent principles is the principle of superior priority of the International Commission on Nomenclature which can rule on any case contrary to the Code (ICZN: xiv).

Taxonomy-dependent principles

There are three taxonomy-dependent principles.

1. The type concept. The principle of name-bearing types is the most important and most demonstrative with respect to the restrictions imposed by taxonomy on nomenclature. According to the Code "The name-bearing type provides the objective standard of reference by which the application of the name it bears is determined, no matter how the boundaries of the taxon may change" (ICZN Article 61a). In other words, a taxon can be introduced into the system ultimately only be referring to its type. To assess this decision we should consider alternative possibilities.

The first thing to consider is the way to introduce a taxon by referring to its characters. This identifies a taxon as a class provided that the characters are defining ones and not merely diagnostic (Ghiselin, 1974, 1987). There are several possibilities of doing this; the simplest is a combinatorial system – a multidimensional matrix with each compartment corresponding to a particular combination of characters and thus harbouring a separate taxon. A version of this is an identification table sometimes used by taxonomists – a rectangular matrix with an upper row of characters and left column of taxa, and with character states at the intersections. This sort of system is really simple and sometimes quite useful. It does not agree with the aims of the general system of organisms, however. It is too inflexible: we cannot improve a combinatorial system locally to fit a particular taxon, for any addition, deletion or alternation of a character will affect many other taxa. That is why such a system is not very common, even as an identification tool.

A more flexible system is one with the taxa identified by ranked characters, as in the standard key for identification, with characters being more highly ranked the earlier they occur in the key. It is quite handy, although it is not as good as the general system because of the evident arbitrariness of the character rankings. Nevertheless, in somewhat modified form (that a few of the highest rank characters are enough to shape the system) this approach has remained popular among taxonomists since Linnaeus (1751), who based his system of plants primarily on characters of fructification. This proposal has been formulated most explicitly by Lubischew (1923, 1966), who called for a search for a few highest rank characters (parameters) that could determine the distribution of all other characters, like the nuclear charge determines the features of atoms and the position of respective elements in the Mendeleev system. This would result in discovering a parametric system, which is able to predict all important characters of the taxa involved from these key characters (the parameters). The task proposed by Lubischew seemed hopeless as applied to taxonomy, and Lubischew himself failed to resolve it. However, meanwhile a solution has been found, albeit in a place other than where he sought for it. Ironically, it was discovered in a field which Lubischew, as a convinced antiselectionist, considered as false.

The field is the cladistic system with its central claim that the characters of organisms and, by inference, the location of their taxa in the system, can be best determined by only one characteristic, viz., their relatedness. Relatedness thus becomes *the* Lubischew parameter by definition. The meaning and potentialities of the cladistic system have been discussed above. Here I only want to draw attention to the fact that the system does not need its taxa to be "typified" because it is enough to refer to *the* parameter to introduce a taxon into the system.

Indeed, "names are synonymous if they refer to clades stemming from the same ancestor" (De Queiroz & Gauthier, 1990: 307). However, De Queiroz and Gauthier failed to draw the self-evident inference from their proposal that cladistic taxonomy should abandon the type concept. This next step has been taken by Sundberg & Pleijel (1994). I am not aware of any practical application of their effort, and I am afraid that this will be a difficult task. Their proposal is that cladistic nomenclature should attach a taxonomic name as a tag to an ancestor of a clade. However, as we have seen, the cladistic approach does not permit us to think about an ancestor as a real group (taxon) that could be identified and studied. Instead, the ancestor is thought about only as a collection of synapomorphies of the clade in question plus a sum of synapomorphies of all more inclusive clades. All these synapomorphies do not result from direct observation, as the type specimen does, but exist only as hypotheses concerning which character states have been acquired at what divergence event. So we are effectively being told to attach a taxonomic name to a collection of hypotheses, which I do not believe will be an easy job to persuade taxonomists to do.

The class, as a group defined by the characters of its members, has the individual as its logical alternative. The suggestion to consider the taxon as an individual (Ghiselin, 1974, 1987, and bibliography therein) is thus quite natural. As an individual, a taxon must then be able to be introduced by referring just to its name. For this, it must have its integrity and spatiotemporal wholeness developed enough to permit the taxon to be born and to die. It cannot be broken down into parts equal enough so that more than one of them might pretend to inherit the taxon name. This makes a difference between the ostensive definition of an individual (direct indication of its member/part) and the use of the type concept. Any part of an individual may be equally used for the intended definition, and hard rules of how to select and to use the taxonomic types are not necessary to introduce individuals into a system.

"Taxon" therefore is a very special kind of individual, if it is anything (see e.g., comments in Ghiselin, 1981), and the issue deserves further consideration. The paradigmatic case of an individual, the organism, has its integrity and spatiotemporal wholeness based on continuous interaction of its parts. This also has been proposed to be true for species, due to the fact that their divergence is suppressed by gene flow (Mayr's biological species concept). The model is limited in its scope, for "The biological species concept has validity only in what I have called its 'nondimensional situation', that is, where populations are actually in contact with each other" (Mayr, 1988: 301–302).

Ghiselin (1981) hypothesized as well that the phylogenetic lineage has integrity sufficient to consider the lineage and the respective taxon as an individual. There is a problem here too, for all of the ancestor-descendent transitions are equally integral. I am equally related to my father and to my son, and so is a species to both its ancestor and descendent species. The only difference results from the asymmetrical distribution of common history: I share a common history with my father but not with my son [thanks to one of my anonymous reviewers for showing me this dichotomy]. This is a precise description of the essence of the cladistic system. It displays very clearly what a special kind of individual a cladistic taxon is: it can be born, exist, and die, but it can never give birth to another taxon. The only thing available to it is to segregate its internal contents into subclades (subtaxa). I can see here an exaggerated, all-depressing role for history: nothing in the world, not a single evolutionary invention, no matter how "brilliant and influential" in determining the history of a clade it could be, is comparable in its taxonomic meaning as is common history itself. The past history is everything, the future is next to nothing – this is apparently a fairly correct characteristic of the cladistic view of the system.

However, the class-individual dichotomy does not necessarily exhaust the existing options. Indeed, the taxon possesses features of both the class and the individual: as a class it possesses characters, as attested to by its diagnosis, and it has members (contrary to Ghiselin, Alex Rasnitsyn is not only a part but also a specimen [example] of *Homo sapiens*). At the same time, similarly to what is so for the individual, a taxon has parts (populations in relation to species), and, what is more important, it can develop (evolve) and still not lose its individuality. While evolving, a taxon retains its wholeness in time, in the multidimensional space of all its characters, and to an extent in geographical space (see e.g., Schram, 1980). Because of this wholeness, the taxon is able to be appreciated after its name is given, as is an individual. In possessing features of both class and individual, the taxon is a notion intermediate between these two, or rather it fills the gap between them, because the class and the individual appear to be two extremes of a single spectrum.

Consequently, the taxon in the above sense is neither a true class nor a true individual. It is most similar to a cloud whose spatiotemporal wholeness is real, though far from being complete. A taxon seems to be best defined as a continuum, in agreement with its phylistic usage. The phylistic approach is well suited to the task of introducing and handling taxa using types: it is the continuum that can be introduced into a system ultimately by using a type. Indeed, unlike an individual, the possibility to identify a continuum depends on similarity instead of integrity, and unlike a class, a continuum can be identified in relation (in overall similarity) to other taxa and not by means of particular characters. If an individual is an integral body and a class is a compartment in the character matrix, a continuum is neither of the two. It is rather a cloud for which it is possible to change its shape and composing elements, but nevertheless it persists as an appreciable thing until it is dismembered or dissolved (becomes extinct). It is possible to characterize the continuum both by its integrity, manifest in the existence of gaps delimiting it from other continua, and by the characters of its diagnosis. Both criteria are not fixed, however, through being easily changeable in the course of both evolution and knowledge acquisition, so that at any particular moment they can be found insufficient to delimit the taxon. That is why the taxon is ultimately identifiable through its name attached as a tag to its nomenclatural type.

The same result can be achieved by means of a different and shorter path of reasoning. Indeed, the aim of any classification is to accommodate all of the diversity to be classified by a system of taxa that should neither overlap each other, nor leave any uncovered space (unclassified residue). This implies that the main aim of a classification is to trace natural gaps ("to cut nature at her joints", to use Plato's metaphor as cited by Hull, 1983: 186) in the field under classification, and to fix and to rank them as taxonomic boundaries (in case of an artificial classification, we just impose such boundaries instead of tracing them). Class does not fit this procedure, for it is defined by a character, for which it is quite natural to overlap with other characters. For individuals, we are aware of no natural forces that could pack them so tightly as to leave no space in between, unless individuals are defined in a sophisticated manner, as is done by cladists. In contrast, the taxon-continuum meets perfectly the demands of the classification procedure, because the only legal way to define a continuum is to trace and to rank border lines between it and other taxa.

Besides the type concept, there are two more taxonomy-dependent principles of nomenclature, both not appreciated as such by ICZN. They are also an implication of the continuum nature of a taxon.

2. The principle of hierarchy. Being continua, taxa cannot be grouped in any other way than in the next more inclusive continua (higher taxa). The latter must be fully inclusive, that is, they must include the subordinate continua as a whole, not in parts. Equally, the taxon-continuum, even as a whole, cannot be a member of two or more higher taxa, for otherwise the latter would overlap and thus would not obey the definition of a continuum. As a result the system takes a fully hierarchic form.

3. The principle of synonymy. If a taxon can be a member of only a single higher taxon, it can only bear a single name, extra names being destined for invalidation because of synonymy.

Reasons for refusing to follow the principles of nomenclature

In the case of taxonomy-independent principles, the reasons for a deviation are necessarily subjective in the sense that there is no taxonomically compelling reason to do so. That is why these cases are not discussed here. The problems with the taxonomy-dependent principles seem more important and deserve consideration. As they have been scrutinized elsewhere (Rasnitzyn, 1986), they will be only treated in a cursory fashion here.

Reasons for not following the principles of nomenclature arise when the shortage of information necessary to classify a particular group comes into conflict with the necessity nevertheless to classify it. The necessity arises from the applied or scientific importance of the group. As regards the incomplete information, the reasons are usually connected with some specific imperfection of the material involved. This is well known in paleontology and in the taxonomy of groups with a complicated ontogeny (such as parasitic worms and fungi).

The least disturbing case is a taxon incertae sedis. It differs from an orthotaxon (normal taxon) in that its incomplete characteristics make it impossible to specify its position at a particular level of the hierarchy. For instance, a genus incertae sedis can be assigned to an order, but not, at least for the moment, to any particular family. This practice can be interpreted as a local rejection of the principles of hierarchy and synonymy. Indeed, a genus subordinated directly to an order can be understood as attributed to a new unnamed family, which can easily be a synonym of an existing family.

Other and more serious cases concern only the principle of synonymy and can all be attributed to a special field called parataxonomy (the definition published by Melville, 1979, is rather narrow in comparison with practical usage). There exist several distinct kinds of parataxa. The term *formal taxon* was proposed (Rasnitsyn, 1986) as a broader interpretation of the largely botanical term form-genus (ICBN Article 3). A formal taxon can be treated as if it is an orthotaxon, but only in the framework of a special system which is parallel to the general one and completely independent of it, except for the principle of homonymy. These are for example taxa in systems created to classify fossil detached leaves, or seeds, or beetle elytra, fossilized animal traces, and other works (e.g., caddis cases), or larval stages of living parasitic worms, or even unassociated males in highly dimorphic insect groups with a traditionally female-based classification. Parataxa differ from orthotaxa only in that any of them are possibly (sometimes even certainly) a synonym of some orthotaxon, and yet they should not be synonymized with the latter. Important considerations on the nature and functions of parataxa can be found in Meyen (1990).

Some cases of this sort are claimed to involve the type concept as well. Some of them are difficult to explain (e.g., the case of ichnotaxa, ICZN Article 66). Others are known to arise as a means of defending parataxa from the persistent drive of some taxonomists to synonymize parataxa, however arbitrary such synonymy might be. As an example I refer to the case of the genus *Laberius* Kieffer, 1914 (see Rasnitsyn, 1986, for details), which was created to house male wasps from the tribes Dryinini and Gonatopodini (Dryinidae), whose generic and tribal position is unknown because of the female-oriented taxonomy of these groups. Nevertheless, the genus *Laberius* has been synonymized with one of the orthotaxa within the Gonatopodini. As A.G. Ponomarenko explained to me, it was this case which had stimulated him to create detypified parataxa for fossil beetles in Rasnitsyn (1985: 47–81). Detypification does prevent ungrounded synonymy. Yet it prevents any synonymy, thus being perhaps a case in which the medicine is more dangerous than the illness itself. I hope that a better understanding of the aims and functions of parataxa will be a defence against their arbitrary synonymization.

The last and poorest kind of parataxon is a collective taxon. It is a parataxon, usually of generic rank, that can be assigned to a higher taxon but cannot be organized there in a special system of the above sort. For example, "*Cercaria* O.F. Müller, 1773, established for a genus of worms [...], is used in the present state of knowledge as a collective-group name for Trematode larvae that cannot be placed with certainty in known genera..." (ICZN Article 67m). The collective taxon is also stated there to be detypified, but this viewpoint is incorrect. According to the above definition, the collective taxon is equivalent in its scope to the respective higher taxon and thus its members are ultimately identifiable by referring to the same type. A species of *Cercaria* can be identified as such simply because it is similar enough to a larva of the trematode type species. It does not matter that this type species is not as yet appreciated. I have little doubt that higher taxa will be eventually typified in zoology, as has been done in botany. Another example is the collective genus *Carabilarva* Ponomarenko, 1985, proposed (in Rasnitsyn, 1985) to house larvae of Mesozoic beetles of the superfamily Caraboidea that are impossible to attribute to a family. Because of this, the type species of *Carabilarva* is the type of the superfamily Caraboidea, that is *Carabus granulatus* Linnaeus, 1758. Thus *Carabilarva* is formally a junior objective synonym of *Carabus* and yet the two must not be synonymized as long as they belong to separate systems.

Table II. Principles of nomenclature.

Taxonomically independent

1 unrestricted taxonomic freedom beyond the restrictions imposed by taxonomically dependent principles
2 restricted area of application
3 homonymy
4 priority
5 standardized and rank-indicating names
6 superior authority of the International Commission on Nomenclature

Taxonomically dependent

1 type (with no good reasons for not following it)
2 hierarchy (not to be followed for taxa incertae sedis)
3 synonymy (not to be followed for all parataxa except those belonging to one and the same particular system)

The preceding considerations on the principles of nomenclature are listed in Table II.

Summary

Phylogenetic inference, like any scientific work, relies on (1) observations (including experiments), (2) search for analogies, (3) creating of hypotheses about the underlying patterns and mechanisms, (4) attempts to falsify these hypotheses (mostly through their implications), and (5) assessing results of the above attempts using a set of presumptions.

The set of phylogenetic presumptions covers the presumption of "knowability" of phylogeny, and an array of more particular presumptions possible to be segregated into two groups, involved either in group analysis or in character analysis (Table I). The group analysis applies to ancestor-descendant relationships and relies primarily on the paleontological presumption for groups. The presumptions used in the character analysis are further separable into those relevant to the study of differences, and those used in the analysis of similarity. The former subgroup covers the presumptions that help us to polarize transformation series, i.e., to discriminate the plesiomorphic (ancestral) and apomorphic (derived) character states. This group comprises a wide array of presumptions, the most important of which are the paleontological presumption for characters, the biogenetic presumption, the presumption of analogy, those of the irreversibility of evolution, of functional efficiency, of complexity, of vestiges, and the outgroup presumption. The presumptions engaged in the similarity analysis concern the problem of the inherited vs. independently acquired similarity. These are, first of all, the presumption of parsimony, and the presumption of weighted similarity.

The objective of taxonomy is to create a system whose taxa are meaningful for the maximum diversity of possible users, i.e., taxa should reveal maximum within-group homogeneity and between-group heterogeneity. Of three main rival taxonomic approaches, pheneticism relies solely upon available characters as such and thus appears to be too myopic (purely empirical). Another extreme represents the cladistic approach, which employs only apomorphies (inferences about the evolutionary history of character states). As a result cladistics is fastidious, and the cladistic system is overburdened with hypothetical content. The phylistic approach is intermediate in a sense. Its ultimate goal is the system that reflects a comprehensive balance of similarities and dissimilarities, while the relatedness is considered to be an important heuristic method to approach this goal. Phylistics defines a taxon as a monophyletic continuum, where discontinuities (gaps) are used to delimit taxa, and monophyly is considered as a means to assess whether the resulting taxon is correctly delimited, or the system deserves re-investigation.

Taxonomic nomenclature is claimed to be built on the basis of 9 principles, 6 of which are purely conventional in the sense that they are independent of a taxonomic concept employed, and 3 are taxonomically dependent principles, as is shown in Table II. Among the taxonomically dependent principles, the most important one is the type concept, which is the only one that more or less stabilizes the name of the taxon, that is designed as a monophyletic continuum. Two other taxonomically dependent principles, those of hierarchy and of synonymy, may be not followed in cases of taxonomically deficient material, which then should be organized either in a taxon incertae sedis, or in a special (independent) system of a particular kind of objects (e.g., of particular detached fossil organs, or of a particular developmental stage of a living group of organisms). There are neither valid reasons found to violate the type concept, nor to violate any of the taxonomically independent principles, which are conventionally designed solely in order to make the taxonomic practice more stable and uniform.

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Notes

1. This problem is ignored by cladists who consider an ancestor only as a collection of plesiomorphies and refuse to try and identify a real ancestor among known organisms, either extinct or extant. I do not believe this approach is fruitful (see below).
2. The fact that we trace groups using their characters is irrelevant to the possibility to discriminate group analysis and character analysis. The problem is discussed at length below (pp. 7–9). In short, I follow Linnaeus who said “Scias Characterem non constituere Genus, sed Genus Characterem” [1751: 169], that is “Know, the character does not constitute the genus, but the genus the character” (translation mine, corrected by M.T. Ghiselin).
3. It can be easily seen from these examples that using the paleontological presumption for groups, like any presumption, is not an easy and straightforward thing. It needs thorough knowledge of, and considerable experience in, the subject and related topics, and even then mistakes are unavoidable. Of course, there is no faultless method of cognition at all. However, there are two different strategies possible here: we could prefer either to avoid mistakes, or to correct them. In the first case, we would consider only the most safe methods (those least dangerous of giving incorrect results). This strategy would reduce dramatically the diversity of our scientific approaches and thus lowers the demands for the abilities, knowledge, and skillfulness of scientists. More people would be able to participate in scientific work, albeit using a reduced diversity of methods, while high abilities of few particularly gifted persons would rest unapplied. This ideal of a mass, standardized science is not mine. I prefer the science which is free to use a broad variety of methods, dares to make and correct mistakes (and to turn the very mistakes to their good, as a source of experience and discoveries), and permits everybody to work at his maximum efficiency. That is why I am trying to develop and support the approaches which promise both interesting new findings *and* pitiful mistakes.
4. I use the traditional interpretation of parsimony following Ockham’s razor and related to the notion of economy, of the least necessary amount of means to reach the aim. There exists another, more wide understanding which includes weighting of the phylogenetic evidence (Farris, 1983). This approach makes the notion of the most parsimonious hypothesis just a synonym of the best hypothesis and thus unnecessary (as Farris himself has said on another occasion, “If everything is ‘phenetics’, there is no need for the term ‘phenetics’; ‘everything’ would do just as well”; 1979: 488).
5. An apomorphic similarity of the living xyelids in the subdivided galea (a lobe of the mouthparts) is possibly of post-Triassic origin. It is proved only for the subclade comprising the subfamilies Xyelinae and Macroxyelinae and is not known for the Triassic Archexyelinae.
6. To be more persuasive, the cladograms presented here possibly should be prepared using one of the popular computerized cladistic methods. I have some experience in this matter (Rasnitsyn, 1995) and could do it. However, it should be a special, and rather extensive work, for it would be senseless without taking into consideration all the new data and ideas available and without the respective reevaluation of all taxa and character states involved. I believe that the data presented here as they are, even if slightly outdated, are appropriate to explain how the proposed approach works, and how it has permitted me to reach the conclusions presented here.
7. Griffiths (1974) proposes to restrict the term classification as applicable only to ordering into classes, not into systems. I do not follow this restriction, because the classes and systems (individuals, in current usage in taxonomic theory) are not such clear-cut things as common belief suggests (see main text, below).
8. E.g. researches on bivalve molluscs inhabiting the Paratethys, a system of epicontinental seas of southwestern Eurasia during the later Tertiary (Neogene). A complicated environmental history of the seas, with rapid, frequent, and often reversible changes in hydrology and pattern of straits inside and outside the system, had a strong effect on the evolution of the biota. The bivalve molluscs of the Paratethys have been a subject of intensive research for more than a century because of the economic importance of oil-bearing strata, and currently they are rather well known. Besides, bivalves have a special meaning in this context. At lower taxonomic levels their classification relies on their shell characters, both in fossil and in living populations. Unfortunately, the results of these extensive studies have mostly been published in Russian. They have been recently summarized, together with relevant literature, by Nevesskaya et al. (1986).
9. I follow Ashlock (1971) using monophyly as a term covering both paraphyly and holophyly, the latter being equivalent to monophyly in cladistic usage. I refuse to follow the cladistic usage for the following reasons. Taxa can be classified phylogenetically depending on how many (one vs. more than one) discernable lines of ancestry (successions of ancestors) cross their lower border line. Equally they are classifiable according to presence vs. absence of descendants of the group, that is whether

its upper (side) border line is crossed by line(s) of descendants or not. A taxon with more than a single ancestral line is universally called *polyphyletic* irrespective of possessing descendant line(s). A taxon with a single ancestral line is called traditionally *monophyletic* also irrespective of its further fate (whether it has descendants or only members). Cladists use the latter term exclusively for taxa with a single ancestral line and without any other descendant ones, while taxa with a single ancestral line and existing descendant line(s) are termed *paraphyletic*. This usage leaves no term for the two notions combined, i.e., for the traditional monophyletic taxon. The cladistic approach needs no term of so broad a meaning, for cladistically the paraphyletic taxon is a nontaxon and a combination of nontaxon and taxon is nonsense. This is not the case for phylistics (or phenetics) which considers paraphyletic taxa as valid and thus badly needs a term covering all taxa with a single ancestral line. The broad usage of monophyly has priority over the narrow one, and there exists a replacement term, *holophyly*, for the latter. That is why I follow Ashlock in the usage of these terms.

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