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Ontology of Evolution and Methodology of Taxonomy

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Abstract—The theoretical basis of evolutionary biology is presented and discussed to introduce the reader to problems of evolutionary theory and particularly to the problem of paradigm selection. Advantages of the epigenetic hypothesis over the synthetic one are demonstrated, and a wide array of inferences is analyzed including the hypothesis of adaptive trade-off, which considers the organism as a finely tuned comprehensive whole that is restricted in modification unless under more or less serious destabilization. The basic premises of phylogenetics, taxonomy, and taxonomic nomenclature are also analyzed; this results in the inference that the phyletic (refined traditional, Linnean) methodology has advantages over the cladistic one. The nature of the biological taxon and the problems of taxonomy of taxonomically imperfect material (paleontological, parasitological, etc.) are discussed.

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FROM THE AUTHOR

This work is essentially a summary of my reflections on the taxonomically oriented aspect of theoretical biology. In my view, this aspect includes branches of biology that consider the structure and origin of biodiversity at the organismal level. The structure of biodiversity is developed by taxonomy, with its methodological and linguistic apparatuses (including taxonomic nomenclature), while the formation of biodiversity is studied by evolutionary theory with its methodological basis called phylogenetics.

My interest in evolutionary theory is natural; at the time of my formation as a biologist (1950s and 1960s), this was true of many, or even most the biologists. The summary ideas and inferences form Chapter 1 of this book.

I became involved in methodological issues for a number of reasons. One of them is the old crisis of taxonomy that appeared as an endless conflict between the traditional and novel methods of taxonomy, pheneticism and its successor cladistics; in my opinion, this crisis is still far from resolved. An intuitive feeling of the advantage of the traditional approach forced me to join the discussion: the results are in Sections 2.1 and 2.2.

The case of nomenclature was different again: this interest has its roots in my paleontological research. Although taxonomy and taxonomic nomenclature have a long history, the basic principles of the latter are not yet all fully discovered and outlined. This is because many of them are so simple and self-evident that they escape the attention of a student until he or she enters a remote corner of our research field, to classify difficult matter: organisms incomplete in taxonomically important features. This is an ordinary occurrence in the study of fossils, parasitic worms, and asexual forms of fungi. While attempting to classify these incomplete objects, one is often forced to violate some nomenclatural rules that had previously seemed to be unbreakable. This is unsatisfying, and a way is usually sought to resolve the contradiction between a wish to observe the rules and the necessity to classify these difficult objects because of their applied or theoretical importance. Eventually, the student reaches the understanding that the standard rules are simply inapplicable to defective material, which must nevertheless be classified, and that this is because of the very nature of some of the basic principles of nomenclature, which thus become better visible. Principles of taxonomical nomenclature are considered in Section 2.3.

Until recently, these two major topics of my theoretical reflections, the ontology of evolution (Rasnitsyn, 1971a, 1971b, 1975, 1984, 1986a, 1987a, 1988a, 1988b, 1989a, 1989b, 1989c, 1989d) and the methodology of taxonomy, phylogentics, and nomenclature (Ponomarenko and Rasnitsyn, 1971; Rasnitsyn, 1972, 1982, 1983a, 1986b, 1987b, 1988c, 1990a, 1991, 1992a, 1992b, 1996, 2000; Rasnitsyn and Dlussky, 1988) proceeded independently. Only recently, their deep interconnection has become more apparent to me (Rasnitsyn, 2002).

1. TWO EVOLUTIONARY THEORIES

1.1. Introduction

It is plain that many evolutionary theories have been proposed, viz., synthetic, epigenetic, neutralistic, nomogenetic, and lamarckian, to name but a few of the first that come to mind. Why am I speaking about only two? This is because most of them, including the last two listed above, appeal to unknown and apparently unknowable agent(s) responsible for adaptation such as gradation (J.B. Lamarck), or immanent ability of adaptive response even to essentially new evolutionary challenges (L.S. Berg, the author of the theory of nomogenesis). In my opinion, these theories lie beyond the scope of science, as I understand it. This leaves us with only the selectionist hypotheses, that is, with those which address to natural selection as the only natural process that explains adaptation of biological objects toward essentially novel evolutionary challenges. Of them, the neutralist approach is a redundant construction aimed to overcome Haldane's nightmare, the problem of transitional load that appeared fatal for the selectionist (Darwinian) approach, but was eventually found to be an illusory effect of unfortunate nomenclature of the agents considered by population genetics (for details, see Rasnitsyn, 1989b, 1989c).

The two selectionist hypotheses left for examination are the synthetic theory of evolution (customarily abbreviated as STE) and the epigenetic hypothesis. A comparison between them has been provided by Shishkin (1987, 1988a, 2006) and Grodnitsky (2000, 2002); the following account further develops their results.

1.2. Synthetic Theory of Evolution

This approach is widely accepted, and therefore selected to start with here. It represents an explicitly reductionist concept that aims to explain the evolutionary process, while addressing to agents and processes that act at the population level and affecting the allele frequency dynamics in evolving populations. This is the only and limited level of the synthesis achieved by STE which attests this version of the evolutionary hypothesis as a population genetic rather than synthetic theory. However, this is not to suggest changing the name. Names commonly live on their own and very incompletely depend on changes in the named object and in our opinion about it. The name 'synthetic theory of evolution' is too well established now for us to expect any possibility of its change.

Thus, STE considers heredity, that is, the ability for stable reproduction of the phenotype and its characters in succeeding generations, as a property of special entities, genes, which are currently identified with particular sections (loci) of chromosomes and further with sections (sites, cistrones, etc.) of DNA. In agreement with this inference, the evolutionary process is considered to be a selectively controlled dynamic of the allele frequencies in evolving populations. The selective control is put into effect by means of the viability evaluation and, hence, the differential reproduction of alleles within the population. The effect of the selective control is moderated, up to complete reversion, only by stochastic processes in populations. Characters appear and modify as a result of mutations and recombination. Both mutations and recombination lack the property of immanent adaptiveness, it is only selection that is responsible for the composition and adaptive features of a population, the resulting adaptiveness being only stochastically limited. The only other agent that can moderate and modify the process of the otherwise unlimited adaptation is the gene flow, which unifies the population structure according to the averaged rather than local characteristics of natural selection operating on the population.

This approach makes the organization of living beings a plastic clay in the hands of natural selection, or rather a set of characters easily shuffled by natural selection. As a result, the evolutionary pace is about as even as the environmentally defined variations in characteristics of natural selection. Because of this evenness, it is only divergence and extinction events that split lines of ancestry and so create the natural systems of organisms.

No question, the synthetic theory appreciates both the pleiotropy of genes (each gene has effect on more than one character) and polygeny of characters (each is defined by more than a single gene; cf. the gene balance hypothesis), so as in a sense each character depends on the entire genome and each gene defines the entire phenotype. However, this awareness has little effect, since appreciation of this total interdependence makes it impossible to reduce the evolutionary process to the dynamics of allele frequencies, or more so, to events at the molecular level.

The above observations indicate a considerable simplistic element of the synthetic theory which accounts for the not uncommon disagreements between the predictions of the theory and observations. A few such cases follow concerning the superorganismal (mainly taxonomic) level of analysis. The issues pertinent to the ontogeny and its genetic basis are considered in detail by Shishkin (1987, 1988a, 1988b, 2006) and Rautian (1993). First of all, let us consider the tempo of the evolutionary process.

The pace of evolution is commonly evaluated by the tempo of the first and last appearances of taxa. This approach is far from ideal, because in different groups, taxa are comparable to a very limited extent, even if the very existence of the system of taxonomic ranks is to provide at least some comparability of taxa. As a result, the comparability of taxa is guaranteed by nothing more than the intuition of taxonomists, a weak guarantee indeed. However, unfortunately we have no better clue, since the other means available are even worse (less informative concerning the pace of the evolutionary process). It is well known that changes that are similar in appearance can be a similar external manifestation of strikingly different internal processes and changes, so that the use of these characters as a measure of the tempo of evolution will be misleading. For instance, the environments of isolated islands often permit a wide diversification of few founder species, so that the island dwellers may differ in characters pertinent to high rank taxa on continents. However, this should not be taken, and in fact is not normally taken, as indication of a respectively high taxonomic rank of these insular taxa, because their seemingly profound differences are in fact superficial (imbalanced, inadaptive); this immediately becomes evident upon contact with continental invaders. Plenty of examples are available, such as the dodo, and New Zealand that has lost many endemic species after acquaintance with man in general and Europeans in particular. The early stages of the paleontologically observed diversification of a phylum that has entered a new niche or adaptive zone, are equally often demonstrate a wealth of short-living branches that experience deep and rapid but imbalanced modifications (the paradigmal case of inadaptive evolution).

Another index that suggests itself as a measure of the pace of evolution is the rate of molecular evolution, viz., the rate of nucleotide replacement in various sections of DNA. It is the best available pace measure for processes that are very important per se but they are not those we consider now. As Van Valen (1974) has outlined, there are two forms of evolution, standard and epistandard. The first comprises substitution of amino acids in proteins and the evolution of numerical and meristic characters, with comparable rates in different groups. The second type addresses the appearance and extinction of taxa, structural innovations and progress, changes in chromosome number and reproductive incompatibility. The rate of the second type of evolution varies widely between taxonomic groups. Nucleotide replacement is probably a prominent example of the standard evolution in respect of the evenness of its pace, which makes it possible to serve as a kind of clock (*molecular clock*). The molecular distances (measured using the DNA–DNA hybridization method) between various apes and man, as presented by Cacone and Powell (1989), may be an example. The respective cladogram is (outgroup *Papio hamadryas* + (*Hylobates syndactylus* + (*Pongo pygmaeus* + (*Gorilla gorilla* + (*Homo sapiens* + (*Pan paniscus* + *P. troglodytes*)))))). The calculated distances are found to be near identical between a terminal branch and any terminal within its sister clade implying one and the same rate of nucleotide substitutions in each subclade and terminal within that sister group. Indeed, the distances between baboon and each ape or man (that jointly form a sister clade of baboon for the purposes of this particular research) vary within a limited range of 6.58–7.43% of reassociation. The distances between gibbon and other apes + man vary within a smaller and nonoverlapping range of 4.48–5.13%, the same between orangutan and the remaining apes + man (3.28–3.57%) is still narrower and equally nonoverlapping with the previous range, and so on (2.34–2.76% between gorilla and chimpanzee + man, 1.58–1.59% between chimpanzee and man, and 0.77% between two chimpanzee species).

Similar results were received for nucleotide substitutions in the cytochrome b gene of elephantids, i.e., in the cladogram (*Mammut americanus* + (*Mammuthus primigenius* + *Elephas indicus* + *Loxodonta africana*)) all genetic distances from *Mammut* to other taxa in question are within the range of 0.056–0.067, while all distances between *Mammuthus*, *Elephas*, and *Loxodonta* are within the range of 0.032–0.042, and all intraspecific distances measured for the latter three taxa (except for the *Mammuthus primigenius* which might result from a technical error) are within the range of 0.010–0.011 (Rautian et al., 2006).

The pace of nucleotide substitution is a reasonably good clock for the evolutionary meaningful time intervals, but to measure time and to measure evolution is not the same thing. Otherwise we would not consider ourselves as something taxonomically distinct from apes.

As a result, we are left with the dynamics of taxa through time as a measure of the rate of evolution. We remember that it is not a very good tool for this work, but we still have an additional way to check how it is good or bad. The basis of this trial is the generally accepted inference that taxa of the same rank are not only imperfectly comparable. They are additionally differ in the extent of this comparability, viz., species-rank taxa are considered as the most comparable (at least in biparental organisms), and those of higher rank are much less so. If this inference is more or less correct, we can consider similar patterns of the taxonomic dynamics of various groups of organisms at different taxonomic levels as indicative of the respective comparability of their taxa of supraspecific rank. Otherwise, if the patterns are essentially different, their higher taxa should be assessed as of low comparability. Keeping this inference in mind, we can now address to available quantitative data on the evolutionary rates of various groups of living beings. However, we should first consider predictions of either evolutionary hypothesis about the rate of evolution to compare these predictions to the pattern observed. Again, we start with the synthetic theory.

The population genetic approach states that evolution is controlled by the same factors and mechanisms as those dealt with by population genetics, that is, the dynamics of the allele frequencies as controlled and/or modified by the mutation rate, differential reproduction, elimination, and migration, by the features of mating systems (if any), stochastic factors, etc. ("Quantitatively, the basic equation of evolution states that the rate of evolution within a population equals the number of mutations arising per unite of time multiplied by the fraction of those mutations destined to be fixed"; Wilson, 1985, p. 155). In other words, the evolutionary rate must be defined by the rate of flow of adaptively competent genetic variations through the evolving population. Thus, the rate of evolution should be higher if the rate of mutation is higher, the generations are shorter, the population is larger, and the reserves of variation that could be mobilized in the case of emergency are larger.

Paleontological material does not enable direct assessment of most of these parameters, but those that are correlated with other characters (e.g., size and taxonomic relationships) can be indirectly estimated in fossils. For instance, if the genetic approach to evolution is correct, the minimum rate of evolution should be observed in mammals that have both a relatively slow turnover of generations and small populations due to the relatively large size of individuals. In contrast to mammals, unicellular organisms should be characterized by the maximum rate of evolution, while invertebrates should exhibit intermediate rates.

Table 1. The age of the half-modern fauna, Ma

Group	Order	Genus	Species
Mammalia	40[1]	4[3]	
Insectivora + Chiroptera + Rodentia			0.5[3]
Proboscidea + Artiodactyla + Perissodactyla			0.2[3]
Aves	100[1]	10[4]	0.7[4]
Reptilia	70[1]	20[1]	
Amphibia	170[1]	10[1]	
Pisces	150[1]	30–50[5]	0.7[5]
Insecta	300[2]	40[6]	3–7[6]
Chelicerata	300[1]		
Araneae		30[1]	
Acari		50[1]	
Mollusca	400[1]	60[7]	3[9]–6[10]
Foraminifera	500[1]	230[8]	
Diatomeae			15[8]

Note: Half-modern fauna is a fauna with half of taxa of given rank had become extinct, whereas the remaining half survived. The data differ in reliability; hence, the results should be considered as more or less approximate. Initial data from (1) *Fundamentals of Paleontology*, 1959–1964, for molluscs, changes according to the system of Nevesskaya et al., 1971; (2) Rohdendorf and Rasnitsyn, 1980; (3) Kurten, 1968; (4) data from E.N. Kurochkin; (5) data from P.G. Danil'chenko and E.K. Sytchevskaya; (6) material of V.V. Zherikhin; (7) Tasch (1969); (8) Bozhich, 1971; (9) Stanley, 1978; and (10) Gladenkov, 1978.

The data available (cf., e.g., Tables 1, 2) show, first, that the observed pattern is similar at different taxonomic levels. Even if the figures are in part insufficiently precise (this particularly concerns Table 1 based on rather diverse primary data), the general tendencies remain similar at levels of species, genus, family, and order, and uniformly suggest the highest rates of taxonomic turnover in mammals, particularly in those of larger body size, followed by other vertebrates, then by invertebrates, and, then by unicellular eukaryotes. This suggests that taxa, even those of high rank, are sufficiently comparable in different groups of organisms to legitimize their use in comparative analyses like the present one.

The second result inferred from the tables is that the general pattern of distribution of evolutionary rates is precisely opposite to what the synthetic theory predicts. The taxonomic turnover at any taxonomic level is found to be higher the larger the average body size, the longer the generation time, and the smaller the characteristic size of populations. That is, the higher the turnover is, the lower is the flow of adaptively competent genetic variations running through the evolving population.

The results obtained cannot question the genetic basis of natural selection as depicted by population genetics. Natural selection is absolutely automatic: if the flow of variations running through a population results in the appearance of phenotypes that differ in their fitness, they will necessarily reproduce differently, and do so in strict agreement with their relative fitness, only moderated by stochastic rules. To the extent of heritability of these variations, the adaptively differing phenotypes will participate differently in formatting the gene pool of the following generation, and again they will do it in strict agreement with their relative fitness (including all effects of gene interaction, of mating and genetic systems, etc.), as well as with relevant stochastic rules. Population genetics is really and exhaustively defined by the extent and parameters of the flow of selectively competent (that is, adaptively stably differing in real circumstances and over relevant time intervals) and heritable variations running through a population. This is a theory, and the practice confirms it perfectly: everybody knows the difference between characteristic times required to select a new strain of a microorganism and a new breed of cattle. Potential rates of speciation in insects are also indicative, which can be realized in the course of insular evolution, when, for example, an invasion of 17 founder species of the longhorn beetle genus *Plagithmysus* (Cerambycidae) to Hawaii Island has resulted in 46 speciation events (Gressit, 1978) during at most 0.5 m.y. (the age of Hawaii Island according to Rotondo et al., 1981). Thus, the *average* interval between speciation events was at most 0.15–0.2 m.y., which is comparable to the characteristic species half-life of several million years, as Table 1 implies for insects. Still more remarkable are the results of Shaposhnikov (1960–1966) who *almost* created a new aphid species during a single season (see below).

Thus, the inference that it is the amount of selectively competent heritable variation running through a population that controls the rates of evolution holds

Table 2. The time of half-extinction, Ma (after Rasnitsyn, 1987)

Group	Families	Genera	Species	Group	Families	Genera	Species
Mammalia	17	3.3	0.54^1	Trilobita			
Chiroptera			1.6^1	early	2.5	6.3	
Insectivora			0.49^1	late	50	14	
Primates		2.3	0.23^1	Ammonoidea Pz	25	14	
Rodentia		3.1	0.49^1	Ammonoidea Mz	6.7	3.3	
Carnivora		4.2	0.61^1	Nautiloidea	30	17	
Proboscidea		8.3	0.18^1	Gastropoda	130	25	
Notoungulata		2.9		Pelecypoda	60	25	7^4
Litopterna				Rudistae		10	
Perissodactyla		4.2	0.26^1	Archaeogastropoda		25	
Artiodactyla		4.2	0.49^1	Monoplacophora			
Cetacea		2.5		Brachyopoda	30		
Reptilia	17			Articulata		11	
Osteichthyes	30	17		Inarticulata		20	
Teleostei	25	14	3.5^2	Bryozoa	70		
Holostei	40	20		Zoantharia	50		
Chondrostei				Foraminifera	50		
Sarcopterygii		17		benthic		25	18–24^5
Acanthodii		17		planktonic		17	5
Graptolitha (S)		17	1.3^3	giant		10	
Echinodermata			4.2^3	Dinoflagellata		25	9
Echinoidea	50	20		Coccolithophyceae		20	
Ostracoda	50	20		Diatomeae		10	5.5
Malacostraca	40	17					

Note: Time of half-extinction is the time within which half of taxa of given rank included in given fauna becomes extinct. Unless otherwise stated, the estimates were obtained based on the extinction rates published by Van Valen (1973); other sources are (1) Kurten (1968), the Quaternary of Europe; (2) Stanley (1978), Late Cenozoic freshwater fish; (3) Raup (1978); (4) Raup (1978), Cenozoic; (5) Stanley (1978), Late Cenozoic.

generally true and needs only limited correction. I mean that either this amount of variability can control only the upper limit of the evolutionary rates, while actual rates are further limited by some other agents that act at the evolutionarily meaningful time intervals. Or, rather, the pattern observed is because variations that appear as selectively competent when analyzed in the framework of population genetics become different when are seen from other aspects and particularly over much longer time internals.

There are observations that are not in agreement with the predictions of STE which do not concern rates of evolution. Being a soft clay in the hands of natural selection, the organization of living beings should be predictable in its evolutionary changes, at least as far as the selective parameters are known. In particular, we should expect that a similar way of life in comparable environments should result in similar adaptations. At the same time, innumerable contrary examples are known, partially collected in various anti-selectionist publications. To select only one of them, I mention here the case of the spotted hyena (*Crocuta crocuta* (Erxleben)), which is highly extravagant in its reproductive morphology and biology (Harrison Matthews, 1939, cited in Gould, 1983), and the striped hyena (*Hyaena hyaena* L.), which is closely related and similar to the above species, and yet quite ordinary reproductively.

Still less understandable from the "synthetic" point of view is the quite ordinary situation when relationships of higher taxa are found to have more apparent and understandable relationships than those between their subordinates, in spite of the fact that the latter were diverging later than the former and so should retain traces of the respective processes better preserved. Certainly, the phylogeny of the insect orders is generally more or less resolved, except for a handful of really difficult cases (Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005). Relationships between superfamilies and most families in one of the largest insect orders, the Hymenoptera (wasps and their relatives) are also mainly resolved (Rasnitsyn, 2002), except for the families within the superfamily Chalcidoidea, which might have been somewhat oversplit because of its economic importance. The next taxonomic level is less fortunate; the internal structure of a number of families is under acute and long-lasting discussion, and for some of them, including the largest family Ichneumonidae, is still mainly obscure. The same holds particularly true for the generic level, because relationships of their species, especially in large genera, often remain essentially unknown.

Equally difficult to understand is the fact that many taxa are discrete, that is, separated by more or less clear hiatuses (breaks in character distribution). It would be acceptable if this concerned only species-level taxa in biparental groups; their discreteness is predicted by the synthetic theory as a result of the gene flow that operates only within and not between reproductive communities, which are interbreeding species. However, discreteness is not a unique feature of species in biparental groups. Referring again to my taxonomic experience, I can witness that the vast majority of the insect orders, and most of the hymenopteran families, are clear-cut enough to make it a rare occasion to find a specimens that poses a problem in its attribution to a particular order or family. This holds particularly true for extant insects and is often correct even in the case of fossils which should particularly abound in intermediate forms. Yet these are not as common as expected by the synthetic theory.

A similar case is that of uniparental (asexual and parthenogenetic) species, which are equally provided with no means of discreteness by the STE. In spite of this, there are enough indications that these species are also sufficiently clear; students refer to lower algae (V. Poljansky, 1956), ferns (Farrar, 1990), protists (Yu. Poljansky, 1957, G. Poljansky, 1977), rotifers (Mayr, 1963), and weevils (Ivanova, 1978; Zherikhin, 1986, personal communication).

Observations of extraordinary longevity of species are problematic for the synthetic theory as well, because no stabilizing agents like unifying gene exchange can be inferred as operating over a succession of millions of generations, as in the case of insect and mite species found to have remained almost identical morphologically from the Baltic Amber Time (ca. 40 Ma) till now (Zherikhin, 1999). Identical morphology of insect galls on plants indicates biochemical stasis of insect species for 3–5 m.y. (Zherikhin, 2002a). The still greater longevity defined by the age of breakage of the main continents can be hypothesized for some species of the hexapod order Protura, because these animals are wingless, incapable of surviving desiccation, and, hence, never leave the soil. Yet, four or five of the 30 Australian species of Protura are indistinguishable specifically from populations from Java, Japan, South Africa, and Europe (Tuxen, 1967). Even a classically mobilistic range covering both coasts of the Atlantic is known in the proturans, viz., *Delamarentulus tristani* Silv. found in both Costa Rica and West Africa (Tuxen, 1963).

The above cases of longevity in tens of millions of years are modest compared to the tadpole shrimp *Triops cancriformis* (Schaffer), which is virtually unchanged since the Early Triassic (ca. 230 Ma), and even species-level distinction of the Permian populations is not yet confirmed (Tasch, 1969). Morphologically hardly distinguishable Japanese populations of the living species *T. longicaudatus* (LeConte) subjected to the molecular clock studies have been shown to have diverged some 15 Ma, while species of *Triops* (including *T. cancriformis*) are found to have diverged 25–45 Ma (Suno-Uchi et al., 1997).

Taken together, the above results convincingly certify that the synthetic theory of evolution is insufficient to explain the respective observations, and so they prepare us to switch attention to the epigenetic hypothesis.

1.3. Epigenetic Hypothesis of Evolution

Unlike the synthetic theory of evolution, the epigenetic one (the name referring to a level overlaying that predominantly addressed to genetics), considers evolution as a process of evolutionary transformation of ontogeny (Shishkin, 1987, 1988a, 1988b, 2006; Rautian, 1993). The integrity of ontogeny is particularly stressed, which means that both the ontogenetic process taken as a whole, and its result (the resulting organization at succeeding stages of development), are much more stable (and, hence, more important biologically) than any elementary parameters and processes it consists of. Normal development is equifinal, that is, able to suppress or level a wide range of external and internal disturbances, including the phenotypic effect of mutations, recombinations, and other errors of normal development.

The epigenetic approach considers the entire ontogeny, rather than particular traits, as inherited (stably reproduced in succeeding generations). In addition to the norm, there are numerous aberrations of development, which are realized rarely and unstably in normal circumstances. In unfavorable circumstances resulted from either a strong external agent or for internal reasons (developmental errors caused by an imbalanced epigenotype due to mutations, recombinations, hybridization, etc.), the development securing system may be destroyed, or its stability threshold may be overcome; as a result, the development will follow an aberrant (deviated and unstable) pathway.

The epigenetic approach employs a genetically wider basis of evolution than the synthetic theory does. This is because endogenous aberrations of development are found to be easily observable not only under usual sexual (biparental) but also under uniparental (asexual and parthenogenetic) breeding system, which is considered more rigid (modifiable, according to STE, mainly in full dependence on the concomitantly

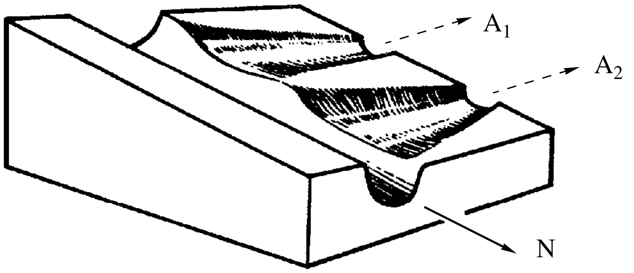


Fig. 1. A segment of an epigenetic landscape, demonstrating abrupt changes in the wall height (thresholds of stability) of the creod at the points of deviation of aberrant valleys. Designations: (A_1, A_2) aberrant valleys, and (N) the major valley, creod (after Shishkin, 1987).

appearing new favorable mutations). The most convincing evidence of this process is given by the above-mentioned experiments by Shaposhnikov (1960–1966), who demonstrated rapid (a few tens of generations) and almost perfect transition of a species into another, already extant species, in a strain of parthenogenetic aphids (‘almost’ is because the experimental strain lost its reproductive compatibility with its parental species and gained compatibility with another species, but the new compatibility was not complete). Shaposhnikov’s results, as well as others of this sort, can be interpreted as a phenomenon of cryptic (suppressed) developmental pathways (creods) that become available for realization in sufficiently modified conditions of development. New characters that resulted from realization of these apparently new, but in fact previously hidden developmental pathways are interpretable as a result of exposure of the previously hidden heterogeneity of a population, which is a property of both interbreeding and clonal breeding systems.

It is aberrations of normal development rather than alleles that are the object of natural selection according to the epigenetic approach. From this standpoint, evolution proceeds because natural selection suppresses some of potential developmental pathways and facilitates others. This results in modification of normal development and stabilization of the new norm. Because of the total interconnection between creods, both available and hidden, the above modification and stabilization of some of them results in more or less deep reorganization of the creod system including appearance of new aberrations (and disappearance of some old ones). In other words, new developmental pathways and new characters appear in the course of routine selectively controlled reorganization of the developmental system.

The above process is easier to grasp using the metaphor of an epigenetic landscape (Waddington, 1942, 1957, 1966; Shishkin, 1987a). Normal ontogeny is a stabilized system of tightly interconnected epigenetic (developmental) processes. The relatively clear-cut sections of this system are called creods. Given an image of a generalized landscape (Figs. 1, 2), a creod appears in the form of a valley with the ontogenetic process running downward along its bottom (Fig. 1). The shallow-sided valleys entering the main (deep) one represent aberrations. To realize an aberration, the ontogeny should follow a side valley, that is, it should be displaced there, either being modified by a sufficiently strong external effect (Fig. 2a; this can be, for instance, a thermal or chemical shock routinely used in genetic studies to obtain phenocopies of mutations), or modification of the landscape itself, e.g., due to a factor or factors that deepen a side valley and level the main valley (Fig. 2b), or else because of combination of both processes (Fig. 2c).

Aberrations are not stable (‘nonhereditary’; the more common of them are called modifications). However, they are permanently, even if unpredictably in detail, reproduced in populations, because the adaptive norm of a species is the epigenetic landscape with all its main and side valleys. That is why it is the aberrations which form the raw material of natural selection in spite of (and, moreover, due to) their low hereditability. If certain aspects of manifestation of an aberration are found to be adaptive, natural selection will selectively support the ontogenies better securing realization of these aspects. This gradually enhances stability (repro-

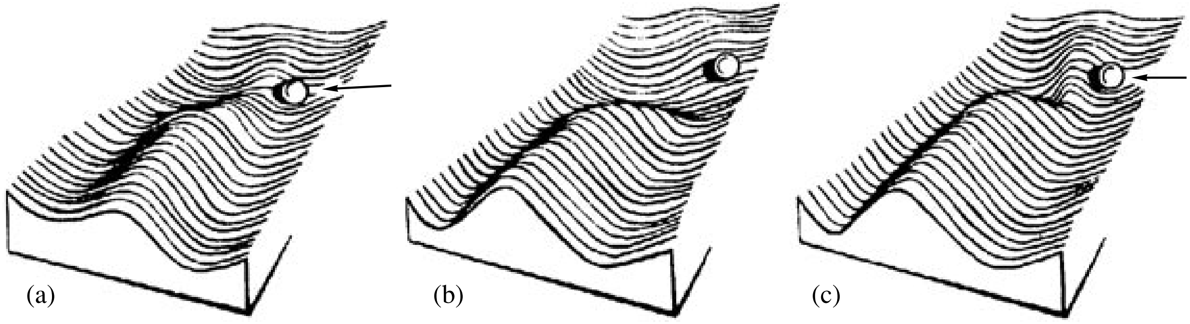


Fig. 2. Deviation of development to a lateral valley due to (a) an impact (long arrow) of an external factor or particular gene; (b) a deviation similar in definitive phenetic manifestation, but caused by a change in the epigenetic landscape due to external or internal causes; and (c) both an individual factor and a change in the epigenetic landscape.

ducibility in varying environments) of the latter, and eventually can make it part of the norm, while the former norm may have become the aberration. In our metaphor, the new adaptive valley becomes deep, and the main valley of the former norm becomes shallow, that is, aberrant. Or both valleys may remain deep and represent two versions of the new (stably polymorphic) norm, a likely exit for two norms each fitting a particular circumstance. If this is the case, adding a specialized environmentally driven switch makes our system a case of typical adaptive polymorphism. Being of more internal (e.g., recombinant) nature, the switch brings Mendelian traits into the system; this is the likely method of origin of some natural polymorphic systems (e.g., many systems of sex determination), as well as the mechanism responsible for the stabilization of pure lines in the laboratory.

In short, according to the epigenetic hypothesis, *the epigenetic landscape is a representation of the spectrum of potential lines of development* (that is, creods and aberrant valleys determined by the creods system), *kept (saved) in the adaptive norm of a species, the essence of a living being*, its ontogenetic potential, which defines its existence and chance of survival under the action of natural selection. As to the level of allele frequencies, mutations, recombinations, and other effects dealt with by the synthetic theory, it lies much deeper and hardly able to define specifics of the evolutionary process, likewise the specifics of quantum mechanic processes is hardly traceable at the macroscopic level. Actually, the genes come and go, while the creods persist; it is well known that characters change slower than genes, which would define these characters, replacing each other.

The genetic aspect of ontogenetic processes, as seen by the epigenetic hypothesis, are considered more closely by Schmalhausen (1938, 1949, 1968) and Waddington (1942, 1957, 1966) (see also Shishkin, 1987, 1988a, 2006), while a more detailed consideration of this topic is beyond the scope of the present study.

1.4. Adaptive Compromise

The integrity of living beings, arisen due to their complex ontogeny, in turn, deeply affects their evolution. At the morphogenetic level, this effect results in deep interdependence of changes in various creods and, hence, between changes in various properties and characters of an organism, that is, its organization appears stable. As a result, natural selection meets considerable resistance in attempts to change organization of a living being beyond the limits of the normal intraspecific variability (the limits set by selection of numerous previous generations of the species). The successful exit beyond the limits of normal (stabilized) epigenotype (i.e., normal phenotypes and their developmental pathways), occurred infrequently and with hardly predictable results (because it is difficult to predict, in which particular way, if at all, the complex, well-balanced epigenotype will be changed in a particular case and circumstances).

In other words, the organization of a living being shows itself to be of a brittle, capricious material, evolutionary changes appear more or less saltatory, and the resultant biodiversity more or less discrete. This discreteness is not absolute and sometimes not apparent because of the intra- and interspecific variability that can obscure it (even if this discreteness does exist). And yet it exists and is widespread, even if biologists and particularly taxonomists are not much inclined to notice and mention it, because the very specifics of their work predisposes them to concentrate themselves on exceptions and difficult cases. The existence of these exceptions is expectable because the stabilized epigenotype (the adaptive norm) embraces a particular spectrum of variation that represents the result of selection of the previous generation, like the epigenotype itself. The ranges of variation may overlap, posing problems to taxonomists, although the epigenotypes remain discrete.

The problem is that we are not aware yet what the epigenotype looks like in itself, and can see only its external features. Like an atom or neutrino, it is inaccessible to direct observation, but not because of its small size but because epigenotype represents a too complex system of interactions and interdependence. However, like the atomic charge, it closely defines features and behavior of an organism and so it is deducible from these with almost equal confidence as the atom.

The high integrity of the epigenotype and deeply buffered character of its evolutionary changes makes it appropriate to consider using one more metaphor, the metaphor of adaptive compromise (Rasnitsyn, 1987, 2002). The stability of a well-balanced epigenotype can be understood as an implication of the systems theory and, particularly, its statement that no system can simultaneously be optimized for more than one parameter. Indeed, a swift cannot run, a penguin is unable to fly or run rapidly, and an ostrich is both flightless and a poor swimmer. Actual systems are open only toward incomplete optimization as a result of seeking for a trade-off between contradictory demands of optimization of their parameters. In living beings, with their various structures and functions being deeply interconnected and sophisticatedly correlated, this trade-off should be particularly stressed. That is why stable epigenotype cannot be organized otherwise than a deeply involved compromise between the contradictory needs of optimization of all its adaptive functions.

The view of the organism as an adaptive trade-off is not strictly new. Mayr apparently meant precisely the same thing when wrote that “Almost any change, but particularly a major change, of the phenotype in such a well-balanced system will be deleterious. Although minor gene substitution may be frequent, the well-buffered system of developmental canalizations shields the phenotype from mayor changes. There is opportunity for speciation, but a major alteration of the morphotype is impossible as long as the epigenotype is intact." (Mayr, 1970, p. 367). A similar idea of the struggle (competition) of body parts has been earlier expressed by Roux (1896) and Weismann (cf. Weismann, 1904). Still earlier, essentially the same principles of compensation or balancing by Göthe and Geoffroy Saint-Hilaire (citing Darwin, 1859, 1905 edition, p. 133), and well before all of them, Aristotle as the principle of economy (cited after the Russian translation of 1937).

The metaphor of the adaptive trade-off is particularly appropriate because it permits inference of a number of the clearly falsifiable implications. The first coming to mind is that the well-balanced organization cannot easily be modified without a considerable loss of fitness. Certainly, this is not the final prohibition of any changes, and as much as changes are possible, the loss of a particular adaptation that has missed its actuality allows additional optimization of some other systems. This appears to be a more natural explanation of the rudimentation of a structure that has lost its function than a simple accumulation of mutations due to the loss of selective control of the affected structure. This also concerns stabilizing selection sensu stricto (as is defined by Schmalhausen, 1941, 1949, that is, when one of modifications becomes the only adaptive norm, while the others are lost along with their complex morphogenetic pathways; e.g., in the case of the loss of males (transition to permanent parthenogenesis) or, on a lesser scale, the loss of a well-pronounced sexual dimorphism (recall the example of the spotted hyena, with the perfectly malelike female). Stabilizing selection in this (narrow) sense results in considerable reduction of creods and their switches.

For our purposes, however, it is the stabilized nature of the well-balanced epigenotype which deserves particularly close attention, that is, the resistance to changes of the adaptive norm, with its development system (stabilized epigenotype). This resistance can be interpreted as the existence of barriers, which are not easy to overcome, that separate one adaptive norm from another. This makes the customary visualization of the metaphor of the evolutionary landscape as a system of ridges separated by selectively inferior valleys and mounted with adaptive peaks unrealistic. Rather, the correct visualization would the Schram's (1983) model of adaptive holes (traps) separated by barriers of adaptive instability.

The assumption that the successful compromise, once found, is hard to modify has far reaching consequences which form and control the entire evolutionary process. The first noticeable effects are the above mentioned hampered and uneven pace of evolution, discreteness of taxa, and relatively low evolutionary effect of elimination. Population genetics displays a wide array of apparently selectively competent population variability, that is, the presence of numerous kinds of phenotypes that differ in their fitness and so rapidly change their population frequencies in agreement with their selective control. And yet, on the evolutionary time scale, species may change slowly or experience an evolutionary stasis that continues for millions and tens of million years. When they occur, the evolutionary changes appear more or less saltatory, that is, display rare and ephemeral intermediate steps, resulting in clear cut types of well-balanced epigenotypes and, hence, a rather distinct system of taxa; this makes taxonomy far less arbitrary and less subjective than it might otherwise be.

As for the population genetic processes, which are so apparent and well known, and, hence, leave little space for doubt in their reality and importance, and which nevertheless show little effect on the evolutionary process which reproduces little, if any, of the population genetic specifics, this effect also receives a likely explanation. The genotype diversity subjected to intrapopulation dynamics is in fact a result of the past evolution of species and is selected for (molded as) an adaptation to meet and level (moderate) environmental diversity, like animal behavior is formed to survive the permanently changing circumstances of life. This genotype diversity has its natural (selectively imposed) limits of variation, which leave it little space, if any, for development to the extent of the appearance of an evolutionary novelty. The most extravagant mutations of *Drosophila* have little to do with the origin of new species (even if some existing species look similar to some of these mutants, as comprehensive textbooks on the taxonomy of the genus witness, cf., e.g., Hardy, 1965) until a balanced epigenotype using one such character is reached.

The above features of the evolutionary process, which are so hard to anticipate and explain when looked at from the viewpoint of the synthetic theory of evolution, are easy to explain from the epigenetic point of view. However, this approach naturally raises other difficult questions and problems. First of all, evolution proceeds despite all the above barriers, even if it is at the expense of the extinction of innumerable imbalanced epigenotypes that have failed to overcome these barriers and form a new balanced adaptive norm. How are the successful lineages ever able to cross those barriers? Which kinds of gaps and holes can be imagined allowing them to penetrate? The problem is that the traditionally postulated mechanisms do not seem to help. Interaction between the interpopulation polymorphism and isolation do not work properly toward this end, so that reproductive isolation neither secures evolution nor even stimulates it (Gritsenko et. al., 1983). Actual populations are always heterogeneous and, being combined with the ordinarily extremely high rates of elimination (see below), they would have provided an equally high tempo of evolution, in splendid contradiction to the normal taxonomic stasis over tens and hundreds of thousands of years (sometimes much longer: see above).

The above-mentioned fact of the normal (standard) rate of elimination, which is always very high, is plain but commonly overlooked. It is known in Russia as Beketov's (1860) rule that, on average, of all the progeny of a particular female, only a single female has a chance of breeding successfully, while the rest are destined to perish without reproductive success. This inference follows inevitably from the very nature of breeding: the Malthusian geometric progression can be stopped only while Beketov's rule is observed. Commonly broken for short periods (particularly in population outbreaks), it is generally observed on the evolutionary time scale, simply because this scale cannot resolve such short-time processes, and if a species is observed or hypothesized to exist during evolutionary meaningful time intervals, its population density should change on average very slowly in respect to the breeding rate. As a result, the average elimination rate is nearly equal to the breeding rate, that is, it cannot be higher. However, if high population diversity coupled with the highest possible elimination does not secure evolution, what does drive it?

The above result can be understood as the inference that, in normal circumstances, the available population diversity simply lacks evolutionary competent variants, that is, those which are adaptive beyond the limits of the current adaptive norm and so possess evolutionarily meaningful advantages over other conspecifics. All conspecifics are equal, and no conspecifics are more equal than others.

Having no reply yet on how evolution can ever proceed, let us try to act in a different manner. We can consider, for instance, actual cases when evolution does proceed, and proceeds relatively rapidly.

1.5. Actual Evolution: The Insular Test and the Inadaptation–Euadaptation–Stasis Cycle

As already mentioned, reproductive isolation is not a particularly important factor of evolution. At the same time, it is well known that evolution proceeds particularly rapidly on isolated islands and in insulated water bodies, and often results in highly modified, even grotesque forms there. Shvarts (1980) analyzed this problem and found that the likely reason for this effect is the lower intensity of competition in impoverished, not tightly packed insular ecosystems. This impoverishment allows one-sided specialization of island dwellers, and this inference perfectly agrees with the adaptive trade-off concept, because the founder species, when finding itself in the softened environment of a loosely packed insular ecosystem, can additionally optimize its organization at the expense of functions which have been left there out of strict selective control.

The above scheme of insular evolution displays a striking similarity to the old concept of inadaptive evolution by Kowalewsky (Rasnitsyn, 1986a). At the same time, it demonstrates an actual mechanism to overcome stability of the well-balanced organization that is the hardest obstacle for the evolutionary process. The question is, whether a similar scheme is applicable to other circumstances. In response, we consider some other occasions when a group finds itself in supposedly softened environments, to seek circumstances favorable for rapid and maybe one-sided (imbalanced) changes of organization that might indicate similarity to inadaptive evolution.

One such case is the invasion of an ancestor into a new ecological niche, or creation of a new niche due to respective change of organization. Before descendants of that ancestor sufficiently fill the new niche, they exist in a somewhat underexploited environment, that is, in relatively soft circumstances favorable for somewhat imbalanced, inadaptive evolution. Taking the Shvarts's (1980) metaphor that each taxon represents its own niche, it is possible to infer that similar temporary softening of environments is a common occasion at the earliest stages of evolution of a taxon. This inference suggests that characteristic of early stages of existence of a taxon might be, first, a higher pace of evolution, and, second, higher extinction rates of newly born inadaptive taxa during the succeeding filling of the adaptive zone.

Both the above inferences agree with observations on present and past biodiversity. The well-grounded paleontological observations that stages of intense diversification usually occur almost simultaneously to, usually slightly after major extinction events (e.g., Grant, 1977, text-fig. 32.3) indicate that abandoned niches stimulate rapid evolution of surviving groups. The rapid differentiation of taxa soon after their origin, as implied by near coincidence of the age of a genus and many of its constituent species (Shvarts, 1980), also supports this inference. The high structural diversity of early offshoots of many higher taxa results in that these early offshoots, even those of lower taxonomic rank, differ in characters otherwise characteristic of taxa of much higher rank ('the rule of archaic diversity', Mamkaev, 1968). At the same time, these early offshoots usually show lower evolutionary stability, which is striking in the majority of phylogenetic charts for groups with a relatively rich fossil record in form of the wealth of short branchlets surrounding the bases of the main phylogenetic lineages. Taken together, these two inferences indicate that evolutionary events (those resulting in the origin of a new adaptive norm) do appear commonly as rapid and one-sided (imbalanced) adaptation deserving the name of inadaptation, and that these events are apparently facilitated by temporary softening of strict selective control of an evolving entity.

In other words, we come to the conclusion that evolutionary events are stimulated by the penetration of a group into a relatively free (incompletely packed) ecological space and, if they occur, they take the form of an inadaptation. Certainly, the new adaptive norm would experience an additional change in the form of an adaptive adjustment to become an evolutionary successful group. To gain a better understanding of this rather complex process, let us consider a relatively well controlled experiment of artificial creation of a new adaptive norm. I refer to the famous publications by Shaposhnikov (1961–1984), who was able *almost* to transform one existing aphid species into another.

Shaposhnikov took a common aphid, *Dysaphis anthrisci maicopica* Shap., that fed on the umbelliferous plant *Anthriscus nemorosa* MB. and placed it initially on another, hardly appropriate umbelliferous food plant *Chaerophyllum bulbosum* L., and, then, after initial adaptation to that host, onto the previously completely inedible *Ch. maculatum* Wild. During one season of raising on *Chaerophyllum*, with the main changes taking at most ten generations, the experimental aphid strain underwent considerable morphological changes that made it hardly distinguishable from the related species *Dysaphis chaerophyllina* Shap., which normally feeds on *Chaerophyllum bulbosum.* Moreovere, the experimental strain had lost the reproductive compatibility with its parent species *D. anthrisci* and acquired a distinct even if somewhat incomplete compatibility with *Dysaphis chaerophyllina* (!) (incompleteness of the compatibility was expressed in certain disturbances of developmental processes).

The conditions of this experiment do not look very easy for the aphids, but neither were they particularly difficult. The death rate reported for various stages of the experiment varied from 15–22 to 53–75%, while the fecundity (indicated for the concluding stages of the experiment only) was 36.6 offspring from a parthenogenetic female, thus, resulting in about tenfold growth of the population even at 75% mortality. The experimenter succeeded in the elimination of all major mortality agents (predators, parasites, unfavorable weather conditions) other than the inappropriate food plant. The experimental population survived for 50 generations, a duration that does not seem ordinary for individual strains of aphids in nature.

We can conclude that success of the experiment was provided by particularly severe experimental conditions. As mentioned above (concerning the Beketov's rule), the ordinary life and circumstances are cruel enough to make their further deterioration unlikely. If almost 100% of the progeny of a living being is destined to death before reproduction, how is it ever possible to change the life to the worse, so as to appreciably affect the pace of evolution?

Equally, the success of Shaposhnikov's experiment was not a result of a mere transfer of an aphid onto an unusual food plant, which is an ordinary event in nature: a wind can transfer a winged founder aphid into the wrong habitat, another time rain washes a wingless aphid onto a different plant. We rarely notice these cases because normally an insect out of its correct places dies rapidly instead of producing something new.

In general, neither overall environment deterioration, nor growing mortality by a particular agent per se can cause the evolutionary process. They can only result in extinction, which is a trivial event on the evolutionary time scale. Nor can amelioration secure evolution. We can already see that the ecological space (space of resources), if underexploited for a moment, becomes well exploited in a few generations due to the ordinary Malthusian factor (geometric progression of reproduction). That is, an underpopulated space exists on an ecological rather than evolutionary time scale and, hence, cannot facilitate the process of evolution. A large-scale oscillation of the population density is an ordinary feature of many, if not most populations, with a low evolutionary effect at best. It is evident that an actual cause of successful evolutionary transformation has different source(s) that may depend in a way on one or another of the features highlighted by the Shaposhnikov's experiment. I propose that one-sided (nonthorough) selective control of an epigenotype (developmental system) is the acting cause of the initial steps of successful evolutionary transformation.

A characteristic of the above experiment is really an imbalanced selective control of the population, control intended to resolve only one, crucial, task: to make the population to feed on a previously inappropriate host plant. Certainly, this result cannot be achieved other than at the expense of some other adaptive functions, like resistance to predators, parasites, diseases, weather factors, etc. We are not aware in detail which of these functions did suffer as a result of the experiment, because the study has not been completed. The resulted strain of the "artificial *Dysaphis chaerophyllina*" has not been exposed to the thorough selective control in nature in order to demonstrate whether or not the new epigenotype is balanced enough to survive there. The chances of a positive result for this final stage of the experiment are low. This is because the developmental system of the "new *chaerophyllina*" has been created under one-sided selective control and, hence, it is most probably inadaptive. Only being exposed to the normal environment with all the attendant troubles and hazards might improve the fitness of the inadaptive epigenotype up to the *euadaptive* level.

An individual inadaptive population has low chance of surviving this long and severe test, so the vast majority of newly born epigenotypes are destined to rapid extinction. However, this chance does exist; otherwise life on the Earth would have ceased long ago. Moreover, the system forms a negative feedback that secures its persistence. When a higher than usual proportions of new epigenotypes fails to meet demands of their thorough selective control (e.g., in the case of deteriorated climate, such as at glaciations, or due to mixture of long isolated biotas, as in the Pliocene Great American Exchange), the density of life decreases (either on the planetary scale, or within a particular area/biotope/ecosystem), because extinction continues. This makes thorough selective control less strict, and thus more inadaptive epigenotypes can survive transformation into euadaptive state. The density of life and level of competition grow until a new balance establishes between the rates of extinction and successful euadaptation. Equally, when the thorough selective control becomes easier (e.g., after a mass extinction providing additional ecological space for survivors, or because of climate amelioration that has a similar effect), transformation of new inadaptive taxa into euadaptive ones also becomes easier and more common. As a result, the rate of the emergence of new taxa increases until the density of life grows enough to depress the origin and enhance the extinction of new taxa until new balance is found.

A well-balanced epigenotype is stable because it is a trade-off between the contradictory demands of optimization of various adaptive functions of the organism; the contradiction results from the sophisticated system of interdependences between particular morphogenetic processes that form various structures and features. Because of this interdependence (integrity), any positive modification of a particular function and respective structures always has a negative effect on some other adaptive functions. Darwin's famous example tells us that the white blue-eyed cats are always deaf. There is a more general observation: the artificial selection of any animal or plant for a particular character, after a rapid but slight initial success, becomes blocked by negative side effects on other characters and on general fitness, so that further progress becomes very slow. Nevertheless, we are able to reach necessary results in the evolutionary unattainable time, evidently because we are able to provide our charges with the most favorable environments by taking upon ourselves all care for their survival. Again we meet the same combination of the strict selective control of some (few) adaptive functions with the softened control of the remainder: the combination resulting in one-sided (imbalanced, inadaptive) evolution.

Unfortunately, I am not aware of studies discussing gains and losses in efficiency of particular adaptive functions during the process of insular evolution, e.g., in the famous cases of the Galapagos finches or many groups of Hawaiian insects. Nevertheless, it is well known that dwellers on oceanic islands (and isolated small continents like Australia) usually lose out in direct contact with those that occur on larger land masses: continental species often become established on islands (commonly at the expense of the aboriginal species), while opposite cases are at best rare. This also implies that the selective control of a particular adaptive norm is lighter, the resultant adaptive compromise is less deep and thorough, and the less adaptive resultant epigenotype appears in direct competition with developmental systems of different origin.

The above considerations can be summarized as the inference that stability of a well-balanced adaptive trade-off can be overcome and evolution made possible only, or at least mainly, as a result of one-sided lightening of the selective control of the epigenotype, when only a few of numerous adaptive parameters remain under strict selective control, while the rest can vary relatively freely. This causes deregulation, destabilization of the developmental system which is really observable in these circumstances (Zherikhin in "Activities of Intersectional Seminar …," 1967; Belyaev, 1974; Shishkin, 1984, 1987; McCune, 1990; etc.). Destabilization reduces fitness, so the evolutionary transformation can hardly proceed in normal environments.

Among other things, destabilization that accompanies the origin of new groups makes the common belief unlikely that this origin can proceed while entering an occupied niche and ousting its previous owner. It is much more probable that a new group either uses an unclaimed resource, or creates a new niche of its own. Indeed, we know of examples of a relatively recent origin of immigrant taxa (see above on the Hawaiian cerambycid beetles), sometimes even in historical time (during or after anthropogenic introduction). Some helminthological examples (cited in the discussion on the report by Rausch, 1982, p. 184) are particularly striking, including the case of two succeeding speciation events in a parasite of the house mouse introduced into North America, and divergence of two species of a human tapeworm 16000 or less years ago. In contrast, numerous and apparently better known aboriginal forms display a low tempo of evolution. Even in the highly unstable environments of the Pleistocene Holarctic, almost all fossil beetles belonged to extant species (Nazarov, 1984). In the database by Sher et al. (2006), out of 731 insect species recorded from the Anthropogene deposits of Northeastern Siberia, only 6 to 8 species are considered with more or less certainty to be extinct.

More important is another inference from the above conclusion, that is, evolution proceeds through two steps, the inadaptive step that is the only way to overcome stability of a well-balanced epigenotype, and the euadaptive step that is the only way to restore a balanced epigenotype fit to normal environments (those providing thorough selective control of the entire developmental system of the organism). The resultant stable organization displays itself in an additional stage, evolutionary stasis, that is, the absence of evolution, which could continue for indefinite time (up to tens if not hundreds of million of years, see above). This is because "almost any change, but particularly a major change, of the phenotype in such a well-balanced system will be deleterious" (Mayr, 1970, p. 367). Of this triad, the stasis is the calmest stage, that ends only when environmental changes make the continued existence of the available developmental system impossible (when total elimination exceeds the maximum reproduction rates available for the population affected under the current environment). The likely result is extinction, while less likely is successfully entering the inadaptive stage, that is, one-sided (ill-balanced) modification that also has a high chance of ending in rapid extinction. Otherwise, the population enters the process of euadaptation, that has still less chance of a happy ending. Yet if this rare, lucky chance is successful, a new adaptive norm is established and starts its stasis.

The above inference indicates a high rate of extinction of phylogenetic lineages forced to enter the process of evolutionary change, and so it looks rather pessimistic. This is not exactly true because of an already mentioned feature of the evolutionary process, its buffered nature. The more lineages fail to cross the barrier of the well-stabilized epigenotype, the more of them become extinct, are not replaced with luckier lineages, and the thinner the field of life becomes. This makes thorough control of evolving epigenotypes less severe, and free resources become available for future invaders. As a result, the more lineages entering the evolutionary process dare successful, until a new balance establishes between extinction and origination rates (cf. Flush and Crash model in Carson, 1968).

Therefore, life is reasonably guaranteed from complete extinction on Earth as the result of overly strict selective control of evolving lineages. However, my optimism does not extend far enough to expect that the above oscillations of strictness of the selective control could restore any level of status quo in a wider respect. The past events of mass extinction were less sweeping than is often described: even one of the deepest of them, the Permian–Triassic extinction resulted in the loss of about half of the families and three- quarters of genera in the seas (cf. Alekseev et al, 2001, text-figs. 6b, 6c) and much less on the continents (Alekseev et al, 2001, text-figs. 25b, 32a, 42a), and yet, the living world became essentially different after that event; the total diversity of life on the Earth, if considered for the most general trends, was essentially stable during most of the Paleozoic, and started the unlimited growth that has not yet finished up to now, and surpassed the mean Paleozoic level many time (Alekseev et al, 2001, text-fig. 6). Apparently, the general structure of life has changed on the global scale, and this change opened a way toward much more tight packaging of species and life forms in ecosystems.

The most general character of the evolutionary process, as inferred from the above consideration, is its low predictability, that is, low correlation between the environments where evolution takes place, and the results of evolution (features of resultant taxa). This unpredictability is a distressing feature of our model, and yet it is its highly positive feature. As mentioned above, observations do demonstrate low coordination between characteristics of environments and features of their dwellers, that is, low predictability of evolution. This effect is expectable for the epigenetic approach because epigenotypes (developmental systems) are so complex and integral that the pathways and results of their successful transformation are so far inaccessible for understanding and precise analysis. I consider the inference of unpredictability of evolution as an important positive feature of our model, which gives serious support for the epigenetic hypothesis as an alternative for the Synthetic Theory. It makes possible to unite the selectionist paradigm (*Evolution is a process of interaction between selection and available organization, which is produced by natural selection of previous generations*) with the observed unpredictability of evolution.

Another general characteristic feature of evolution implied by the above results is its highly uneven, saltatory nature, which is well known to paleontologists but difficult to explain within the framework of the synthetic approach. At the same time, our three-step model *inadaptation–euadaptation–stasis* easily finds its counterparts in various models proposed by syntheticists working in paleontology (Simpson, 1944; Eldredge and Gould, 1972; Stanley, 1975; Gould and Eldredge, 1977) and genetics (Carson, 1975). However, this similarity should not be overestimated. The above authors propose models intended to introduce the observed uneven pace of evolution into the framework of the synthetic theory. Accordingly, the proposed mechanisms differ profoundly from ours and are much restricted in their application. Indeed, under the synthetic approach, it is hardly possible to propose any other cause of evolutionary stasis than gene flow. However, the gene flow is much restricted in its ability to suppress differentiation. The gene flow does not act in groups of uniparental organisms, and acts unidirectionally in populations traced through time: in both cases stasis cannot be explained by reference to gene flow. Some syntheticists refer to the stability of the well-balanced organization which resists modification (Mayr, 1970, see citation above; also Van Valen, 1982; Laurin and Bruno, 1988), but this is an appellation to a different paradigm hardly compatible with the synthetic approach.

Now we can conclude that the epigenetic hypothesis of evolution is found to be superior to the synthetic one in explanation of the basic features of the evolutionary process. This does not mean, however, that we can be satisfied with the result. There are enough facts and observations that are waiting for explanation from the epigenetic point of view. It is time to start with them.

1.6. Problems

The first apparent contradiction concerns the basic inference that the adaptive trade-off is the main agent that makes the well-balanced epigenotype stable (resistant to attempts at modification). It is evident that the more complex and integral the epigenotype, the more strict the trade-off, and the more difficult and slow the evolutionary process should be. Equally evident is that the higher forms of life should be more complex and integral and so should evolve more slowly. And yet Tables 1 and 2 show the reverse: in general, the higher position a taxon takes in the system, the more rapid is its pace of evolution.

However, the case is more complex than it might appear at first glance. First, the higher resistance of more complex forms of life to evolution implies a lower frequency of adaptive evolutionary events, but it says nothing about other parameters of resulting changes which might counterbalance the effect of the low frequency. Among these parameters, the first coming to mind is that the logical inference that evolutionary changes will be more difficult and so rarer in higher forms of life compared to lower (more primitive, simple) ones infers nothing about the scale of these changes. It seems equally logical that a complicated and, hence, relatively rigid system, when forced to change, would generally change more deeply simply because of the longer and more intricately interdependent relationships among its subsystems. This effect alone can counterbalance the relative rarity of elementary evolutionary changes of advanced groups and provide higher rates of their evolution.

The directedness of evolution may have a similar effect. Actually, environmental changes usually have an appreciable chaotic component when particular parameters fluctuate to and fro. From the above, we conclude that the evolutionary response of a more complex form of life to a comparable environmental change is generally deeper (affects a wider array of its subsystems) than in the case of a less advanced group of organisms. It is expectable that, if the environmental change then reverses to its previous state, a simpler form that experienced more superficial modification has a better chance to perceive this environmental change as it is (a reversion) and to change itself accordingly (that is, to make a reversion). As a result, the cumulative evolutionary effect of long term chaotic environmental changes could be modest. In contrast, elementary evolutionary changes of higher forms of life generally affect them more deeply, so that once modified, they probably perceive an environmental reversion as a change in a different direction, and will evolve accordingly. This effect would transform chaotic environmental changes into directional evolution and so speed evolution up (Alberch, 1980; Rachootin and Thomson, 1981; Oster and Alberch, 1982).

The rigidity of a well-balanced trade-off depends not only on the internal parameters discussed above. Another side of the system under study is the strictness and particularly comprehensiveness of the environmental, mainly ecosystem, control of adaptations of a living being that controls the possibility of optimization of a function at the expense of others. Unfortunately, we have little, if any, possibility of direct evaluation of this parameter. However, we can try and assess it in indirect way. For instance, we can compare the general resistance of different organisms and taxa to various agents, because environmental factors affect the evolving system via modification of the control of adaptability of particular functions of that system.

It is possible, for instance, to compare the character and extent of individual and population stability in relatively primitive and more advanced groups. According to Beketov's rule, population stability can be measured simply by the reproduction rate characteristic of the group, that is, the fecundity and generation time. It is evident that mean fecundity decreases and the generation time increases with evolutionary advance: a clear manifestation of growing autonomy of the organism, its increasing independence of environmental fluctuations. Per se this would secure slow evolution of the higher forms of life. However, autonomization is expensive energetically, being dependent on rapid and fine evaluation of the state of the environment to identify timely signs of threat as a tool of anticipatory action, which is crucial for high individual stability. The result is increased dependence on energy sources (food). S.A. Severtsov (1941, p. 228) indicated that "the stoat, which needs daily food of half its own weight, and the viper, which hibernates half the year and in summer two or three moles a week suffice, clearly exemplify their metabolic difference. In the zoo, 36 g of meat a day suffices for a crocodile., while panthers of similar weight have 3.5–4 kg."

Furthermore, autonomization systems are as opportunistic as any adaptation they are aimed at to counterbalance customary, evolutionarily typical challenges. Their excellence (paid for by high energy dependence) gives little benefit in *new* (evolutionary nontypical) circumstances and, hence, does not secure general evolutionary stability of advanced forms of life.

Now let us consider the population mechanism of evolutionary stability. It is the excessive (reserve) population density that cause the *density dependent* growth of mortality and/or decrease in the fecundity of population (Van Valen, 1976). This mechanism of evolutionary stability is universal, because a decrease in excessive population density will increase the reproductive potential of a population (through a decrease in the density-dependent mortality and/or an increase in the density-dependent fecundity) irrespective of which particular agent caused the decrease in population density. However, the extent of the reserve population density is limited both above and below. The upper limit is imposed by the capacity of the resource space, which cannot be exceeded, while the lower limit of the population density should not be crossed in view of extinction danger, e.g., because finding of mates becomes problematic.Evolutionary importance of the excessive population density can be illustrated by the example of the phytospreading (Meyen, 1987a), a pattern of prevailing origin of new higher taxa within the equatorial (frost-free) zone, with their subsequent migration to higher latitudes at climatic oscillations (similar ideas have been earlier outlined by Darlington, 1957, and a generalization is proposed by Eskov, 2002). An explanation of phytospreading was proposed based on the effect of reserved population density, whose free supply would be higher in nonseasonal climate (Rasnitsyn, 1989d). Certainly, migration, reproduction, and evolution tend to level the life conditions all over the Earth, because any ecological space that is easy for life (underpopulated) will be rapidly filled, firstly, by propagation of local forms, then, by migration of the adaptively superior ones from other places, and, finally, by in situ evolution. No free space can exist at least in long run, but, nevertheless, some long-term differences do exist. In particular, the abiotic conditions are easier in the nonseasonal climate than in the seasonal one, and this difference should be compensated by biotic stresses including the additional excessive density of populations. The higher the available reserve of the population density, the longer a population can survive under negative reproductive balance, and, hence, the deeper evolutionary reorganization it can survive. It is understandable that abiotically smooth frost-free environments provide more chance for the evolutionary reorganization of the adaptive trade-off than the temperate climate with cold winters.

However, of importance for our aims is whether or not a correlation exists between the level of organization and the available amount of excessive (density dependent) population density. A direct comparison of, for instance, prokaryotes and mammals in that respect seems risky; so, we again take a roundabout way of analysis of agents defining the position of the limits of stable population density and, at the same time, dependent on the evolutionary level of respective organisms. The upper limit of stable population density ultimately depends on the energy flow available for the population. In case of the stable flow, the upper limit depends on the energetic demands of an individual (we speak in terms of individuals rather than biomass, because the individual is a natural unit while considering the position of the low limit of population density; see below). It was already concluded that the individual needs in energy increase very rapidly with the evolutionary progress, because individuals of advanced groups are generally of larger body size, and additionally because autonomization is energetically costly. As a result, the upper limit of population density decreases rapidly with evolutionary progress, thus threatening the evolutionary success of the higher forms of life.

The low limit increases stepwise when, for example, the sexual process is acquired, particularly since two individuals, and not any two, need to meet for reproduction. A similar effect appears as a consequence of environmental conditioning (favorable modification of the environment by the combined activity of several individuals). The first acquisition of sexuality was undoubtedly connected with the growth of the level of organization, although later its influence was probably negligible in that respect, and the correlation of the ability for environmental conditioning with the level of organization is probably moderate at best. Therefore, the position of the upper limit of the population density is probably the main agent that influences the amount of reserve population density in correlation with the evolutionary level of respective organisms. As we can already see, this agent reduces that reserve with the growth of the level of organization and, hence, their evolutionary stability, that is, increases the tempo of their evolution.

Population and evolutionary stability in a changing environment also depends on available refuges with less modified conditions. Refuge availability depends on many parameters, but the most influential are probably the dispersal potential and body size. Analysis of the tempo of evolution (Rasnitsyn, 1987) does show taxa with pronounced dispersal adaptations as evolving slowly (Tables 1, 2); the age of half-modern order-level fauna (when half of orders are extant and another half extinct) is about 100 Ma in birds vs. 70 Ma in reptiles and 40 Ma in mammals. Equally, the species half-life (mean time of extinction of half species set) is 1.6 Ma in bats vs. 0.18–0.49 in other mammals. However, a significant correlation between the evolutionary level and dispersal potential is questionable.

More important in our context is absolute body size which is correlated positively with the organization level and negatively with the availability of refuges. Correlation with the level of organization is clearly understandable even if not at all strict; to become complicated, it is necessary to have some additional space and material, and conversely, to secure appropriate functions of a larger organism, additional regulating systems are necessary that are efficient at respectively long distances.

The negative correlation between the body size and availability of refuges is also plain, since the larger is the body size, the greater is the minimum space necessary for the population to survive, and so the larger a refuge would have to be to house it. Accordingly, this reduces the chance of respective organisms finding an appropriate refuge during available dispersal time. As a result, the groups of generally larger body size would have become extinct more often and so evolve at higher rate than taxa of smaller body size. As mentioned above, the half-modern species-level fauna of small mammals is 2.5 times as old as that of large mammals (0.5 Ma for rodents, insectivores, and bats, vs. 0.2 Ma for elephants and ungulates; Table 1). At the same time, it is still 10 times younger than that of insects (some 5 Ma). During the Quaternary, most characteristic large-sized mammals of the so-called tundra-steppe biome became extinct before or during the Early Holocene, while the majority of small mammals survive, and most insects have survived through all the Quaternary virtually unchanged (Nazarov, 1984; Sher, 1997a, 1997b; Zhegallo et al., 2001). Evidently the positive correlation between the extinction rates as dependent on the shortage of refuges, and the body size (and hence, the evolutionary level), is quite real.

The above features hardly exhaust the entire diversity of interconnections between evolutionary stability and the level of organization that control the tempo of evolution. However, other regulatory mechanisms of the pace of evolution are less apparent. As a result, we have identified several mechanisms that control the evolutionary rates in different and in partly contradictory ways whose cumulative effect cannot be unambiguously predicted without special research. Of them, one system of forces should decrease evolutionary rates of higher forms of life, providing the adaptive trade-off concept is correct: advanced forms have their organization more complicated and, hence, are more resistant to adaptive modifications (they have a more stressed trade-off between the contradictory demands of optimization of different adaptive functions, the adaptive remodeling of which is particularly risky for their survival).

The contrary effect, viz., increasing evolutionary rates of higher forms of life, results from several other mechanisms, as follows.

(1) better expressed directedness of their evolution,

(2) reduced evolutionary stability of higher forms due to

(a) the lower upper limit of stable population density because of the larger average size of individuals as well as because of high energetic cost of autonomization,

(b) the higher lower limit of stable population density of bisexual organisms which should be high enough to secure meeting of mates,

(3) refuges are less available for more advanced organisms because of their generally larger body size.

It would be important to get independent information on the actual efficiency of the above mechanisms, to make it possible to assess their cumulative effect and so to confirm or disprove our explanation of the paradoxical distribution of the observed rates of evolution in various groups of organisms. These data do not seem easily available in the near future, and for the present we must draw conclusions based on what we have now. The results at hand look sufficient to infer that the concept of the adaptive trade-off as a part of the epigenetic theory of evolution supplies us with an adequate explanation. It agrees with the majority of accumulated observations, including those difficult to explain from the standpoint of the synthetic theory of evolution. The epigenetic approach is not sophisticated yet enough to give reliable and detailed predictions about the rates of evolution in various groups of organisms; this is a goal of future research. Nevertheless, it is possible to conclude that, in general, the epigenetic theory of evolution is in agreement with a wide array of observations and inferences not only in the field of ontogenetic realization and evolutionary modification of individual development of organisms (original domain of the theory), but also with the results of paleontological study of the organic evolution. This inspires the hope that the problems outlined above will find their resolution in the not very distant future.

2. METHODOLOGY OF PHYLOGENETICS, TAXONOMY, AND NOMENCLATURE

2.1. Elements of General Methodology: Presumptions

Normally, the scientist does not take notice of the methodological grounds of his or her work. However, when the standard, custom, means and methods of the work time after time fail to give satisfactory results, a temptation appears to raise a kind of a scientific revolution (Kuhn, 1970), that is, to abandon those means and methods along with their underlying methodology and to replace them with something different. Revolutions, even scientific, are rarely bloodless; however, they usually result in rejecting approaches that are well workable, albeit in a somewhat different domain, and data obtained under these approaches that are still meaningful and worthy of being reassessed rather than rejected. Therefore, it seems preferable to examine the methodological background of a scientific approach prior to abandoning it, in the hope of identifying and improve its methodological deficiencies, and thus to save the approach and the results of its application.

The present revolution in taxonomy and in the closely connected phylogenetics has continued for about half a century and is caused, in my opinion, by an intention to formalize, automatize, and standardize the scientific process, that is, to make it more objective and reproducible. A natural subsidiary result of this drive is the suppression of researchers' individuality, and particularly of their intuition. Explosive computerization has particularly intensified this process during the last decades. Chronologically, the first was the clash between traditional taxonomy and phenetics (reviewed by Sneath and Sokal, 1973), which had no natural result because the latter has been ousted by the newly emerged (since Hennig, 1966) cladistics. Currently, we are apparently observing molecular phylogeny ousting the customary (morphological) cladistics.

Traditional taxonomy was scarcely affected by pheneticism. Cladistics is more aggressive and supported by more influential proponents, and it has been more successful in oppressing traditional taxonomy, in spite of its evident shortcomings (see below). Yet I do not consider the battle to be over. However, I have to start with a more general issue.

Each step in cognition, while acquiring knowledge, in my opinion, proceeds through six successive stages (Table 3). First, based on previous knowledge, we formulate the aim of research and plan observations and/or experiments. Second, following the above aims and plans, we collect material for study. Then, if we are happy to observe an essentially unknown (not yet understood) pattern, we start seeking known elements there. Based on our background experience and/or on the results of a preliminary contact with the pattern, we are sorting these known elements into important (relevant to the goal of our job), or unimportant. In this context, the known element of an essentially unknown pattern is considered as important, when we suppose that our knowledge of it permits us to discern (is correlated with, or otherwise reflects in one way or another) important features of the pattern. In turn, important features are those which have more profound influence on, or are correlated with, or otherwise permit to appreciate and foresee, the structure of the pattern and its behavior

Table 3. Steps of cognition

1	Target setting and planning of data gathering
2	Observation and experiment
3	Seeking for analogies, i.e., for known elements in a new pattern, and selecting those promising to help in the revelation of the basic structure of the system under study
4	Constructing hypotheses about the basic structure and underlying processes creating the pattern observed
5	Attempts of falsification of the hypotheses proposed by drawing the longest chains of consequences and testing these predictions against results of earlier and new observations and experiments
6	Assessing of the testing results using a system of relevant presumptions

under various circumstances. For example, when a taxonomist encounters a completely new insect group to classify (for the moment I mean only internal classification, not the general taxonomic position), he will ignore the features, how profound they are per se, which discriminate males and females, or adults and larvae (except to segregate these and those to classify each subgroup separately and eventually to compare results). Further, he will probably give preference to the morphological similarity over that in the color pattern, etc.

The fourth stage of cognition begins here. We create a hypothesis about the particular similarity between the patterns under examination and a class of patterns that have been already studied but seemed dissimilar to the pattern in question. The hypothesis should be predictive, i.e., we should propose the existence of a particular mechanism that is responsible for the similarity, or clarify that the similarity also exists in many other characters. This then allows us to hypothesize that the similarity can predict the behavior of the pattern in question in various environments and conditions. To continue with the above example, the taxonomist will possibly hypothesize that the similarity in morphological characters could indicate a higher (say, generic) level of overall similarity, while the similar color pattern concerns a lower one (say, species level). In other words, the taxonomist would hypothesize that the inferred tentative classification be more natural, e.g., less burdened with homoplasies, then the alternative one that gives more weight to the color pattern.

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

The fifth stage is to test the hypotheses proposed. To reach that end, we should propose the longest and most diverse chain of implications in order to have more opportunity to compare them with the results of observations and experiments (for more detail, see below).

The sixth and last step of cognition is to decide concerning the availability of each hypothesis proposed: whether any of them can be retained for further testing, or must be rejected. Again, examples and discussion follows.

The fifth step of cognition has been well studied by Karl Popper (1968), who clarified the fact that there is no way to verify a hypothesis definitely. Moreover, it is impossible to completely falsify a hypothesis, since this would mean the verification of an alternative hypothesis, namely, that the falsifying result occurs neither by chance nor due to neglected external influences (circumstances) (cf. Farris, 1983). In practice, if you claim that all swans are white, and yet encounter a black swan, prior to abandoning your claim you should reject possibilities that (1) your black swan is not a swan (e.g., it is a convergently modified goose, or a skillful mystification, or something of the like), (2) your black swan is not naturally black (e.g., artificially stained black). I believe that these possibilities are always a matter of likelihood and not just of yes-or-no reply. It is for this reason that the sixth stage of cognition appears necessary when we consider competing hypotheses and assess relevant falsifying evidence in order to reach a decision.

Implication of the above consideration is that all our knowledge is a Mont Blanc of hypotheses relying one upon another, and Mont Blanc upside down, because the basic hypotheses are few, and those resting upon them and upon each other are many. There is an additional problem in that our analytic tools do not fit the material they handle. They are designed to seek for the truth and not to manipulate hypotheses. Proof relies on statements taken as the truth, but even the mathematical axioms are found questionable, while biology can present us with nothing comparable. The rules as empirical generalizations of high reliability are not perfectly reliable, even the most reliable of them, the law of conservation of matter and energy. As to the laws in biology, like the famous biogenetic law, the law of irreversibility of evolution, or of the nonspecialized ancestor, their reliability is low. The explanation, that is, reduction of a pattern toward processes of another level of generality that are not further analyzed in the given research (that is, taken for the truth there) is also not a reliable tool. First, results acquired at other levels of analysis are not necessary more reliable than ours and anyway not absolute; therefore, to be certain in results, research should be continued further through all levels, an evidently hopeless venture.

Second (or, rather, first), the same evolutionary phenomenon can often be explained satisfactorily, in the opinion of respective students, in the framework of selectionist, lamarckian, and theological approaches. It is not at all infrequent that the subjective initial impetus that drove Popper to develop his falsificationist approach was his Freudian experience, when he discovered that there is no imaginary case that cannot be explained from the Freudian position. This was the very reason why he claimed that Freud's doctrine (as well as Darwin's and Marx's) were nonscientific (it is a different question whether he was always correct). In my opinion, Popper was incorrect in the unambiguousness and final character of his verdict. Apparently, he meant *experimentum crucis*, the conclusive experiment that gives the final reply to a question; we have already seen that this is impossible. I believe that only the whole body of evidence can falsify a hypothesis probabilistically (not absolutely).

Both final verification and falsification being impossible, we can never be certain of any of our observations and considerations concerning the nature of things. Our knowledge is not reliable, and our tools are not fit for their use. If so, how can we live and work in a world which offers nothing definite for us and thus seems so unreliable? Apparently, the above pessimistic inference is not correct: we should have more adequate means of gathering the knowledge, otherwise mankind would have become extinct long ago. We are skillful enough at making correct decisions with insufficient information (when information is sufficient and all is plain, we act almost automatically and do not say that we are making a decision). We do make mistakes, but they are (or, rather, were until now) not bad enough or numerous enough to lead mankind to extinction. Therefore, we possess the correct means, and the task is to identify them.

The instrument in question was first identified in the present context by the author (Rasnitsyn, 1988b, Rasnitsyn and Dlussky, 1988), although it has been known for centuries in other context (in courts of justice). I believe that this is because it is in this domain where information is so often insufficient and where a *correct* decision is vital, given that the time needed for seeking necessary "generalization" has been sufficient. This generalization is termed the presumption. This means that, for a particular class of problems, there exists a decision (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 evidence exists for it, but only in the absence of reasonably sound evidence against it. Otherwise the alternative decision is to be accepted.

The paradigmatic example of presumption is the presumption of innocence: *However, strong is the suspicion, a suspect should not be considered a criminal unless and until the accusation is reasonably proven.* How reasonably it should be proven is a different and very important thing which we consider later on. Otherwise, all presumptions are constructed similarly: **for a particular class of tasks, presumption proposes a model solution to be selected irrespective of the presence and strength of evidence in favor, but only in the absence of reliable contrary evidence**.

Following, there are a few examples of presumptions in biology (those pertaining to phylogenetics will be considered in more detail below). Bed succession in the Earth's crust should be interpreted as displaying the temporal succession, unless and until reliable contrary evidence is presented. Homotaxic (similar in the taxonomic composition) fossil assemblages should be considered as synchronous if no serious contra argument are found. A taxon is to be taken as monophyletic unless the opposite is demonstrated. Similarity should be treated as inherited until evidence of its independent acquisition is revealed. Onthogenetic succession of developmental stages should be taken as a model of a phylogenetic succession unless we have good reason to conclude differently. In general, do not multiply essences (hypotheses in our case) beyond necessity, as Occam's Razor suggests. Or, in other words, let us take a simple decision until more complex ones are well substantiated.

A few more words to conclude this introduction. Presumption is nothing more than a concentrated experience of successful solutions of particular problems. Normally, for the health of society it is safer to leave a criminal unpunished than to punish an innocent. In geology, the normal succession of beds is more common than the reverse one. On the geological time scale, migrations are usually momentary, and appreciably different ages of homotaxal fossil assemblages are rare. Demonstrable polyphyly of a taxon, particularly in higher forms of life, is also uncommon (this inference now appears endangered by the results of the molecular phylogeny, but we should not rush to conclusions). Parallelism in ontogenetic and phylogenetic successions of organisms is usually striking. And so on. However, all the above inferences have exceptions, and sometimes these are numerous. For instance, in prokaryotes, similarity of traditional (nonmolecular) characters depends on similarity of ecology rather than phylogeny, that is, it is commonly gained independently (Woese, 1987; Zavarzin, 1987). In Quaternary paleontology with its fine time scale it is not uncommon to successful identify homotaxa as diachronical. Soviet society was organized specifically so that its health was secured by the presumption of guilt (that is, actual court justice, rather than agencies of investigation which legitimately rely on a presumption of guilt). And so on.

The above appears sufficient to demonstrate that presumption is not a subject of analysis in terms of truth and untruth, rather, a particular presumption should be efficiently applied in a particular context, while another context might rely on a different presumption. To complicate the problem, it should be borne in mind that several different presumptions can be found pertaining to one and the same particular problem, and their suggestions could be contradictory. For instance, different approaches to the identification of the direction of a particular evolutionary trend can infer this direction differently. Many features of the human skull are similar to those of the embryonic ape skull, while the mature ape skull demonstrates characters absent from the human one. Application of the biogenetic presumption to the case naturally results in the unacceptable inference of the human preceding apes phylogenetically. In contrast, the paleontological presumption suggests the reverse, based on the hominoid fossil record.

This particular example is easy to interpret as a case of a secondary retardation of development with the early maturation that resulted in the loss of previous adult features in favor of the embryonic ones changed into new adult characters. Other cases are often less transparent, thus making a decision difficult if, for example, the ontogenetic succession better secures the phylogenetic one, or the fossil record represents a better indicator, or still another indicator prevails in its prognostic quality. Wide experience and deep intuition are necessary to make the correct selection. Of course, there are further presumptions to help there, e.g., if the involved presumptions are more than two, the rule of majority (presumption of parsimony) can be applied to select the hypothesis supported by a greater number of presumptions. However, the majority are not necessarily correct, and those in the minority might be worth following in cases where they have shown reliability in comparable circumstances (see below for more detail and further explanation).

To conclude, using presumptions is anything but plain. It needs experience, intuition, imagination, and courage (the last property because the risk of error is never far away). However, life itself is like that, and making science is particularly so. Apparently, we have no other way.

2.2. Methodology of Phylogenetics

Phylogeny is commonly interpreted as a history of a particular group of organisms, their history being described in terms of both diminishing genealogical relationships between its subgroups and their changing similarity. In addition, evolution is commonly agreed to proceed slowly enough to prevent its immediate perception, so that phylogeny is perceptible only from its results, not from the process itself. These results are traits of form and function of organisms, including morphological, physiological, and behavioral characters, those concerning the response of organism to biotic and abiotic factors, their distribution in space and time, and the like. Textbooks and relevant publications propose a wealth of simple and straightforward (or sometimes less simple but nevertheless straightforward) criteria for recognizing true relationships, phenetic, cladistic, molecular ones, etc. However, simple and straightforward tools are rarely efficient in our science; therefore, we have to use a more flexible but difficult device called presumption (Table 4).

2.2.1. Basic Presumptions of Phylogenetics

The first and central presumption in phylogenetics is the **presumption of knowability of phylogeny**. It claims, *any similarity should be considered as inherited unless and until the reverse is reasonably proven.* Hennig (1966) calls this statement "the auxiliary principle," however, it is far from being auxiliary. It is the central statement of phylogenetics claiming that phylogeny is generally knowable. Actually, "if homoplasy [independently gained similarity] is universal, the characters imply nothing about the genealogy" (Farris, 1983, p. 14).

This is not an evident thing. A man engenders a man, and not an ape, under any conditions, but water can be equally obtained either by burning hydrogen or by oxidizing lipids inside organisms. The difference between the two cases evidently lies in the different level of complexity of chemicals versus 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 as well. It has been suggested that, in prokaryotes, the amount of the independently acquired similarity is so vast that traditional methods are often of little help in discerning prokaryote phylogeny (Zavarzin, 1987). Observations of this sort quite evidently impose restrictions on the domain of phylogenetics.

There is another, less exotic restriction. The divergence of lower taxa takes place generally in a less remote past than that of higher taxa. Hence, it should leave clearer evidence of how such divergence has proceeded. Nevertheless, we often feel that genealogical relationships of species, especially those in large genera, are much less clear and more difficult to sort out than relationships of, for instance, families or subfamilies (cf. Saether, 1986). I am aware of the only acceptable explanation of this phenomenon, 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 makes it possible for them to respond similarly to similar factors. The problem certainly deserves close examination, which, however, lies beyond the scope of the present study.

When a group is studied thoroughly in great detail, both with regard to paleontological and contemporary material, it is evident that extensive parallel evolution, resulting in the abundance of homoplasies, is often characteristic of higher taxa as well as of species. Vertebrates may serve as an example, since they show numerous cases of parallel transition from the level of

Table 4. Phylogenetic presumptions

Scope	Name	Statement
General	Knowability of phylogeny	Any similarity should be considered as inherited, unless and until the reverse is reasonably proven
Group analysis	Paleontological	Of two apparently closely related groups, the one entering the fossil record earlier should be considered to be ancestral, unless and until sound contrary evidence is presented
Dissimilarity analysis	Paleontological	Transformation series should be polarized accordingly to the succession of the respective character states in the fossil record, unless and until sound contrary data are presented
Dissimilarity analysis	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
Dissimilarity analysis	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
Dissimilarity analysis	Functional efficiency	Of two character states, that corresponding to a more efficient adaptation should be considered apomorphic, until and unless reliable contradicting evidence occurs
Dissimilarity analysis	Of complexity	Complex structure should be regarded as apomorphic in relation to a more simple one, unless and until we have strong reason to decide otherwise
Dissimilarity analysis	Vestiges	The character state showing any signs of being modified from another state is apomorphic with reference to the latter, unless and until strong contrary evidence exists
Dissimilarity analysis	Irreversibility	When we 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
Dissimilarity analysis	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	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
Similarity analysis	Weighted similarity	In the case of conflicting similarities, that known to be more reliable in other cases (especially in closely related groups) should be regarded as inherited, unless and until strong contra-arguments appear

organization (grade) of fish to that of amphibians (that is, independent acquisition of the characters generally characteristic of amphibians) and further to the level of organization of reptiles and mammals (or birds). During the past three decades, this old theme was under close examination of Russian students (Tatarinov, 1976, 1987; Shishkin, 1987; Vorobyeva, 1992; Ponomarenko, 2005). Under the old name aristogenesis (Osborn, 1934), this pattern is discussed by Rautian (1988). Current molecular studies display a particularly wide occurrence of parallel evolution (see below).

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; the term of similar albeit not identical meaning is key aromorphosis, proposed by Iordansky, 1977, 1979). The notion of underlying synapomorphy implies an apomorphy (any change in structure or function) which has been gained by the common ancestor of the group and which induces independent (parallel) development of new and similar changes in some or many members of the group. For instance, the acquisition of the resilient longitudinal string (the chord and its successor the backbone) that permits accumulation of the mechanical energy of the body bending was the common basis for various chordate animals to independently obtain a fish-like general appearance whenever they become a strong swimmer (whales, dugongs, ichthyosaurs, tadpoles, etc.). Another case is costal breathing, a remote cause of independent development of homoiothermy, as was concluded by Iordansky (above references). Unlike these examples, we are rarely aware of concrete causes that are responsible for the repeated acquisition of a particular feature by a particular group of organisms. Nevertheless, I believe that an actual common reason (common feature), albeit unknown yet, should underlie the majority of cases of massive parallel evolution. This feature should once appear as an apomorphy, hence, the name underlying synapomorphy.

Wide distribution of parallel evolution does not permit us to think of taxa as simple products of divergence of the 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" (the term proposed by Mamkaev, 1968). The process of parallel evolution as a whole can be described as taxon maturation, that is, accumulation of similar changes combined with elimination of unbalanced (inadaptive in the sense of Rasnitsyn, 1987b) intermediate groups. This approach returns us to the old and well-known hypothesis of Darwin (1859) that gaps between taxa are in part (probably in a large part) due to the extinction of the intermediate forms. This maturation often takes quite a long time. Therefore, higher taxa at later stages of their evolution are often more clear cut and seem to have a more easily discernable phylogeny as compared to lower taxa, or even to themselves at an earlier stage in their history.

The hypotheses involved to explain the pattern of extinction of intermediates are described above (for the problem of discreetness of the life, see Section 1.4). Here it is important to note that the pattern described above seems to cause less difficulties for the phylogenetic study of eukaryotes than in the case of prokaryotes. Anyhow, we are still able to construct a phylogenetic tree, although assessment of its generality is restricted. We can never be quite certain about the tree and particularly about its details, so it becomes pointless to speak about an ancestral species of, for example, a family. In some (often many) cases, thorough and sophisticated research fail to identify even the ordinal position of the common ancestor of a class. And this may be true even if the actual ancestor is already collected and described, albeit not yet identified, among other fossils (Vorobyeva, 1992). In short, parallelisms affect cladograms in filling them with unresolved (polytomous as opposed to dichotomous) clades, but otherwise the above considerations change 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 the history of either groups or characters. 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 (Section 2.3.2). In short, I follow Linnaeus, who said "Scias Characterem non constituere Genus, sed Genus Characterem" [1751, p. 169], that is, "Know, the character does not constitute the genus, but the genus the character" (translation is mine, corrected by M.T. Ghiselin).

2.2.2. Presumptions in the Group Analysis

The main method of group analysis is the **paleontological** one (redefined as stratophenetics by Gingerich, 1979, 1990). It is based on the presumption that, *of two apparently closely related groups, the one entering the fossil record earlier should be considered ancestral unless and until sound contrary 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 well known to be incomplete. However, this incompleteness is neither vast nor due to chance but is 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, for example, Briggs and Crowther, 1990; Zherikhin, 2002b). In many cases, it is already known which kinds of organisms have a good chance of being buried, fossilized, and excavated, and which do not; which kinds of environments have a greater chance to contain fossils, and which do not. Additionally, deposits vary greatly in their degree of informativeness. 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 its real nonexistence, 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). Therefore, the majority of fossil insects are either flying or aquatic/semiaquatic, shore-dwelling forms. The bristle-tailed insects (Thysanura sensu lato) are wingless, terrestrial, and not especially common along sea and lake shores. Thysanura entered the fossil record later than the Pterygota [that is, in the Westphalian versus Namurian; 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]. The absence of bristletails from the Lower Carboniferous (Mississippian) fossil record cannot be seriously taken as evidence that they could not be the Pterygota 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.

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 study of the subject and related topics, and even then mistakes are unavoidable. Of course, there are no faultless methods of cognition at all. However, there are two different strategies possible there: we could prefer either to escape mistakes, or to correct them. In the first case, we would consider as respectable only the safest methods (those with the least danger of giving incorrect results). This strategy would dramatically reduce the diversity of our scientific approaches and thus lower the demand for ability, knowledge, and skill in scientists. More people would be able to participate in scientific work, albeit using a reduced diversity of methods, while the exceptional abilities of a few particularly gifted persons would remain unused. This ideal of a mass, standardized science is not mine. I prefer science that is free in using a broad variety of methods, dares to make and correct mistakes (and to turn the very mistakes to its advantage, 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 that promise both interesting new discoveries and pitiful mistakes.

There are 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 evolve in their distributional routes, so the distributional history of a group could correlate in a way with its genealogy, so phylogenetics 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. The major factors of the distribution are thus supposed to be (1) the geographic structure of the space, (2) the dispersal potential of the group, (3) chance. Similar distributional 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 the three will be essentially similar, so we should suppose that the pattern of similarity is often by chance. Therefore, under the classical concept of biogeography, the biogeographical method of phylogenetic analysis as appears to be of doubtful value.

In contrast, the cladistic concept of biogeography (treated here based mostly on the summary by Humphries and Parenti, 1986) considers the distribution of plants and animals as a result, both phylogenetic and geographical, of barriers imposed by various physical agents (primarily connected with continental drift, but also of 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 evidence of the respective area-dependent genealogy of all the groups concerned.

Cladistic biogeography seems to perfectly fit the objectives of phylogenetic analysis of groups, for giving a particular repeating pattern of area cladograms, we should simply hypothesize isomorphic cladograms for each group involved. The matter is not so easy, however. The dispersion of organisms is well 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 is not disorderly), is not necessarily so chaotic as to be easily sorted out as producing unique area cladograms. When regular, the dispersal events may produce repeating patterns of area cladograms easily but deceptively interpretable in terms of cladistic biogeography. Until purposeful research demonstrates a subordinate role of the dispersion in the origin of area cladogram patterns, I would refrain from using the biogeographical method in reconstructing genealogy.

There is one more, serious, reason to be cautious concerning the prospects of the biogeographical method as a phylogenetic tool. Both classic (dispersalist) and cladistic biogeography pay little attention to extinction events. However, these are not only very common but often regular enough to concern the entire biota. The area cladograms affected by this form of extinction produce a pattern easily but wrongly interpretable by the cladistic method. For example, there are numerous cladistic reconstructions of the austral ("Gondwanian") distribution (for a review, see Humphries and Parenti, 1986). I am afraid that most of them are in vain, since the fossil record, when it exists, very often shows that some time in the past these austral groups existed on the northern continents and then died out there (for more detail, see Eskov, 1987, 1992).

The austral paleontology is less complete than the boreal one, and yet there are austral fossil findings known for groups that are now of strictly boreal distribution (the same references). Similarly, extinction could well be responsible for the amphitropical (bipolar) distribution of many taxa. These amphitropical geographic ranges, instead of being a heritage of a hypothetical Pacifida continent (Humphries and Parenti, 1986), are more likely remnants of the past worldwide ranges disjuncted by the tropical biota which emerged in the equatorial zone probably during the Eocene (Razumovsky, 1971; Zherikhin, 1978, 1993; Eskov, 2002). Unfortunately, the tropical paleontology is less developed yet than even the austral one. Nevertheless, it is of importance that there are no sound indications of the equatorial Late Cretaceous nonmarine biota comparable to the tropical one of the present day (Meyen, 1987b). The only known relevant and rich fossil arthropod assemblage buried in the late Early Cretaceous (latest Albian) amber from Burma; (Rasnitsyn and Ross, 2000; Shedrinski et al., 2001; Grimaldi et al., 2002) lacks characteristic tropical forms. Instead, among the fossils already identified, there are several groups very common in assemblages from the Late Cretaceous fossil resins of northern Siberia and Canada, such as the hymenopteran genera *Serphites* Brues and *Palaeomymar* Meunier (Rasnitsyn, 1980; the latter genus is extant and predominantly extratropical bipolar now). Additionally, the assemblage includes a group (snakeflies, insect order Raphidiida; Engel, 2002) of a currently northern extratropical distribution.

There is still stronger evidence that the past Burmese forest that yielded the fossiliferous amber differs cardinally from the tropical rain forest as we know it. Unlike the tropical assemblages from the later (mid-Tertiary) Mexican and Dominican ambers, as well as those from the Oligocene of Sicily and the North Apennines, the Burmese assemblage is completely free of the isopteran family Termitidae, social bees, and higher social ants. As was demonstrated by Zherikhin (1978, 1993, 2002c), these are three animal groups that play key roles in the functioning of the tropical rain forest, and their possible functional equivalents are known neither now, nor in the past.

Hence, it is possible to conclude that the repeated pattern of area cladograms is still of obscure meaning unless 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 biogeographical presumption for group analysis.

The same seems true for other apparently relevant methods, e.g. the parasitological one, which suggests using the host cladogram as a model for that of the specialized parasite, or vice versa, depending on which cladogram appears more sound.

2.2.3. Character Analysis

Character analysis has twofold application. It can be used to polarize the transformation series (morphocline), that is, to identify the direction of evolutionary changes in an apparent set of character states. In the example above, the task of character analysis is to reveal if the respective characters of the ape and human skull are generalized (plesiomorphic) or advanced (apomorphic). Another function of character analysis is to resolve conflicts between hypotheses of unique origin of observed similarities whenever these conflicts are encountered (see below for details). These two functions can be termed analyses of differences and of similarities, respectively.

2.2.3.1. Analysis of differences: polarizing transformation series. There are several methods of identification of the direction of character evolution in a particular group of organisms. One of them is the **paleontological method**, which is similar to the paleontological method for groups described above (Section 2.2.1). However, these two applications are independent. Homoplasies are shown paleontologically to be not only fairly common but also often to have a similar direction in various contemporary groups. The cases of mammalization of theromorph reptiles, angiospermization of gymnosperm plants, arthropodization of worms, and ornithization of theropod reptiles (Tatarinov, 1976, 1985; Krassilov, 1991; Ponomarenko, 2004; Kurochkin, 2006) are good examples. Therefore, in many cases, we can use the presumption that a *transformation series should be polarized accordingly 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 and with their morphology inconclusive (either simple and thus poor in characters, or replete with homoplasies).

Another and very similar method is the **ontogenetic** 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" on the differentiation through ontogeny, claiming that *"Aus dem Allgemeinsten der Formverhältnisse bildet sich das weniger allgemeine und so fort, bis endlich das Specialliste auftritt"* (p. 224; von Baer's italics). Or, in translation, "From the most general structural relations [that is, beginning from synapomorphies of the most inclusive taxon (AR)], develop the less special ones [synapomorphies of the less inclusive taxon], and so on, until the most special characters [synapomorphies of the terminal taxon] appear."

There is a widespread belief that the biogenetic law has extraordinary importance (as a "direct argument") in phylogenetics (see, e.g., Nelson, 1978; Bonde, 1984). I do not believe that. Ontogeny is flexible, with any of its stages subject to secondary modification or loss due to paedomorphosis, pre-adult adaptation (cenogenesis), or in the process of rationalization (streamlining) of the developmental path. As a result, the biogenetic method is highly effective in deciphering phylogenesis of some groups and misleading in other cases. It has no a priori advantage compared to other methods, and does not work as a rule of thumb, but only as a presumption. Certainly, the ontogenetic succession of developmental stages is a result of direct observation. The same is 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 keep 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 a 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 our 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 the taxonomic pattern of various character states, particularly DNA structure, see below). Otherwise, based on the ontogeny per se, we should infer the human skull features to be symplesiomorphic with gibbons and monkeys, while those of the great apes would be synapomorphic.

The next important method and presumption are the method and **presumption of analogy**, which reads *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.* Indeed, if we are reasonably sure that the bat wing is a modified leg, we can legitimately believe this to be the case for pterosaurian and avian wings as well.

A similar hypothesis concerning the insect wings is less evident because of great differences that exist between the groups and the deep dissimilarity in 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 both are modified parts of a biramous ancestral leg. Likewise, we know that most mammalian lineages evolved in the direction of increasing body size ("the 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 is true for many other so-called empirical laws of evolution.

The well-known polarizing method using functional efficiency can be formalized as based on the **presumption of functional efficiency**, i.e., *of two character states the one corresponding to a more efficient adaptation should be considered apomorphic, until and unless reliable contradicting evidence occurs.* For example, viviparity is generally considered as apomorphic in comparison with oviparity, because it secures progeny better than the latter (it permits viviparous animals to survive despite the low mean number of their offspring).

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

Such secondarily simplified structures commonly display rudiments or other signs of their lost complexity, indicating one more polarizing method, the **presumption of vestiges**, which reads *the character state showing any signs of lost complexity from another state is apomorphic with reference to the latter, unless and until strong contrary evidence exists* (e.g., until it is found that what we took for the vestige is in fact an *Anlage*).

It is worth recalling the famous rule of irreversibility of evolution that is also the subject of plentiful exceptions and so represents rather the **presumption of irreversibility**, i.e., *when one possible direction of transformation is found as realized, it should be selected as repeated in other comparable examples, unless and until a different direction is supported strongly enough.*

The last and most popular polarizing method analyzes discribution of the respective character states within and beyond the group under analysis. It is called the outgroup comparison and represents a probabilistic test for conformity of a cladogram with our basic phylogenetic model that evolution is generally divergent, while homoplasies are not abundant enough to make similarity irrelevant to genealogy (cf. the presumption of knowability of phylogeny, Section 2.2.1). 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 appearing later in the same group. When we 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 that the first character state is plesiomorphic, while the second is apomorphic (unless there are strong contrary arguments). This is because, when doing so, we could infer only one evolutionary change which took place at the origin of a subclade of the group in question. Otherwise, hypothesizing the first character state as apomorphic and the second as plesiomorphic, we should imply a minimum of two identical evolutionary changes, one within the group, and another beyond its limits. If we agree that inherited similarity is a more likely (more common) thing than an 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 some related reptiles: Tatarinov, 1976). Similarly, feathers are only known in birds (and, again, in some related reptiles, see, e.g., Xu et al., 2003). These cases are typical subjects to application of the **outgroup presumption**, which claims *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.* Applying this presumption to the above transformation series should result in a hypothesis that both hairs and feathers are apomorphic, while scales are plesiomorphic.

The outgroup comparison and presumption should not be confused with the outgroup method used in the computer cladistics (see below, Section 2.2.5).

2.2.3.2. Analysis of similarity. The similarity analysis was characterized above as designed to resolve conflicts between hypotheses of unique origin of observed similarities whenever these conflicts are encountered. Conflict appears when we encounter similarities that are distributed in a contradictory way, that is, when they cannot be all considered as inherited. Indeed, if we accept the similarity of whales to other mammals in homoiothermy as inherited, we must treat their swimming adaptations as acquired independently of fish, and vice versa. Independently acquired similarity is termed homoplasy, so the similarity analysis can be redefined as identification of homoplasy.

There are two main methods to detect homoplasy. The first and more straightforward is based on 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, p. 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.*

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 the characters are not even. If we consider similarity between mimicking butterflies and count each similar element in their color pattern separately, and then we count similarities of each mimicking species to its relative, I am not sure that the result will be always in favor of the true relatedness. Similarities do vary in how reliably they indicate relatedness, depending on what kind of character states are involved. We generally assess similarity in the type of symmetry or in the gross structure of basic organs as usually more important phylogenetically than, for instance, a color pattern or details of the surface structure. However, exceptions exist even here; in particular, all mammals are similar in the absence of blue pigments from their hair, not to mention the importance of differences in the pigment sets for the prokaryote and plant taxonomy. And nevertheless color pattern is generally considered as only of subsidiary phylogenetic importance.

The above observations indicate that the phylogenetic importance of the same sort of similarity differs greatly, depending on what taxa are compared and what characters are involved. Therefore, I believe, we should operate weighted characters when discriminating homoplasy. Hard rules seem to be impossible to use in this situation, at least for the present. That is why we have to rely on one more presumption, the **presumption of weighted similarity**. In fact there are quite a number of such presumptions, and some of them have been already discussed elsewhere (Rasnitsyn, 1988b; Rasnitsyn and 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 the similarities cannot be accepted as all being inherited), *that known to be more reliable in other cases (especially in closely related groups) should be regarded as inherited, unless and until strong counterevidence appears.*

2.2.4. Example

How we can use the above presumptions is better illustrated using an example. I think that the early evolution of hymenopterous insects and, particularly, the problem of the phylogenetic position of the sawfly family Xyelidae, seems adequate, since it is a difficult case and the subject of long-lasting debates. Unless stated otherwise, the discussion below is based on my previous papers (Rasnitsyn, 1969, 1980, 1983b, 1988a, 1988c, 1990, and references therein). The results of the latest publications are not considered here, even if new findings (Rasnitsyn and Zhang, 2004a, 2004b) are relevant to the problems under discussion. This is because these results further confirm my inference below, which already looks sufficiently grounded.

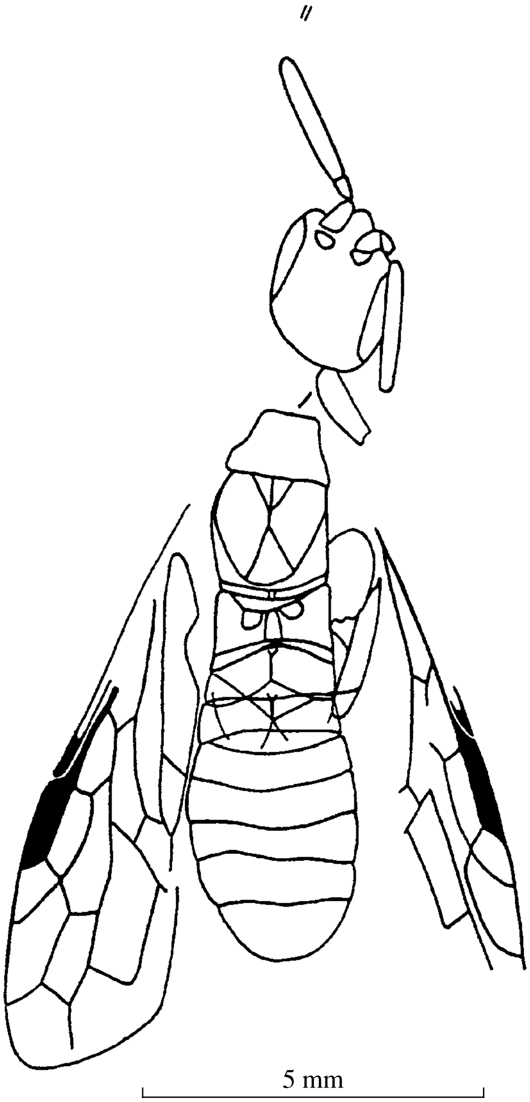


Fig. 3. *Triassoxyela foveolata* Rasnitsyn, 1964 (Vespida, Xyelidae); Middle or Late Triassic of Kyrgyzstan (after Rasnitsyn, 1969).

Hymenopterous insects (order Vespida; the reasons for using this name instead of Hymenoptera are given in Rasnitsyn, 1982, 1988a, 1989) first occur in the fossil record in the second half of the Triassic. These Triassic species have been found in both Australia (one species) and Central Asia (two dozen species); all belong to the family Xyelidae, as indicated by their characteristic wing venation and antennal structure (Fig. 3). The family (Fig. 4) persists in the Northern Hemisphere as a relict group comprising five genera and some three dozen species, but, until the mid-Cretaceous, it was among the leading hymenopteran groups, at least in relatively temperate climates.

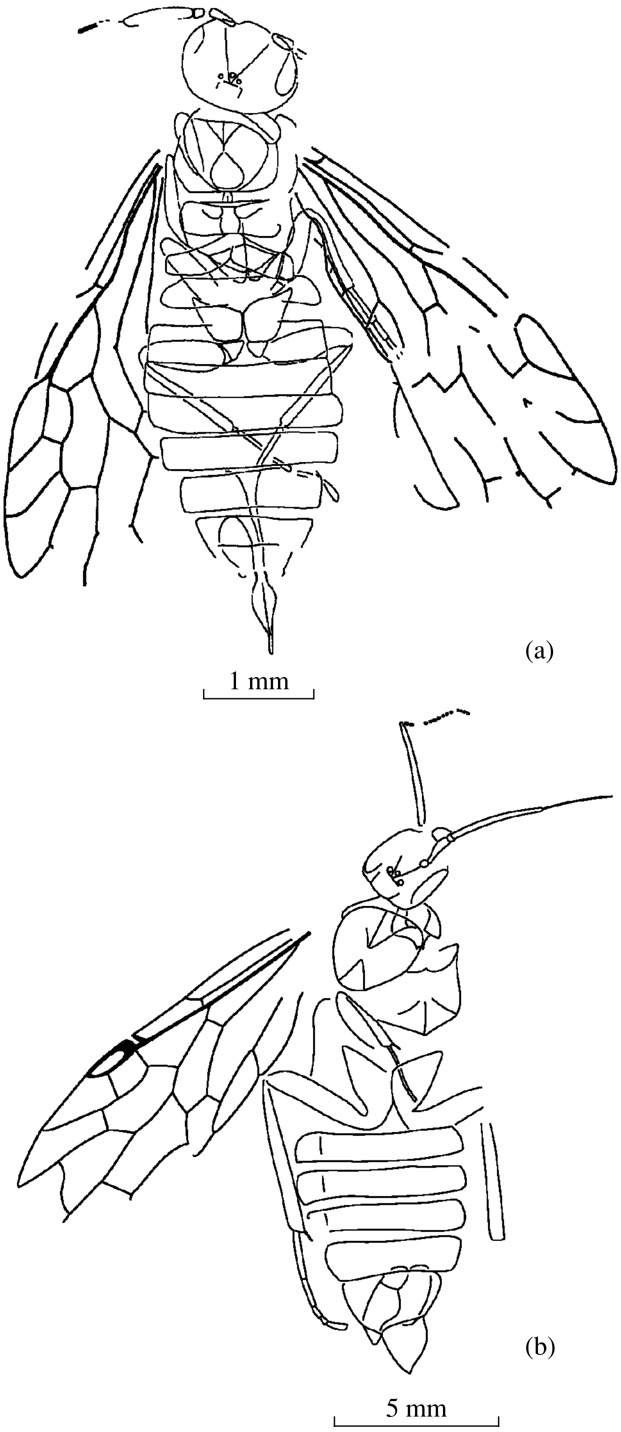


Fig. 4. Early Cretaceous Xyelidae from Transbaikalia: (a) a representative of the extant genus *Xyela, X. (Mesoxyela) mesozoica* Rasnitsyn, 1965 (Xyelinae) (after Rasnitsyn, 1995); and (b) a representative of the extinct genus, *Anthoxyela turgensis* Rasnitsyn, 1990 (Macroxyelinae), Lower Cretaceous of Transbaikalia (after Rasnitsyn, 1990).

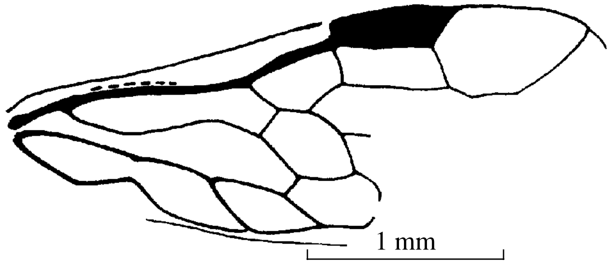


Fig. 5. The earliest hymenopterous insect not belonging to Xyelidae, *Sogutia liassica* Rasnitsyn, 1977 (Sepulcidae) from the Early Jurassic of Kyrgyzstan (after Rasnitsyn, 1977a).

Other hymenopteran groups appeared later than Xyelidae, remaining unknown before the Early Jurassic (Fig. 5). This makes it possible to use the paleontological presumption for groups and to propose a hypothesis that Xyelidae could be an ancestor of all other hymenopterans. This hypothesis is in agreement with most other observations that show this family to be the most plesiomorphic within the order in regard to all its characters, with the only exception discussed below. Actually, the xyelid wing venation is the richest and most similar to that of other insects; the fore wing with 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 is true concerning the body morphology and supposed generalized bionomic features. Particularly relevant is the suggestion that their development inside gymnosperm staminate cones was possibly retained from the earliest holometabolans (Fig. 6). However, plesiomorphies are unimportant cladistically; hence, we have to scrutinize the nature of the xyelid antenna, the only character not easily disregarded as an autapomorphy of the family. As to the putative synapomorphy of living xyelids in subdivided galea (a lobe of the mouthparts), it might have a relatively late (post-Triassic) age. This character state is proved only for the subclade comprising the subfamilies Xyelinae and Macroxyelinae and is not known in the Triassic Archexyelinae.

The xyelid antenna is evidently apomorphic in respect to a standard insect antenna, with several basiflagellar segments fused into the long and thick compound third antennal segment. This is mounted apically with a thread of ordinary (thin and short) flagellar segments. The apomorphic nature of such an antenna is supported by application of a number of the above presumptions. The paleontological presumption for groups is relevant because the closest and oldest nonhymenopteran group (extinct order Palaeomanteida = Miomoptera, Fig. 6) has normal antennae. The respective presumption for characters is also applicable, because all known pre-Triassic insect antennae display no xyelid apomorphy. The same holds true for the biogenetic presumption, because, at the early developmental stage (Fig. 7), the antennal segmentation is more

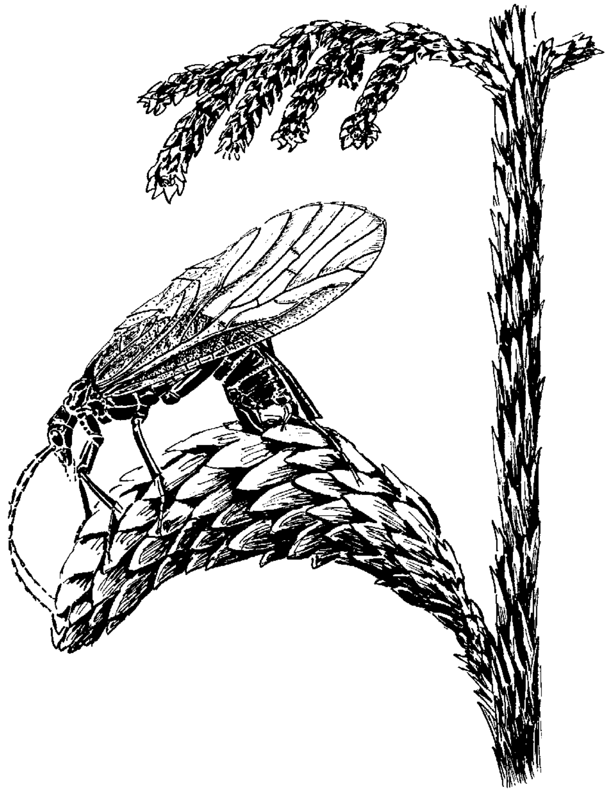


Fig. 6. *Palaeomantina pentamera* Rasnitsyn, 1977 (Palaeomantiscidae, order Palaeomanteida); Lower Permian of the Ural Mountains (reconstructed by A.G. Ponomarenko, after Rohdendorf and Rasnitsyn, 1980).

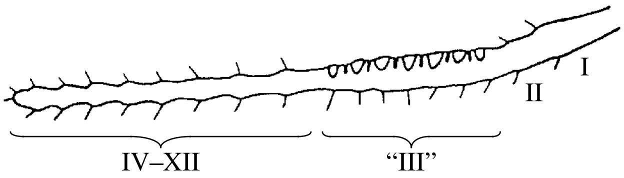


Fig. 7. Pupal antenna of *Xyela julii* Brébisson, 1818 (Xyelidae) (after Rasnitsyn, 1968). Designations: (I–XII) segments of antenna and ("III") compound third antennal segment.

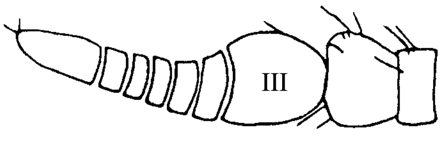


Fig. 8. Antenna of the primitive fly *Glutops semiformis* Nagatomi et Saigusa, 1970 (Rhagionidae) (after Nagatomi, 1982).

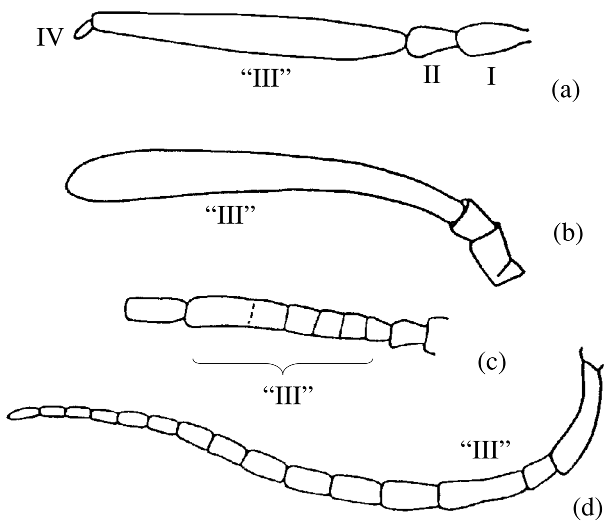


Fig. 9. Antenna of extant sawflies and horntails: (a) *Blasticotoma filiceti pacifica* Malaise, 1931 (Blasticotomidae); (b) *Arge ustulata* (Linnaeus, 1758) (Argidae); (c) *Caenolyda reticulata* (Linnaeus, 1767) (Pamphiliidae); and (d) *Xiphydria camelus* (Linnaeus, 1767) (Xiphydriidae) (after Rasnitsyn 1968).

homonomous than in the adult insect. Equally important is the presumption of analogy, because the similarly inflated (although not evidently compound) third antennal segment of flies (Fig. 8) is certainly apomorphic. The outgroup presumption suggests the same conclusion, since the xyelid antenna is only found within the order Vespida, while the ordinary one is common both within and outside it.

Some of the above presumptions seem to give the same result when applied intraordinally as well. It seems especially true for outgroup comparison, because the ordinary antenna is widespread within the order, and this is not the case for the xyelid-like one. This inference is probably wrong, however. Indeed, although among living insects, the xyelid-like antenna in its full appearance occurs only in that family, antennae of some lower hymenopterans (sawflies and horntails) may also be described as variously modified xyelid-like antennae (Fig. 9). The least modified of them are the antennae of the tenthredinoid families Blasticotomidae (Fig. 9a) and Argidae (Fig. 9b). Both have the third segment even hypertrophied compared to that of Xyelidae themselves, but the following segments are reduced to a single one (Fig. 9a), or completely lost (Fig. 9b).

Another source of evidence is living pamphiliid sawflies and siricoid horntails. Pamphiliidae (except some species of *Pamphilius*) have the third segment subdivided but relatively small, several times longer than the fourth and of subequal width (Fig. 9c). Less known, though no less important, is the antenna of the primitive horntail genus *Brachyxiphus* (Siricoidea, Xiphydriidae), which has a rather thick and long third segment (subequal in length to three more distal segments combined), and additionally subdivided into four primary segments in males of *B. grandis* (specimens are studied in the collection of Smithsonian Institution, Washington, DC). Most if not all other Xiphydriidae also have this segment somewhat enlarged (Fig. 9d); thus, this character state is possibly a part of the family ground plan.

The above distribution of the compound third antennal segment can be explained by its independent development in five different groups. Moreover, this number doubles when we consider the data provided by Van Achterberg and Van Aartsen (1986, tables 1, 2, text-fig. 366) and suppose that the composite structure of this segment has never been lost (cf. Fig. 16).

The cases of independent acquisition of the compound segment become even more numerous if we take fossils into consideration. The fossil collection of the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN) are particularly demonstrative in this respect. These collections contain the overwhelming majority of Jurassic and Lower Cretaceous hymenopterans collected worldwide; they mostly come from Kazakhstan, Siberia, and Mongolia. Among them, 515 specimens of the above age are sawflies and horntails (lower hymenopterans composing the suborder Siricina). Of these, 120 display their antennal structure clearly enough to identify the antennal type; 65 of these specimens belong to Xyelidae and have the respective antennal type. Among the remaining 55 fossils, 23 also have the xyelid-like antennae, including those with the third segment not so huge as in Xyelidae but still clearly thicker and much longer than the distal segments. The remaining 32 fossils have ordinary antennae or nearly so.

Among nonxyelid fossils displaying the xyelid-like antennae, we see, first, four genera (Fig. 10) that share several important putative synapomorphies with living Tenthredinoidea. These genera have the fore wing with 2r-rs meeting RS distad of 2r-m, and 1mcu cell enlarged so that the 1st abscissa of RS is short or lost. Most genera have also SC stock fused, albeit only distally, with R, so that its fore branch, when present, forms an intercostal crossvein (*Pseudoxyela* Rasnitsyn is exceptional in retaining SC free and, thus, probably forms the sister group for the rest of the tenthredinoid clade). The four genera also share synapomorphies with the Tenthredinoidea in regard to their antennal flagellum, which is thick, with the segment number reduced (supposing that the antenna is secondarily multisegmented in Diprionidae and some Pergidae). I consider *Xyelotoma* Rasnitsyn, *Xyelocerus* Rasnitsyn, *Dahurotoma* Rasnitsyn, and *Pseudoxyela* Rasnitsyn as forming the extinct family Xyelotomidae. No autapomorphies are recorded for the family, implying its ancestral position with reference to other Tenthredinoidea.

The next five extinct genera with the xyelid type of antenna (Fig. 11) show the important synapomorphy of the superfamily Pamphilioidea, including the reduced clawlike ovipositor of characteristic general form and position in the body. The general appearance and wing venation are also similar to those of living pamphilioids. Among these taxa, *Xyelyda* Rasnitsyn, *Prolyda* Rasnitsyn, and *Mesolyda* Rasnitsyn are assigned to the extinct family Xyelydidae which lacks autapomorphies and, hence, is supposed to be ancestral to other Pamphilioidea. *Praesirex* Rasnitsyn and *Turgidontes* Rasnitsyn 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 Megalodontidae.

One more group marked by xyelid-like antenna comprises several genera (Fig. 12) which are now assigned to the extinct family Sepulcidae (Rasnitsyn, 1993). Sepulcidae are attributed to the superfamily Cephoidea because of their synapomorphy with living Cephidae (Rasnitsyn, 1988c). Both families have their fore wings with the costal space moderately narrow and bandlike (secondarily very narrow or lost basally), with SC fused with R (except sometimes basally), and lacking the apical SC branch crossing the costal space. Sepulcidae lack characteristic venational synapomorphies of living Cephidae and are probably ancestral to cephids. As to Cephidae themselves, the observation of its oldest (Early Cretaceous) genus *Mesocephus* Rasnistyn as having xyelid-like antenna (Rasnitsyn, 1988c) has been found to be erroneous.

The last group with xyelid-like antennae is rather loosely outlined. I include here *Protosirex* Rasnitsyn (Protosiricidae, Fig. 13), which seems to belong to the horntails (Siricoidea) because of its general appearance and some siricoid plesiomorphies (e.g., the presence of free SC). Otherwise, it could have represented a group ancestral to both siricoids and cephoids. Other siricoids with xyelid-like antennae are *Syntexyela media* Rasnitsyn, 1968 and *S. inversa* Rasnitsyn, 1968, (Figs. 14a, 14b). They surely belong to the Siricoidea, as witnessed by their characteristic synapomorphy (strong needle-like ovipositor). They represent the predominantly Mesozoic family Anaxyelidae (with a single living species), as confirmed by the synapomorphic reduction of SC stock and of 2r-m crossvein in the fore wing and of 1r-m in the hind wing. It is important that these two species have the third segment slightly modified in comparison with that of 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 as either normal or with the third segment only slightly enlarged (Figs. 14c, 14d; for details, see Rasnitsyn, 1969).

Now we can take all the above data into consideration for assessing the meaning of the xyelid-like antenna with

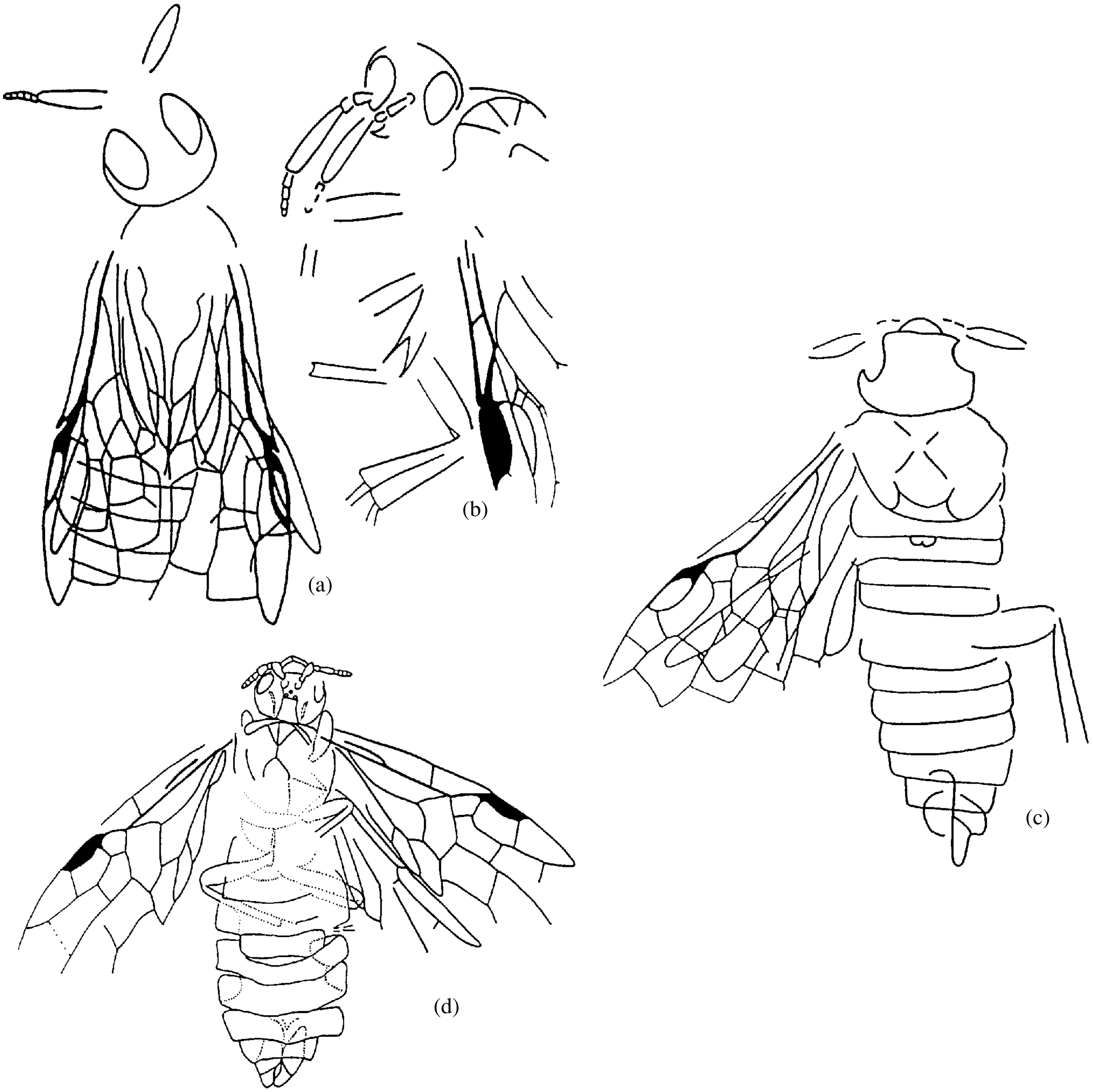


Fig. 10. Jurassic and Cretaceous sawflies of the family Xyelotomidae: (a) *Xyelocerus admirandus* Rasnitsyn, 1968; (b) *Xyelotoma nigricornis* Rasnitsyn, 1968; and (c) *Pseudoxyela heteroclita* Rasnitsyn, 1968 from the Upper Jurassic of southern Kazakhstan; and (d) *Dahurotoma robusta* Rasnitsyn, 1990 from the Lower Cretaceous of Transbaikalia; (a, b) after Rasnitsyn, 1969; (c) after Rasnitsyn, 1996; and (d) after Rasnitsyn, 1990b.

regard to the early evolution of hymenopterans. In fact, we encounter here the conflicting putative synapomorphies. The above-mentioned genera are supposedly synapomorphic with Xyelidae in their antennal structure, while their various other characters seem to be apomorphies shared with some other sawflies and horntails. These hypotheses cannot be simultaneously correct, i.e., the above similarities cannot be **all** synapomorphies. Therefore, our next task is to decide which of the conflicting putative synapomorphies can be falsified (reassessed as symplesiomorphies or homoplasies) to receive the most likely and consistent cladogram.

It is possible to propose the following four hypotheses:

(1) similarity in the xyelid-like antenna is a synapomorphy, while the alternative set of similarities of the listed genera are symplesiomorphies;

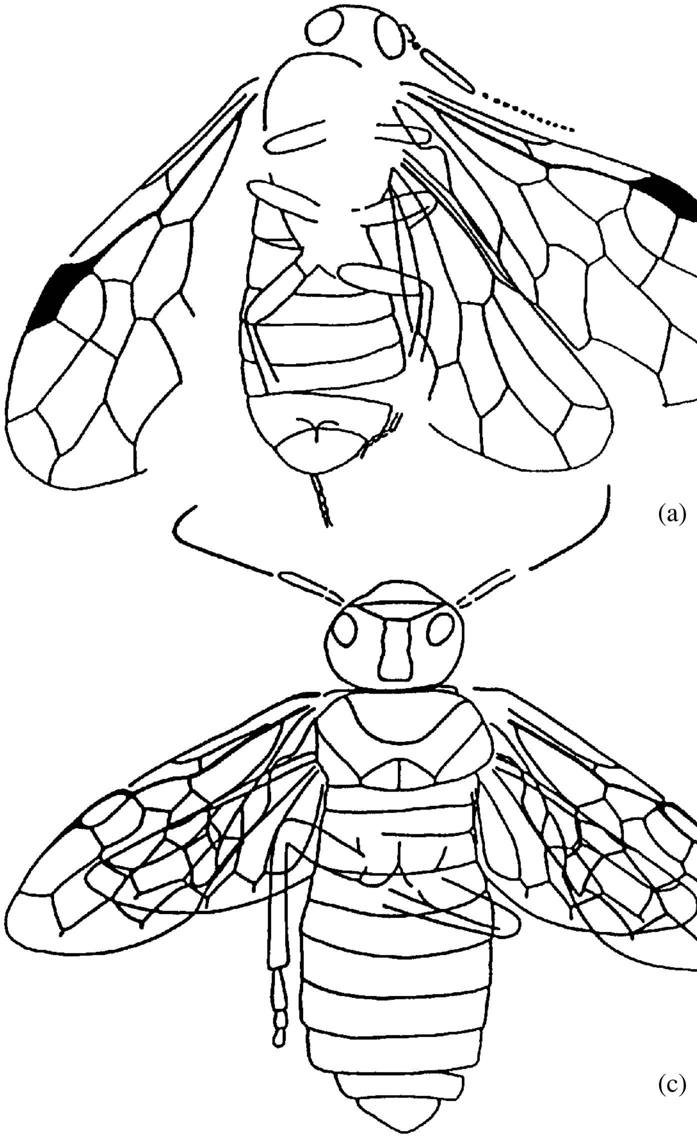


Fig. 11. Jurassic and Cretaceous sawflies of the families (a–c) Xyelydidae and (d, e) Praesiricidae: (a) *Xyelyda excellens* Rasnitsyn, 1968; (b) *Prolyda karatavica* Rasnitsyn, 1968; and (c) *Mesolyda depressa* Rasnitsyn, 1968 from the Upper Jurassic of southern Kazakhstan; (d) *Praesirex hirtus* Rasnitsyn, 1968 and (e) *Turgidontes magnus* Rasnitsyn, 1990 from the Lower Cretaceous of Transbaikalia; (a, b) after Rasnitsyn, 1969, (c) after Rasnitsyn, 1996, (d) after Rasnitsyn, 1983b, and (e) after Rasnitsyn, 1990b.

(2) the same as (1), but the alternative similarities being homoplasies;

(3) the alternative sets of similarities are synapomorphies (the above groups of genera are monophyletic, with the respective nonxyelid superfamilies and families), while the xyelid-like antenna has been acquired independently (as a homoplasy);

(4) the same as (3), but similarity in having the xyelid-like antenna is a hymenopteran symplesiomorphy.

The first two hypotheses (1), (2) mean that all the genera in question are monophyletic with Xyelidae (cladistically belong to the family), while their similarity to other groups is either (1) inherited from a remote ancestor or (2) of independent origin. The hypothesis (1), being applied to all those similarities, seems the least probable because it implies that the direction of evolution of the respective characters is opposite to that generally accepted as normal (that is, most common and thus satisfying the relevant presumptions). This seems possible in some cases but hardly so in others. 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 to the sawlike ovipositor of Xyelidae and Tenthredinoidea. Indeed, several presumptions suggest the reverse direction of evolution. In the majority of nonhymenopteran winged insects, and, particularly,

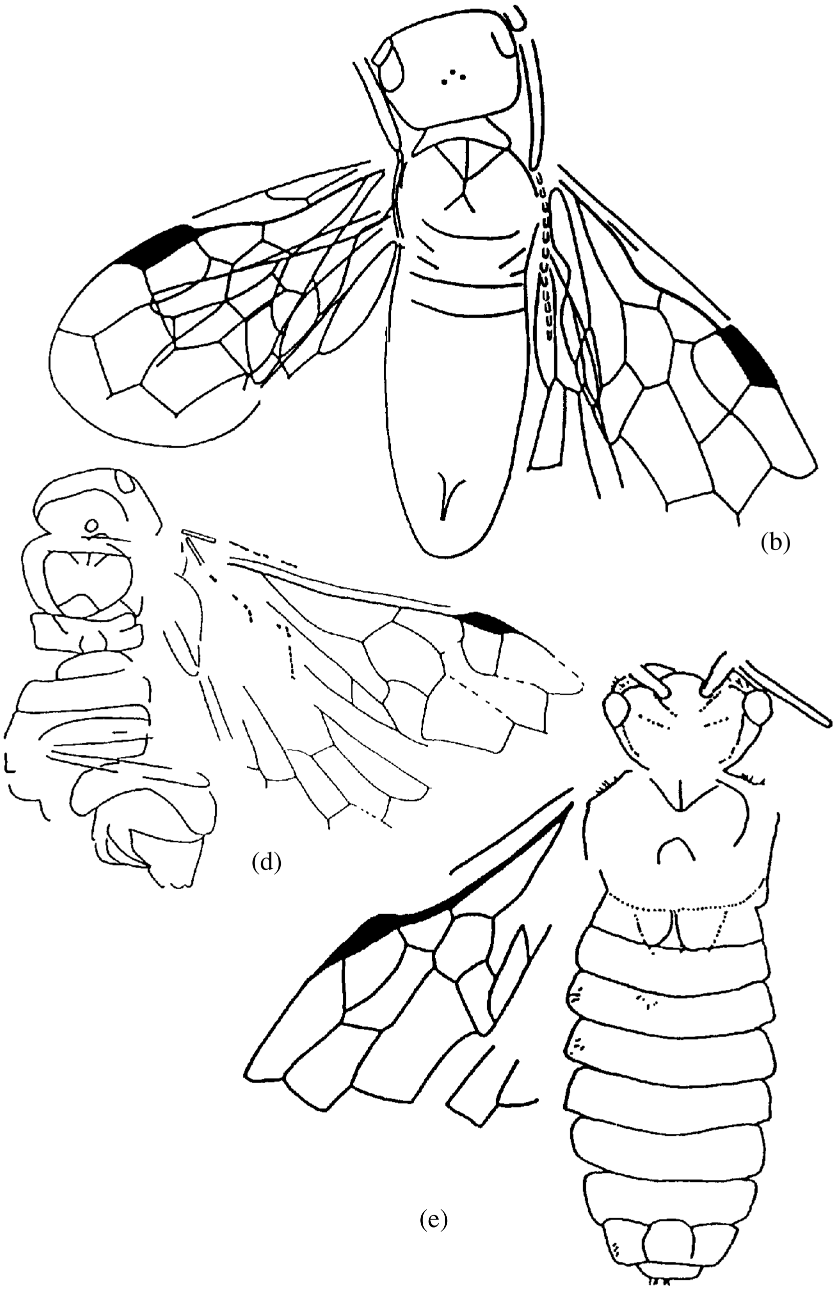


Fig. 11. (Contd.)

among Paleozoic ones (including Palaeomanteida, the order supposedly ancestral to hymenopterans,see Rasnitsyn, 1980), the ovipositor, unless reduced, is a flat leaf- or sawlike structure (Fig. 6). Other (nonhymenopteran) 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 sawlike ovipositor of the sawflies. The same judgment of apomorphy holds true for the reduced anaxyelid wing venation, which is hardly possible to suppose as ancestral to the more complete xyelid and pamphiliid venation, because again many presumptions confirm that, for hymenopterans, a more complete wing venation is plesiomorphic.

Unlike the following hypotheses, I cannot illustrate the present one with a respective cladogram. This is because this hypothesis infers incompatible polarization hypotheses, as is seen in the case of the ovipositor (see above).

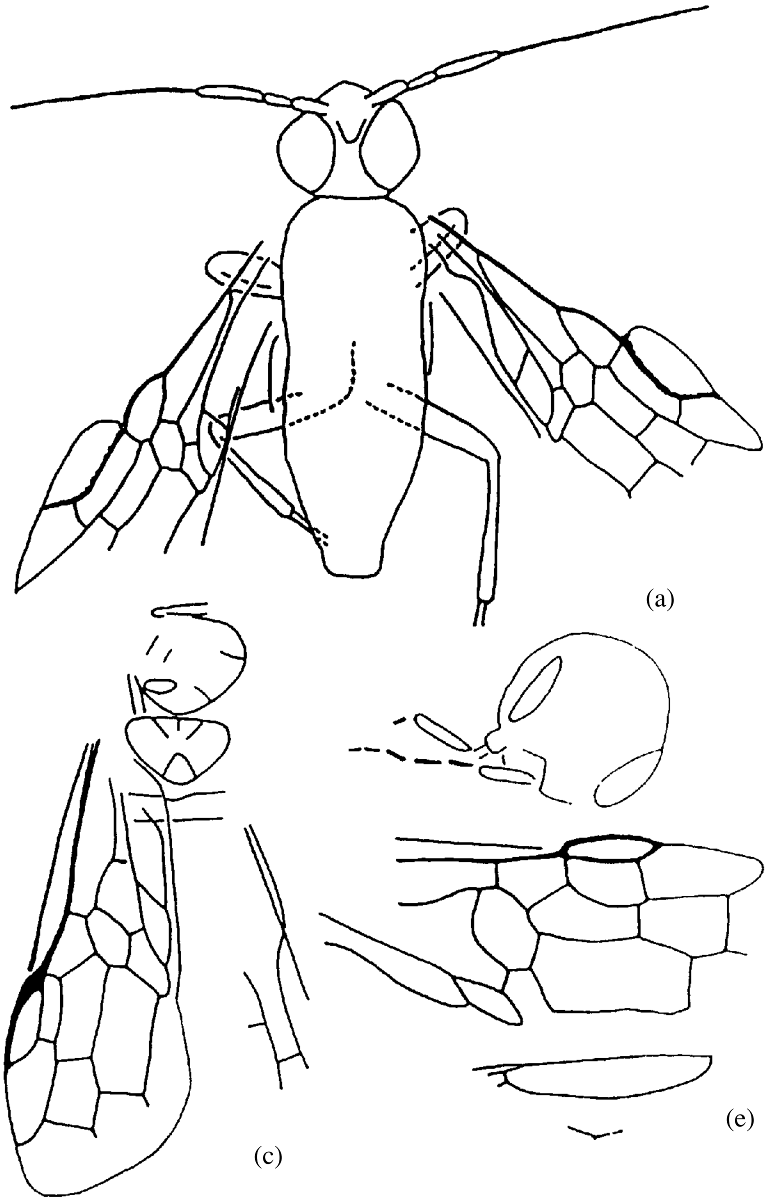


Fig. 12. Jurassic and Cretaceous sawflies of the family Sepulcidae with the xyelid antennae: (a) *Xyelula hybrida* Rasnitsyn, 1969, (b) *Onokhoius aculeatus* Rasnitsyn, 1993, (c) *Parapamphilius confusus* Rasnitsyn, 1968, (d) *Pamparaphilius mongolensis* Rasnitsyn, 1993; and (e) *Micramphilius minutus* Rasnitsyn, 1993; (a, c) Upper Jurassic of southern Kazakhstan, (b, d) Lower Cretaceous of Mongolia and (e) Transbaikalia (after Rasnitsyn, 1993).

The hypothesis (2), suggesting the homoplastic nature of similarities between the genera discussed and the respective nonxyelid 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 appearing independently (Fig. 15, *italics*). This seems unlikely, since these traits have been established by generations of taxonomists as sound diagnostic characters for families and superfamilies. These characters were observed as not especially prone to homoplastic development in related groups and, hence, agree with the presumption of weighted similarity.

One more reason to consider either of the above hypotheses as difficult to accept is the intermediate antennal types described above for two species of *Syntexyela* (Figs. 14a, 14b). Indeed, the antennal structure of *S. media* is easily interpretable as intermediate stage of transformation of an ordinary antenna into the xyelid-like one. In contrast, in *S. inversa* (and several other congeners), the basiflagellar segment, being rather large but seemingly entire, is either a reduced xyelid-like segment (impossible under the above

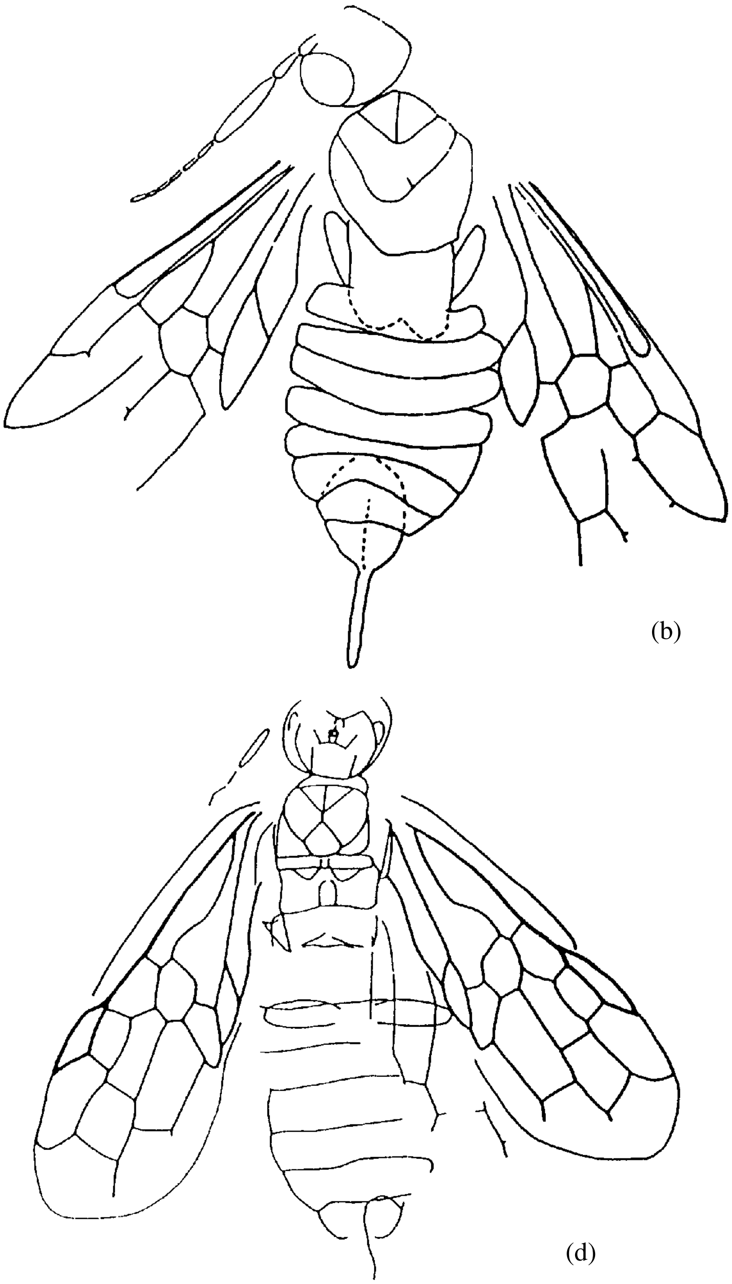


Fig. 12. (Contd.)

hypothesis), or models an early stage of the formation of the enlarged (as in Xyelidae), but entire (unlike that of Xyelidae) third antennal segment. In both cases, the two species cannot be close relatives, and all their deep similarity should be homoplastic.

So, we now turn to the last two alternative hypotheses (3), (4). Both claim that the similarity of the above-listed genera (those possessing the xyelid-like antennae) to certain nonxyelid groups is synapomorphic. These hypotheses differ from each other in proposing that the similarity of possessing the xyelid-like antennal structure is either homoplastic or symplesiomorphic in nature. The hypothesis (3) (Fig. 16) means that the genera in question have acquired the compound third segment independently, while the hypothesis (4) (Fig. 17) supposes that this character has been uniquely acquired by a common ancestor, and then was lost independently in groups with ordinary antennae. Both hypotheses seem more probable compared to the first pair of hypotheses, since they propose little more than numerous homoplasies in a single character (either in the acquisition or loss of the hypertrophied third seg-

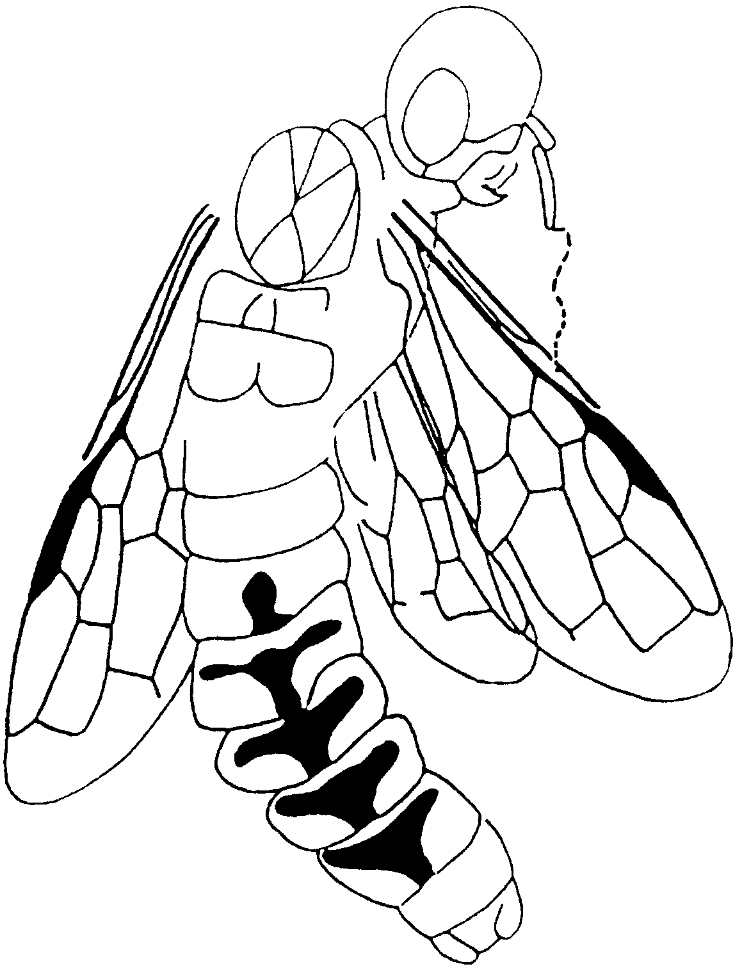


Fig. 13. Primitive horntail *Protosirex xyelopterus* Rasnitsyn, 1969 (Gigasiricidae) from the Upper Jurassic of southern Kazakhstan (after Rasnitsyn, 1969).

ment) and do not imply falsification of the existing and apparently well-based ideas of the evolutionary pathways of other characters.

At the same time, the two hypotheses are not equivalent in terms of being the best based. The hypothesis (3) of homoplastic origin of the xyelid-like antenna from a homonomously segmented one results in more abundant cases of homoplasy compared to the alternative hypothesis (4) of homoplastic loss of the character state (cf. the number of italicized character states in the captions to Figs. 16 and 17). 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 less easily and, thus, to be less prone to multiple origin compared to their multiple loss. Equally it seems logical to believe that, for a structure of enigmatic function, a unique origin and succeeding multiple reduction is generally more likely than 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 multiple loss of the compound antennal segment needs only a single and a quite remote event of acquisition of the enigmatic structure, and thus it seems superior relative to the hypothesis of multiple gain of the obscure adaptation. This is especially so taking into consideration the above case of *Syntexyela.* It forces us to make a choice between the different hypotheses that claim the enigmatic structure arose either by reduction or by multiple origin. The option again seems to be clearly in favor of the multiple loss hypothesis.

The comparison of hypotheses is still not complete, for we have missed one more relevant presumption. Indeed, the above considerations are mostly rather plain, especially those concerning the hypotheses on

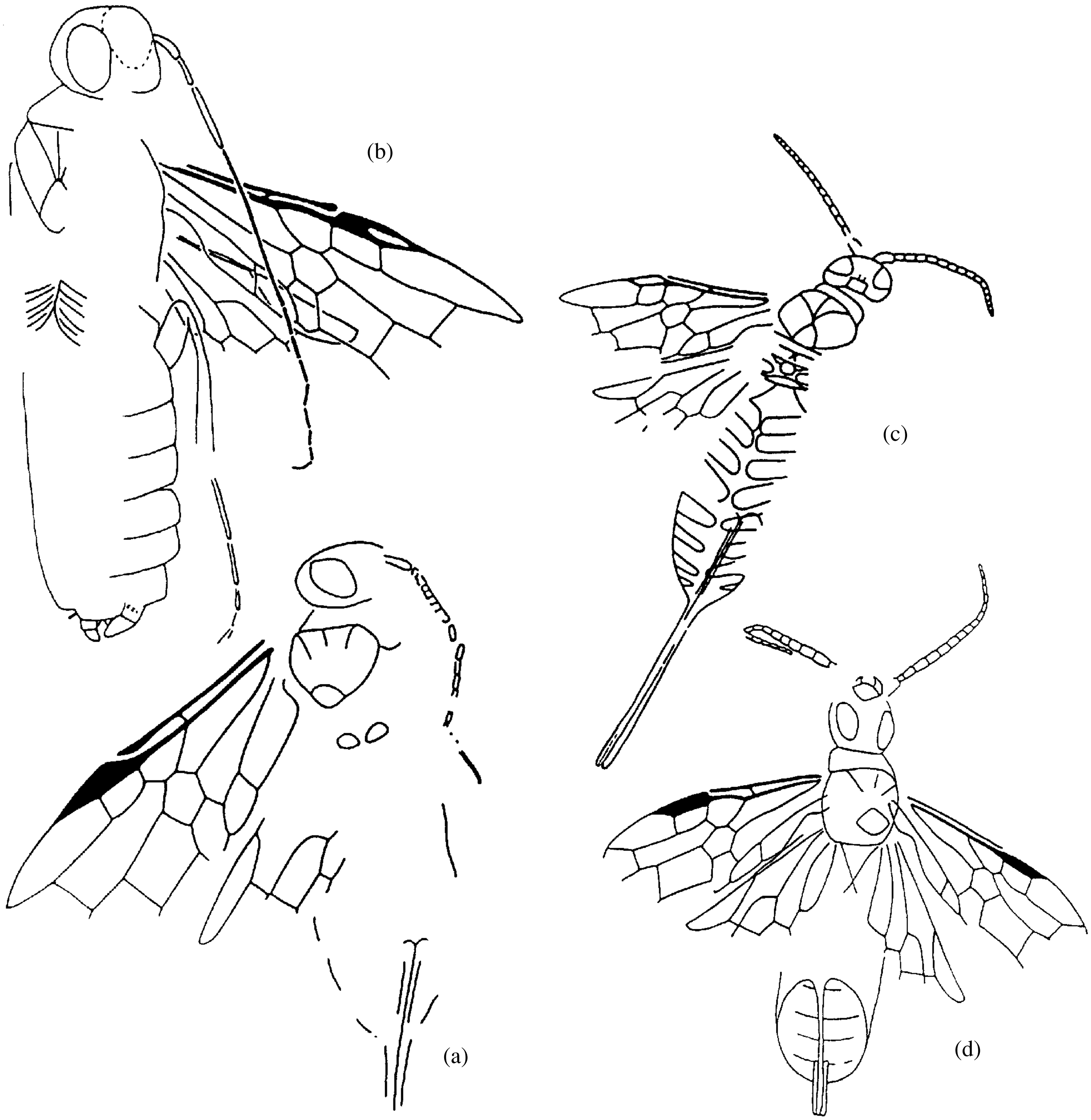
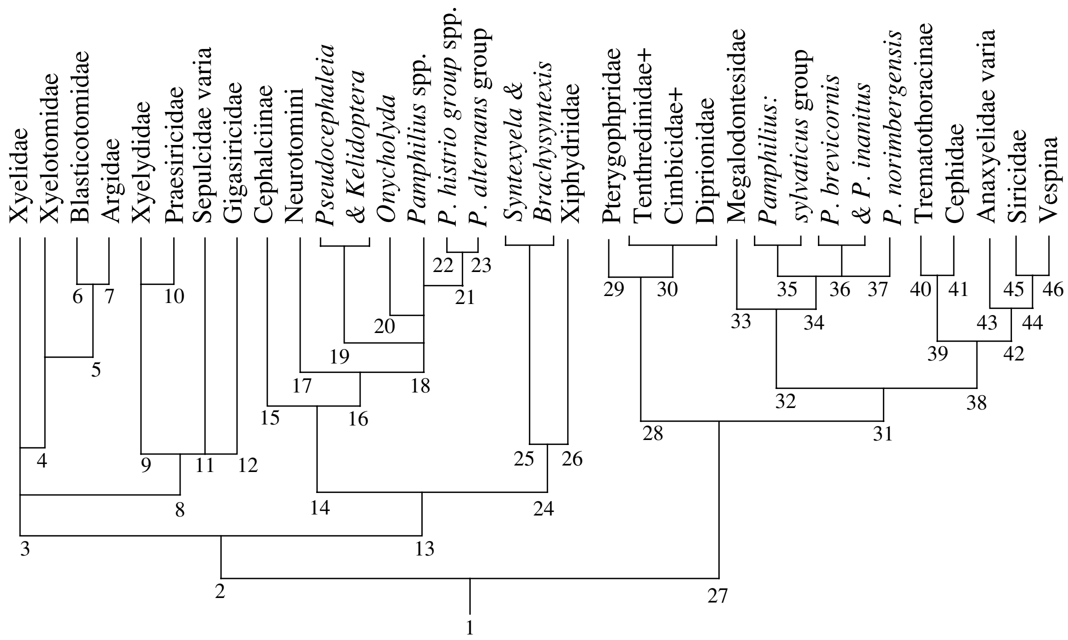


Fig. 14. Jurassic horntails of the family Anaxyelidae with (a, b) modified xyelid and (c, d) more or less normal antennae: (a) *Syntexyela media* (Rasnitsyn, 1963); (b) *S. inversa* Rasnitsyn, 1968; (c) *Anaxyela gracilis* Martynov, 1925; and (d) *Brachysyntexis micrura* Rasnitsyn, 1969 from the Upper Jurassic of southern Kazakhstan; (a, c, d) after Rasnitsyn, 1969 and (b) original, based on the holotype.

the monophyly of all groups possessing the xyelid-like antennae. As far as I know, they have never been proposed before, and to analyze them looks a little like creating a straw man. I need them, however, to make a complete picture. The other two hypotheses actually have been actively debated. The one considering the xyelid-like antenna as homoplastic can be found in Ross (1937) and, in more explicit form, in Königsmann (1976). The hypothesis proposing multiple loss of the xyelid-like antenna within the order Vespida is mine (Rasnitsyn, 1968, 1969, 1980, 1988a, 2002a).

As portrayed here, the last hypothesis looks evidently preferable, but the position of Ross and Königsmann is not at all weak. The shortage of knowledge about (Ross) or with respect to (Königsmann) the fossil record provides only partial insight. The point of view of Ross and Königsmann is based additionally 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 one more 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 commonly asymmetrical, with one direction appearing to be realized more often than alternative ones. Therefore, *when we see one direction of changes as definitely realized, we should prefer the cladogram supposing no changes in the opposite direction, or the least their number, unless and until we have strong contrary evidence.*

The contrary evidence do exist, as I tried to show above, so the final decision depends on what we consider as the stronger and sounder arguments. I argue in favor of the higher probability of the multiple loss versus gain of the complex organ of enigmatic function when more than one mode of change was used, and against the irreversibility of evolution. In fact, this claim is now additionally supported by the latest studies that use modern computer techniques and molecular phylogeny (Ronquist et al., 1999, text-fig. 2; Vilhelmsen, 2001, text-fig. 11; Sharkey and Roy, 2002, text-fig. 8A; Schulmeister, 2003, text-figs. 1, 2). Both approaches unanimously produce cladograms generally similar to Fig. 17 (with the contents of superfamilies Tenthredinoidea, Pamphilioidea, and Siricoidea traditional and not split each into two distant parts as in Fig. 16). But irrestective of this, I hope that the example selected, convincing or not per se, does permit us to assess the proposed approach to cladogram reconstruction.

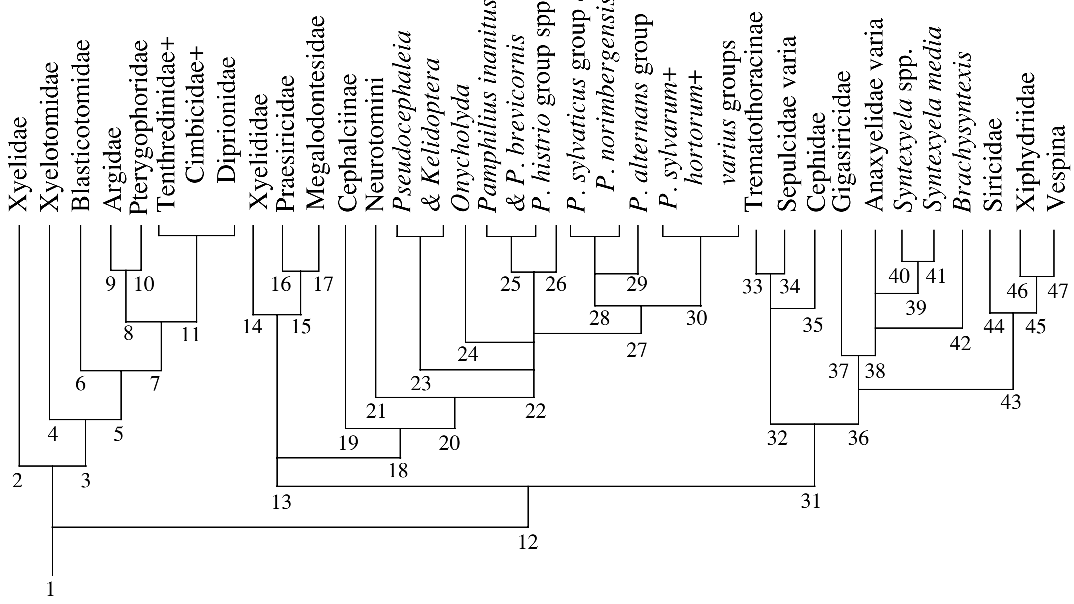
2.2.5. Computer Cladistics

If we imagine replacing the above system of presumptions (Table 4) with various intuitive criteria of apomorphy vs. plesiomorphy and synapomorphy vs. homoplasy, the above description of methodology of phylogenetics (Sections 2.2.1–2.2.4) will be a rough description of the phylogenetic methodology of the original, Hennigian cladistics, also referred to as manual cladistics or the cladistics of pen and paper. Now it is considered outdated and uncommon in use (but see Bechly, 2000; Kluge, 2000). The currently dominating version, computer cladistics, is essentially different from the Hennig's (1966) proposal.

Modern cladistics is different. A wealth of computer programs have been developed to automate assessment of relationships based on a simplified principle of parsimony that claims to produce the cladogram of minimal length, that is, the one inferring minimum number of the cladistic events (acquisition of apomorphies, including homoplasy and reversal). Outgroups are used as well, but only in order to locate the root of the resulting cladogram. All the work of identification of sister groups is made automatically by calculating the shortest cladogram. As to polarization of transformation series, this is generally not of interest, although it can be drawn *post factum* from the cladogram. As a result, all our knowledge, accumulated over many years of how evolution proceeds, what are its patterns, and whether there are any rules and regularities of its pace, is in fact irrelevant to cladistic phylogenetics.

There is a different approach in computer phylogenetics, which is potentially less arrogant toward the past knowledge, the maximum likelihood method. It pur-

Fig. 15. Cladogram of the lower hymenopterous insects (suborder Siricina), constructed consistent with the hypothesis (2) (see the text) that similarity in the xyelid-like antenna is synapomorphic, while alternative similarities are homoplastic. Figures under the ancestry lines refer to the sets of synapomorphies of respective clades (or terminal taxa), as follows (based on Rasnitsyn, 1988a, and, for Pamphiliidae, on Van Achterberg and Van Aartsen, 1986; homoplasies are in *italics*): (1) synapomorphies of the order Vespida (wing venation specialized, flight dipterous, haplo-diploid sex determination, etc.; for more detail, see Rasnitsyn, 1988a); (2) 3rd antennal (basiflagellar) segment compound; (3) basiflagellar segment much enlarged (antenna xyelid-like); (4) *antennal flagellum short (up to 5 segments beyond basiflagellar segment), rather thick; forewing 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; forewing with SC lost except crossvein-like fore branch*, and *with RS$_2$ lost* (for other possible synapomorphies, see Rasnitsyn, 1988a, p. 120, *items 2-3, 3*); (6) forewing with RS lost between submarginal cells; larva boring fern stem, with caudal structures modified; (7) flagellum lost beyond composite segment; *forewing lacking 2r-rs; male genitalia rotated at 180°; larva with eye and antenna distant, with antenna 1-segmented, with mandible lacking incisive molar flange, with suprapedal and subspiracular lobes merged*; for numerous further synapomorphies, see Rasnitsyn, 1988a, p. 120, items 5, 6, 8, 9); (8) *propleurae contiguous ventromesally; forewing with RS$_2$ lost*; (9) *ovipositor small, claw-like modified*; (10) *both wings lacking SC; pseudosternum extending over all* or almost all *length of mesothoracic venter*; (11) forewing with SC short, appresed to R, *lacking fore branch*; (12) *forewing with costal space narrow; ovipositor needle-like* (not known with certainty); (13) *propleurae contiguous ventromesally; forewing with RS$_2$ lost; male gonostylus with gonomacula subapical*; etc. as described in Rasnitsyn (1988a, p. 121, item 13); (14) *lower tentorial bridge intervening between hypostomae; mandible of cutting type (with cutting edge twisted into moving plane); forewing 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; hypopygidial depression large; (16) *forewing membrane more or less folded apically; larva on Angiospermae*; (17) *forewing 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) forewing 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 lost in *P. betulae* (Linnaeus) and *P. festivus* Pesarini et Pesarini]; (22) female forewing with distal third of costal cell glabrous (23) *female with inner tooth of hind claw shorter than apical tooth*; (24) *propleurae contiguous ventromesally; forewing with costal space narrow; ovipositor needle-like*; (25) *forewing and hindwing with single crossvein r-m each*; (26) *head capsule with hypostomae contiguous and with postgenae subcontiguous between oral cavity and occipital foramen; tentorium issuing anterior arms from below tentorial bridge*; pronotum short medially, dorsally; propleurae neck-like elongate; *mesoscutum bearing transscutal suture* and incipient adlateral lines; *prepectus concealed under posterolateral edge of pronotum; fore tibia with hind (outer) spur rudimentary (or lost); mesofurca with fore arms long, fused for some distance; forewing 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, p. 122, *items 19 and 22,* possibly also synapomorphies listed there at item 21 and 22); (27) *forewing with RS$_2$ lost*; (28) *pronotum short medially; forewing 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 at 180°; larva with eye and antenna distant, with mandible lacking incisive molar flange*; also numerous synapomorphies as described in Rasnitsyn (1988a, p. 120, *items 2-3, 3, 5*); (29) *forewing lacking 2r-rs;* hind wing lacking m-cu crossvein; *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 basad 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; forewing with basal sections of RS and M forming entire straight line, and with A_{2+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; forewing with M+Cu angulate; ovipositor small, claw-like; larva exophytic on Angiospermae, silk-protected, with appendages setiform, antenna distant from eye; forewing membrane more or less folded apically*; (35) *ovipositor sheath with large stylus* [possibly secondarily lost in *P. nemorum* (Gmelin)]; (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; forewing with costal space narrow; larva xylophagous* on living plants, modified as described by Rasnitsyn (1988a, p. 122, *item 19*); (39) *forewing with SC lost* and with Cu straight within 1mcu cell; (40) mesonotum membranous except laterally; forewing with costal space very narrow in basal third or half; ovipositor long exerting; (41) metanotum with cenchri lost; forewing *with 1st abscissa of RS very short and with cell 1mcu large*, with crossvein 1r-rs long, with Cu straight before 1m-cu, with A_2 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, p. 122, *item 22*); (43) *forewing and hindwing with single crossvein r-m each*; (44) *head capsule with postgenae contiguous; mesoscutum bearing transscutal suture; prepectus concealed under posterolateral edge of pronotum*; (45) mesoscutum with transscutal suture bent cephalad laterally; forewing with basal abscissa of RS subvertical; (46) tentorial bridge narrow stripe-like, n-like bent; mesonotum with adlateral lines; *forewing with SC lost*; 1st abdominal tergum modified into mesosomal propodeum; larva parasitic; etc., as listed in Rasnitsyn (1988a, p. 123, item 28).



sues the maximum conformity between the cladogram and an a priori model of evolution that infers qualitative features to particular evolutionary events, that is, a priori probabilities of the acquisition of particular apomorphies in particular fragments of the cladogram. This has two results; firstly, the objective mathematical procedure applies to highly intuitive data and, thus, makes the resulting cladogram equally intuitive. Secondly, the calculation problem, particularly in the case of the advanced Bayesian procedure, imposes some limitation on its application and, hence, makes its evaluation premature for the present.

There is also a general problem inherent in any automatic method of relationship calculation that seriously affects the resolution of the method. It is well known that the same character can play a different role (define subgroups and subclades of different rank/inclusiveness) in different parts of the same group. For instance, the number of teeth of particular kind is one of the most significant characters in the taxonomy and phylogeny of mammals. Whales are exceptional; when included in a mammalian character matrix, whales significantly downgrade the general input of tooth characters into cladistic analysis of the mammalian genealogy. I am afraid that this is one of the main reasons why the cladistic method results in unresolved or unrealistic cladograms of groups whose genealogy looks intuitively apparent.

2.2.6. Molecular Phylogeny

Molecular methods of phylogenetic study are particularly popular now, for reasons which are manifold. The first is the old belief that genes and proteins reflect phylogeny directly, unlike other characters, which do this only in an indirect manner. The second reason is that the molecular method gives results that are often compatible with the concept of a molecular clock. My favorite example is that by Cacone and Powell (1989) in the apes and man, with the resulting cladogram (*Paphio hamadryas* + (*Hylobates syndactylus* + (*Pongo pygmaeus* + (*Gorilla gorilla* + (*Homo sapiens* + (*Pan paniscus* + *P. troglodytes*)))))), showing the molecular distances (measured in percent hybrid DNA reassociation) always subequal between sister taxa, and not overlapping within subclades of different inclusiveness. Indeed, the distances between baboon and (apes + human) vary from 6.58 to 7.43; those between gibbon and (other apes + human) are 4.48–5.13; between orangutan and (the rest of apes + human) are 3.28–3.57, between gorilla and (chimpanzee + human) are 2.34–2.76, between chimpanzees and human are 1.58–1.59, and the distance between two chimpanzee species is 0.77. The earlier the divergence event took place, the more distant molecularly are its products.

The third reason of the present popularity of the molecular methods is the same as that of the computer phylogenetics: simple basic concept, complicated but straightforward (unambiguous) procedure, and the necessity of a huge computer base that produces impressive results based on financial rather than intellectual strength.

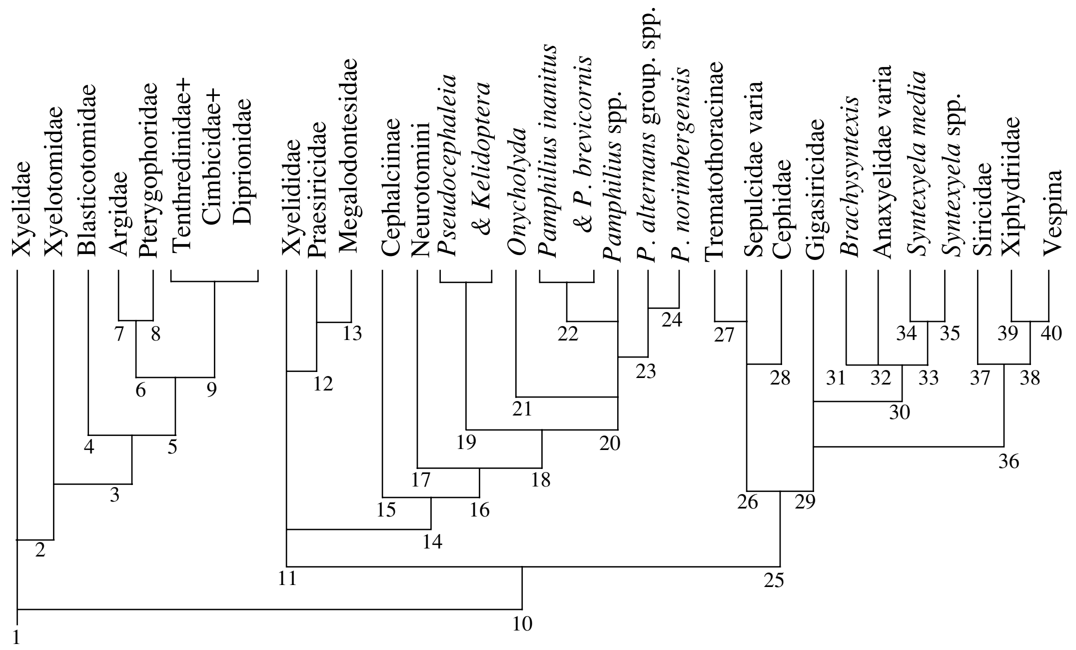
By now (April, 2006), molecular phylogenetic research has not yet resolved any appreciable segment of biological diversity, but has accumulated enough results to reveal some unexpected tendencies. A molecular study of particular taxa shows a considerable dependence of a resulting cladogram on the method and molecules involved, as well as on other agents not

Fig. 16. Cladogram of the lower hymenopterous insects (suborder Siricina), constructed consistent with the hypothesis (3) (see the text) that similarity in the xyelid-like antenna is homoplastic, and the alternative similarities are synapomorphic. Otherwise as in Fig. 15, with the following synapomorphies inferred: (1) the same as in Fig. 15; (2) *basiflagellar (3rd antennal) segment compound and very large*; (3) forewing 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, p. 120, items 2, 3); (4) *basiflagellar (3rd antennal) segment compound and very large*; flagellum short (up to 5 segments), rather thick; (5) pronotum short medially; (6) single flagellomere beyond composite one; *forewing with SC lost except crossvein-like fore branch* and with RS lost between submarginal cells; larva boring fern stem, with caudal structures modified; (7) male genitalia rotated at 180°; (8) forewing lacking 2r-rs; larva with eye and antenna distant, with antenna 1-segmented, with mandible lacking incisive molar flange, with suprapedal and subspiracular lobes merged; for numerous further synapomorphies, see Rasnitsyn, 1988a, p. 120, items 5, 6, 8, 9); (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 crossvein; (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 basad 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; forewing with basal sections of RS and M forming entire straight line, and with A_{2+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); forewing with M+Cu angulate; (19) *basiflagellar segment compound, enlarged*; tibial spurs with soft tips; inner tooth of tarsal claws reduced; hypopygidial depression large; (20) forewing membrane more or less folded apically; larva on Angiospermae; (21) *basiflagellar segment compound, enlarged; forewing 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*; forewing 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*; female forewing 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, p. 122, item 19); (32) forewing with SC short, appresed to R, *lacking fore branch*; (33) mesonotum membranous except laterally; forewing with costal space very narrow in basal third or half; ovipositor long exerting; (34) *basiflagellar (3rd antennal) segment compound and very large*; (35) metanotum with cenchri lost; forewing *with costal space narrow, with SC lost, with 1st abscissa of RS very short and cell 1mcu large*, with crossvein 1r-rs long, with Cu straight before 1m-cu, with A_2 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, p. 122, item 22); (37) *basiflagellar (3rd antennal) segment compound and very large*; (38) forewing and hindwing with single crossvein r-m each; (39) scutellum rounded basally; (40) *basiflagellar segment enlarged though entire externally*; (41) *basiflagellar segment compound, enlarged*; (42) basal flagellar segments enlarged about to form *compound, enlarged basiflagellar segment;* ovipositor scarcely exerting; (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; forewing with basal abscissa of RS subvertical; (45) mesoscutum with incipient adlateral lines; *forewing with SC lost except crossvein-like fore branch*; (46) 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; forewing with SC lost; 1st abdominal tergum modified into mesosomal propodeum; larva parasitic; etc., as listed in Rasnitsyn (1988a, p. 123, item 28).

always identified. This is not surprising at the early stage of development of the method. More worrying are the results that become more and more common with time, when molecular cladograms get some extent of stability and yet display striking disagreement with morphologically based cladograms. The most popular but not at all unique example is the so-called Afrotheria case (Fig. 18), a taxon of solely molecular definition that comprises several predominantly African mammals (aardvark, hyraxes, elephants, sirenians, and two groups of the former insectivores), which cannot be diagnosed and generally have very little in common. Another example is provided by myriapods, which appear rather distant from insects (often near chelicerates) in molecular cladograms. If this trend gains high support, it might result initially oust and replace the morphologically based cladistics as unable to reveal relationships, and at the next step of its development, to falsify the very idea that genealogy should, or even can, form the natural basis of taxonomy (see 2.3 for more detail).

2.3. Methodology of Taxonomy

We need a taxonomic classification of living beings to organize biological diversity in a way that facilitates our activities concerning that diversity. There are many



kinds of classifications created to fulfill particular functions and to meet requirements of particular kinds of users (e.g., a system of pests according to the type of harm caused). They present little problem to biological taxonomy, so I shall concentrate on the system, the very purpose of which is to be universally accepted as a common (interdisciplinary) reference system for all users.

To meet the above conditions, the system must have its taxa 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 have its taxa as within-group homogeneous and as between-group heterogeneous as possible. In other words, it must have the majority of characters similar within taxa and different between them. This property allows the system to fulfill two more functions of no less importance. One of them is to store information in the most compact and available form. Everyone knows much about, say, a sparrow (of course including data on higher taxa). Another function is to predict properties of taxa not yet studied in full detail. Indeed, 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 normal eukaryotic 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 ate. The above considerations are rather commonplace. I need them only to make the background more clear for further considerations.

There are three main trends in the taxonomy of the last decades: pheneticism, cladism, and the third one once called with a misleading name "evolutionary systematics" to distinguish it from "phylogenetic systematics," an original and equally misleading name for what most people now 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: syncretistic, eclectic taxonomy, etc. (Farris, 1979), as well as my previous awkward terms *tradistics* (Rasnitsyn, 1992) and *phylistics* (Rasnitsyn, 1996). However, there is and older and easier term *phyletics* proposed by Ponomarenko and Rasnitsyn (1971) which I restore to use herein.

The three main kinds of taxonomy are more distinct than might be apparent, because their ideologies are rooted in different views on the structure and origin of the biodiversity, which we considered above (Sections 1.2 and 1.3).

One of these concepts is the synthetic or, more correctly, population-genetic theory of evolution. It considers the evolutionary process as the allele dynamics in populations, which is controlled by natural selection and stochastic processes. As a result, the composition of a population precisely meets the limitations imposed by selection, except for deviations permitted by stochastic agents, and also by the interpopulation gene flow that optimizes the population structure toward averaged and not local selective limitations.

According to the synthetist paradigm, the organization of living beings is a set of characters permanently shuffled by natural selection, and the evolutionary process is as even and gradual as much as even and gradual are environmentally driven changes of the selection. This gradual evolution can be interrupted only by divergence and extinction events, the only events that make it possible to split biodiversity into taxa and, so, the only available organizer of the natural system. The nat-

Fig. 17. Cladogram of the lower hymenopterous insects (suborder Siricina), constructed consistent with the hypothesis (4) (see the text) that similarity in the xyelid-like antenna is symplesiomorphic, and the alternative similarities are synapomorphic. Otherwise as in Figs. 15 and 16, with the following synapomorphies inferred: (1) the same as in Figs. 15 and 16, and additionally, basiflagellar (3rd antennal) segment compound and very large; (2) antennal flagellum short (up to 6 segments beyond basiflagellar segment); forewing 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, p. 120, item 2-3); (3) pronotum short medially; *forewing with SC lost except crossvein-like fore branch*; (4) single flagellomere beyond composite one; forewing with RS lost between submarginal cells; larva boring fern stem, with caudal structures modified; (5) male genitalia rotated at 180°; (6) forewing lacking 2r-rs; larva with eye and antenna distant, with antenna 1-segmented, with mandible lacking incisive molar flange, with suprapedal and subspiracular lobes merged; for numerous further synapomorphies, see Rasnitsyn, 1988a, p. 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 crossvein; (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, with subanal appendages segmented, shifted basad 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*; forewing with basal sections of RS and M forming entire straight line, and with A_{2+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; hypopygidial depression large; (16) forewing membrane more or less folded apically; larva on Angiospermae; (17) *forewing 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) forewing 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, p. 122, item 19); (26) forewing with SC short, appresed to R, *lacking fore branch*; (27) *basiflagellar segment seemingly ordinary*; mesonotum membranous except laterally; forewing with costal space very narrow in basal third or half; ovipositor long exerting; (28) *basiflagellar segment seemingly ordinary*; metanotum with cenchri lost; forewing with *costal space narrow*, with 1st abscissa of RS very short, *with crossvein 1r-rs long and cell 1mcu large*, with Cu straight before 1m-cu, with A_2 straight, and with area aspera lost; abdomen compressed; larva boring in angiosperm plants; (29) *forewing with costal space narrow*; probably (unless appearing later as a synapomorphy of all the rest Siricoidea and Vespina) ovipositor needle-like; larva feeding on dead wood conditioned by symbiotic fungi, modified as explained in Rasnitsyn (1988a, p. 122, item 22); (30) basiflagellar segment somewhat diminished in size; forewing and hindwing with single crossvein r-m each; (31) basiflagellar segment dissociated into primary flagellar segments (still widened); ovipositor scarcely exerting; (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 subdivided into primary segments and 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; forewing with basal abscissa of RS subvertical; (38) mesoscutum with incipient adlateral lines; *forewing 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; *forewing with SC lost*; 1st abdominal tergum modified into mesosomal propodeum; larva parasitic; etc., as listed in Rasnitsyn (1988a, p. 123, item 28).

ural synthetic system can be only strictly genealogical, with its taxa delimited strictly through nodes of a graph (cladogram) depicting the genealogical pattern. Therefore, the synthetic paradigm infers delimitation of taxa after restored facts of history of the biodiversity, and not considering its present features: these are important only as evidence of history.

Above is the precise description of the *cladistic* system: strictly hierarchical, with taxonomic ranks not specified (indicated only by the succession of divergence events), and with the ancestral (paraphyletic) taxa prohibited (Table 5).

Unlike the synthetic theory, the epigenetic theory interprets evolution primarily as a process of ontogenetic transformation and, in particular, of evolution of stabilized (selected through generations) epigenetic processes and their assemblages, the creods. The genetic level (allele and mutation dynamics) lies below the epigenetic one and is not considered specially, although it can be hypothesized, for instance, that the epigenotype uses DNA signals to switch between alternative creods.

Deep interconnections between various ontogenetic processes and, hence, between different structures and functions of an entire organism complicate the optimization of these structures and functions. The organism appears as a result of a strict compromise between contradictory demands of optimization of all actual functions. Once being achieved, the trade-off becomes deeply stabilized (buffered), resisting further transformation beyond the boundaries of normal population variability (which is itself a result of selection of past

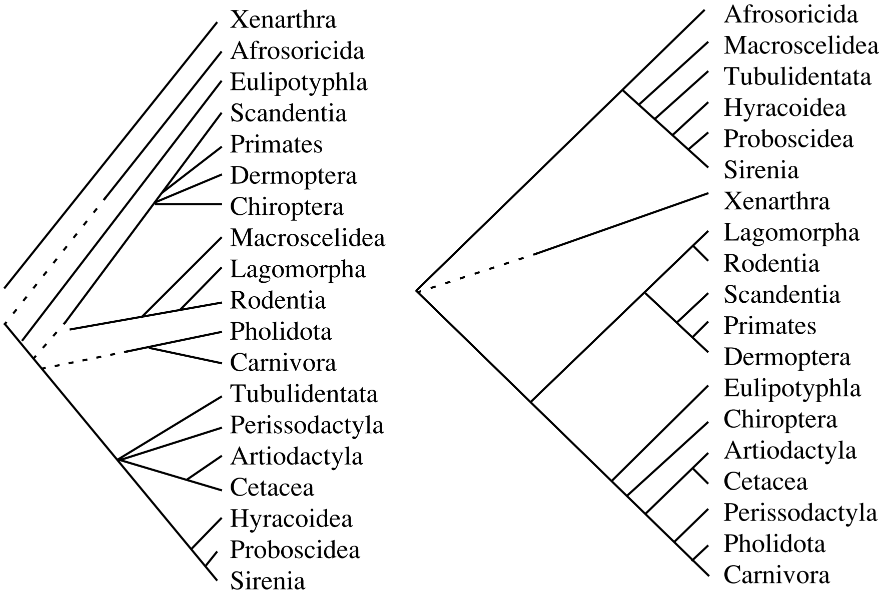


Fig. 18. Two cladograms of placental mammals, morphological (on the left) and molecular (on the right) (Pavlinov, 2005, text-fig. 49).

generations). Therefore, evolution, that is, successful change beyond the limits of the stabilized epigenotype, is difficult, more or less saltatory, and of limited predictability. Therefore, the resulting biodiversity should be more or less discrete. This discreteness of evolution and biodiversity is feature that both pheneticism and phyletics rely on while constructing their respective systems (Table 5). Cladistic, phenetic, and phyletic systems are considered more closely below.

2.3.1. Cladistics

The most profound meaning of cladistics differs in views of different students (cf. e.g., Hennig, 1966; and Platnick, 1979) so significantly that de Queiroz and Donoghue (1990a) apparently propose resurrection of the original name phylogenetic systematics to denote the Hennig's version, and to apply the name cladistics only to its transformed version (the proposal does not look like gaining general acceptance yet, so I continue using the latter term for the whole field). Despite this split, there exists a stable and by inference central cladistic statement, "Phenetic classifications are constructed by grouping accordingly to raw similarity, while phylogenetic ones are recognized by grouping according to putative synapomorphy" (Farris, 1979, p. 478). 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 most effective. Therefore, the system was termed phylogenetic. There is an alternative point of view, however, first, that nature is ordered in a single specifiable pattern which can be represented by a branching diagram or hierarchical classification; second, that the pattern can be estimated by sampling characters and finding replicated, internested sets of synapomorphies; and third, that our knowledge of evolutionary history, like our classifications, is derived from the hierarchical pattern thus hypothesized (Platnick, 1979, p. 538). The pattern is, hence, claimed to be primary, while phylogeny is 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 analyze the proposal independently of classical cladistics, so I shall be concerned only with the latter.

Table 5. Three taxonomies

Taxonomy	Evolutionary basis	Driving process	Workable criterion	Role of similarity	Role of genealogy
Cladistics	Synthetic theory of evolution	Divergence event	Synapomorphy	Ignored	The only basis of the system
Pheneticism	Epigenetic theory of evolution	Discretness of biodiversity	Hiatus	The only basis of the system	Ignored
Phyletics	Epigenetic theory of evolution	Discretness of biodiversity	Hiatus	Workable criterion	Testing criterion

The first question 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 character state acquired can be then lost while an apomorphy is universally treated as unloseable. 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 has ever been acquired* (a fact of the history of a group).

The above considerations are still not enough to explain the cladistic approach, because a problem exists 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. Cladists call all and only groups defined by apomorphies monophyletic although this definition is contrary to the traditional understanding of monophyly. Indeed, implied by the notion of monophyly as used by generations of evolutionists and taxonomists is the means of origin of a taxon, viz., that it roots into an ancestral taxon via a single ancestral lineage rather than several lineages (as a polyphyletic taxon does). The cladistic usage of monophyly (monophyletic = defined by apomorphy) is narrower than the traditional one. The former imposes limitations not only on the evolutionary past of a taxon (upon its way of origin through a single discernible ancestral lineage), but also on its future. Defined by apomorphies is only a taxon that has members (subtaxa) and not descendants, because to have descendants means to be defined by a plesiomorphy, that is, to be a paraphyletic taxon. In other words, traditional monophyly embraces both paraphyly and cladistical monophyly. To avoid this controversy, Ashlock (1971) introduced the term holophyly to denote monophyly in the narrow, cladistical, sense. I follow him terminologically and use monophyly as a generic notion for holophyly + paraphyly.

The cladistic policy to accept only holophyletic taxa (defined by apomorphies) meets a problem in *metataxa*, that is, paraphyletic taxa resisting the procedure of splitting into holophyletic subtaxa, i.e., those unable to be split so as to give subgroups that are all demonstrable as holophyletic (de Queiroz and Donoghue, 1990b). Many fossil hymenopteran groups attested to above (Section 2.2.4) as ancestral for other hymenopterans may serve as examples. The majority of such cases could be settled supposing the difficulties as temporary, a result of our incomplete knowledge (this is especially tempting in case of fossils). The refuge of ignorance is not secure, however, because parallel evolution, as we made clear above, prevents a cladogram from being deciphered in all necessary details. In addition, the manner of obligatory splitting of nonholophyletic taxa inescapably leads us from the stem group to the stem species which cannot be further split in this way (de Queiroz and Donoghue, 1990a).

Some students take refuge in ignorance here again, 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 studies, particularly in case of extensively studied mammals affected by the Quaternary glaciations. Less known but none the less impressive are the results of the study of bivalve mollusks inhabiting the Paratethys, a system of epicontinental seas of southwestern Eurasia during the Late 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 strong effects on the evolution of biota. Mollusks of the Paratethys were a subject of intensive investigation for more than a century because of the economic importance of those oil-bearing strata, and currently they are rather well studied. In many cases, explosive diversification of particular mollusk taxa proceeded in enclosed basins (lacking connection to neighbor basins) with well known fauna which makes possible to exclude migrations and so to be certain on ancestry of the resulting new species and higher taxa. Finally, mollusks have a special meaning in the present context. At lower taxonomic levels, their classification relies equally on their shell characters in both fossil and living populations. Unfortunately, the results of these extensive studies are published mostly in Russian. They have been summarized, along with the relevant literature, by Nevesskaya et al. (1986, 2001). Striking examples of this sort based on the molecular study of several groups of mammals are given by Rautian et al. (2006).

In general, to reveal numerous ancestral species is not at all a surprise, because the total number of ancestral species that ever existed is roughly equal to the number of terminal species, because *every* holophyletic clade must have its own ancestral species. This equation is precise (minus one ancestral species) in case of strictly dichotomous divergence, will shift toward the prevalence of terminal species in the case of polytomy, and toward ancestral species when phyletic (nondivergent) evolution prevails. As a result, we may consider ancestral and terminal species as roughly similar in number.

A species ancestral to more than a single taxon seems to impose insuperable theoretical problems for cladistics, unless it makes the central cladistic statement (taxon definable only by apomorphy) less rigid. This necessary step has already been made by Hennig himself. He considered apomorphy as legitimizing a taxon not by definition but only by implication of another, more hard (basic, central) statement, which is the isomorphism 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, p. 66). This way of reasoning makes divergence itself the only process generating taxa, while the 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 considered to disappear after each divergence event. Even if one product of a divergence event shows not the slightest difference from its ancestor (no apomorphy acquired), it must be considered as a different species. This proposal seems to me a little strange, but it is at least consistent. It gives the system a double advantage. First, it becomes clearly monistic, as it is usually opposed to the claimed syncretistic nature of phyletics (but see below). Second, the system appears as objective and well grounded as the respective cladogram, though not more than that.

The last reservation is important. If some (possibly many) species have no difference from their ancestors, we even have no theoretical possibility to identify cladogram topology correctly. Instead, we can expect only some degree of its approximation. This makes advantages of the approach less evident compared to the alternative one. Indeed, contrary to that claimed above, it seems possible to invert the proposition and to consider the cladistic system as ultimately definable through the sequence of apomorphies, with the divergence events used only as a tool of sequencing. This approach has already been used by Brothers (1975) in his classical study of the phylogeny and taxonomy of aculeate wasps.

As a divergence event is not necessarily coupled with the gain of an apomorphy, the apomorphy can easily proceed unaccompanied by divergence. This results in a fully sequenced array of apomorphies being unattainable even in theory. Thus, the two approaches are at least comparable in their value for phylogenetic study. This is not to say that they are of precisely equal use, but the advantages and deficiencies of either seem to deserve special study. For example, besides the impossibility of being fully sequenced, apomorphies are hardly available just for counting within the framework of Brothers' approach. They cannot usually be hypothesized as appearing in one step (during a single speciation event) in their full form, since most apomorphies are phylogenetically complex, not unitary. This causes problems for identification of the system of internested taxa created by successive steps in acquisition of a complex apomorphy. On the other hand, Brothers' version seems richer in information content compared to Hennig's one, for it takes into consideration both relationships and the amount of change acquired (but see below).

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

To conclude, it is possible to say that the cladistic system should be strictly genealogical (isomorphic with reference to blood relationships, i.e., to the divergence pattern). Hence, its taxa should be delimited at the nodes of the cladogram (divergence events) as identified by synapomorphies (evolutionary innovations acquired by the ancestor and retained by its descendants). Similarity is relevant only as an indication of relationships. Cladistic taxon can be split into subtaxa but cannot give rise to another taxon; no ancestral taxa are permitted there, except for an ancestral species which is considered as an imaginary collection of plesiomorphies. Thus, the event that creates a taxon (either a divergence act or the event of the acquisition of a synapomorphy) is purely hypothetical.

2.3.2. Pheneticism

Of the three competing approaches, pheneticism 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 (including methods of tracing hiatuses), and this way permits one to avoid subjectivity in the similarity calculation. The methods of calculation are called collectively taxometry or, more commonly, though less adequately, numerical taxonomy. Unfortunately, the methods have never been developed to the proclaimed level. In my opinion, this was not because the level was proved unattainable but because pheneticism was forced back by cladistics before it proceeded far enough in its useful work. The methods of taxometry are numerous and diverse, and the choice of the adequate method is not easy and cannot be made in a sufficiently objective manner. However, this is a problem for any approach (including cladistics, see, e.g., Mickevich, 1978), and it evidently needs hard work to evaluate what is the natural domain of a particular method and which are its strong and weak sides. Pheneticism proceeded far in this way before it was consumed by the more vigorous cladistics, but not enough to enable a conscious rather than a chancy option of an adequate clustering method.

However, the above failure does not seem the most important weak point of pheneticism. Probably more important is that the similarity studied by pheneticism is not precisely the same as what the system needs. Pheneticists dealt with similarity in studied characters, which must be reasonably numerous but not more than that. On the contrary, similarity that 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 compared taxa, including the characters not yet studied (and maybe never to be studied). This kind of similarity is a rather abstract thing not available directly but important enough to justify attempts to evaluate it in any possible indirect way. This is quite what both cladistics and phyletics try to do.

2.3.3. Phyletics

Phyletics tries to combine advantages of both phenetic and cladistic approaches in its attempts to take directly into consideration both similarity and relationships. To reach this result, the phyletic 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 and Rasnitsyn, 1971). Monophyly is used there in the traditional sense, that is, covering both holophyly and paraphyly (see above). The continuum means a continuous chain (branching or not) of subtaxa, each of which is phenetically more similar to any of its direct neighbors than to members of any other continuum. In other words, the continuum is an entity delimited from other continua by hiatuses. The definition seems clear and close to the traditional understanding of taxon. It looks eclectic, however, in combining independent criteria of similarity and relationships.

An eclectic approach is bad because it uses independent criteria to define one and the same notion. One time or another, 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 actual or not. 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 phyletics is also escapable. Indeed, the phyletic criteria are conflicting 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 falsified when more sophisticated testing is applied. That was the case with the insect order Neuroptera, which had long been used to cover groups that later were found to be only remotely related. For instance, Sharp (1895, 1899) still comprised under this name, in addition to the Neuropteroidea in the current sense, also the Embioptera, Isoptera, Psocoptera, Mallophaga, Odonata, Plecoptera, Ephemeroptera, Panorpata (= Mecoptera), and Trichoptera. Similar was the fate of the mammal order Pachydermata which was in long use during the 18th and 19th centuries to cover elephants, tapir, rhinos, hippos, and pigs, until it was eventually discarded in favor of more natural (monophyletic) orders.

In other cases, the hypothesis of polyphyly will be falsified, as appears eventually with the hares and their relatives. They were once established as the separate order Lagomorpha, only convergently similar to true rodents (Gidley, 1912), but nevertheless all of them are now considered to form the monophyletic taxon Glires (Wilson, 1989). In theory, it is also quite possible to find cases where both hypotheses (of similarity and polyphyly) appear equally probable. Until recently, this was a rather theoretical possibility, because actual cases usually permitted deepening our knowledge in both the similarity and phylogeny of the taxa involved up to the agreement between the two criteria, or at least they leave hope that such agreement is attainable in the not too remote future. However, current success in deciphering relationships of higher taxa using molecular methods reveal cases that might cast serious doubts on the very possibility of such agreement (e.g., the case of Afrotheria, see 2.2.6).

There are other and less novel cases when traditional taxonomy retains taxa in spite of their undisputable polyphyly. These are examples when polyphyletic taxa cannot be replaced by monophyletic ones without significant loss in usefulness. I refer to various kinds of parataxa in fields such as paleontology, parasitology, mycology, as well as many prokaryote taxa (see the next section for detail). I consider this observation as evidence that the traditional approach relies ultimately on similarity, while relationship (monophyly) is used as an indirect clue allowing us to assess similarity in the total array of characters, including those yet unknown. Relationship is used here to assess indirectly the total similarly in the same way as the apomorphy is used in Hennigian cladistics as a tool to identify the succession of divergence events, and as divergence events are taken to make sequencing of the apomorphies possible in the Brothers' version of cladistics. As a result, all the three are equally consistent (monistic, not eclectic): Hennigian cladistics relies ultimately on the succession of divergence events, and uses apomorphies to mark and identify them. Brothers' cladistics relies ultimately on succession of the events of acquiring apomorphy and uses the divergence events to sequence the apomorphies. Phyletics relies ultimately on similarity (in the most complete array of characters) and uses relationships (as indicated by apomorphies) to improve the results of study of incomplete set of characters. To make the list complete, remember pheneticism; it is monistic and straightforward in relying both proximately and ultimately on similarity alone.

Now, we return to the question of comparative advantages and disadvantages of cladistics and phyletics. In my opinion, the most important phyletic 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 empirical as pheneticism is (in fact, it will be just like pheneticism here). It will use any reliable phylogenetic data when they exist, and because it uses only the more evident data, it is possible that the resulting system is not exceedingly hypothetical. Opposite to this, the cladistic system relies both primarily and ultimately on relationships that are knowable solely from character interpretation (even when studied molecularly). It is based on inferences concerning the evolutionary succession of the character states. As a result, the cladistic system contains inference of the next level up of hypothesis in comparison to phyletics.

Another side of the above result is that phyletics 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. It 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 phyletic system. This makes the domain of cladistics narrow.

Other putative advantages of phyletics seem less important or less evident. It can be claimed that phyletics records both similarity and relationships and, therefore, it stores more information. Farris (1979) objects that the cladistic system in its fullest form specifies the origin of all characters available and, thus, is more informative than pheneticism (and, by inference, phyletics). The claim is not undisputable, 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 available, so as cladistics can always operate with an incomplete set of characters. Phyletics is able to incorporate into its system all the amount of information available for cladistics and to add information about similarity of the taxa involved, which is connected with the nonpolarized characters. Therefore, the phyletic system is potentially richer in its informational content.

The above considerations in fact compare phyletics with the original Hennigian version of cladistics now commonly treated as outdated. This apparently makes the comparison irrelevant to the current problems of taxonomy. However, the classical, Hennigian cladistics is a theory (a system of hypotheses), which is rich in biological contents; it stimulates thinking and helps understanding organization of the nature even if you disagree with the general concept. Computer cladistics is different; it (probably) has rich and complicated mathematical content, but is poor in biological content. As a taxonomic concept, computer cladistics relies on a single biological postulate of isomorphy between taxonomy and phylogeny (both polyphyly and paraphyly are excluded), and as a phylogenetic concept, it relies only on the postulates of parsimony and of strict dichotomy (see 2.2.5, 2.3.1). All the rest of computer cladistics is the matter of mathematics and not of biology. As a result, computer cladistics is, for a biologist, a technique and not a theory, nor a hypothesis. That is, it is more empirical than even pheneticism (which had at least a theoretical problem of selecting the biologically appropriate method of calculation).

There is another side to the problem of information content of a system. The above discussion concerns in fact the information stored not 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 respective dendrogram and on the length of 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 four terminal taxa contains 3 bits of information and not a bit more, unless the rank information is added. Unless ranking is involved, and beyond that the amount of correlated similarity and relationships, 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 reflect the succession in time of divergence events. However, such a practice was found impractical, and now it is virtually abandoned in favor 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 the 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 comblike cladogram should be transformed in a group of taxa of the same rank listed in a sequence with the taxon the earliest to diverge listed first, and the pair diverging most recently listed last (in an arbitrary order). However, we cannot distinguish this list from that sequenced arbitrarily or derived from a cladogram either more complex in form than a simple comb or involving an unresolved polytomy.

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

It is claimed that pheneticism and phyletics, in contrast to cladistics, use taxa characterized only by the absence of characters (Platnick, 1979), that is, paraphyletic taxa which are characterized by the absence of apomorphy. However, it was shown above (2.3.1) that the apomorphy is neither a character nor a character state but rather a hypothesis concerning the history of a taxon. The absence of an apomorphy does not mean the absence of a character. A lizard lacks the apomorphy of snake, it has legs instead.

The problem of symbiotic and hybrid taxa also worth discussing here. The problem is important, because both these 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 Eukaryota, while the latter is very characteristic, for example, of higher plants. As reviewed by Tsvelev (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 these hybrid species. A similar pattern is claimed to hold true in many other higher plant taxa.

Symbiotic and hybrid taxa are polyphyletic, because their lower boundary is crossed by more than a single lineage of ancestry. At the same time, they can satisfy the definition of holophyletic taxon: the nearest common ancestor of all terminal subtaxa and all descendants of that ancestor may easily be included in that taxon, which is 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. It is in no surprise, since they refer to different aspects of the history of taxa (either to their more or less remote, or immediate past, respectively), which are not mutually exclusive. As a result, we have to choose which of these aspects to rely on as an ultimate criterion for accepting a group as a taxon. I vote in favor of the immediate past; if we accept a taxon which is either strictly holophyletic (as a cladistic taxon), or any of holo- and paraphyletic (as a phyletic taxon), and if we exclude those which are neither of the two, we shall avoid polyphyletic taxa in the traditional sense, but not the hybrid and symbiotic ones.

Nevertheless, hybrid and symbiotic taxa do pose a problem for taxonomy. This problem affects not these taxa themselves but their ancestral taxa (the whole chain between both parent species and their common ancestor!), which are paraphyletic by definition. However, this problem concerns only cladistics, and not phyletics nor, of course, pheneticism.

Other considerations certainly exist relevant to the comparison of the three leading taxonomic concepts. Nevertheless, the result already obtained seems enough to conclude that each of them has its own advantages and disadvantages. However, the balance of both does not seem equal. Pheneticism and cladistics demonstrate deficiencies important enough to consider the two as inferior compared to phyletics. These weak points are the short sight of pheneticism, which fails to use the prognostic power of phylogeny, the fastidiousness of Hennigian cladistics, which rejects too large a fraction of the available characters and also produces taxonomic constructions with the high hypothetical content and poor biological content characteristic of the computer cladistics. I believe that phyletics will prevail as the winner.

2.4. Methodology of Nomenclature and the Nature of the Taxon

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 detail and simple basic principles. This is not exactly the case, since the principles are not all appreciated and explicitly formulated in the Codes (ICZN, 1999; ICBN, 2000). In addition, some of these basic principles are not true conventions, being only a reflection of a particular taxonomic concept, or obtained by the inference of a particular evolutionary theory. Indeed, the Linnean principle of binominal nomenclature is fully conventional and easily coupled with any taxonomy accepting a hierarchy formed by genus and species. In contrast, the type principle is essentially different, as is discussed below. The distinction between the two kinds of principles seems useful; so, they deserve their own names and will be further referred to as taxonomy independent and taxonomy dependent principles, respectively (Table 6).

Table 6. Principles of nomenclature

	Taxonomy independent
1	of unrestricted taxonomic freedom beyond the restrictions imposed by taxonomy dependent principles
2	of restricted area of application
3	of homonymy
4	of priority
5	of standardized and rank-indicating names
6	of superior authority of the International Commission of nomenclature
	Taxonomy dependent
7	of type (with no good reason for not following it)
8	of hierarchy (not for application throughout in parataxa)
9	of synonymy (not for application throughout in parataxa)

Due to my personal experience, the following consideration is based on the rules of zoological nomenclature. This seems to make little difference, since the various Codes differ largely in detail rather than in underlying principles.

2.4.1. Taxonomy Independent Principles

These are often plain and need little, if any, comment, 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, Principle (1)). This statement is not fully correct because of taxonomy dependent principles that validate only particular cases in taxonomy. The statement should probably be completed with the words “beyond the restrictions explicitly imposed by the present Code.”

(2) In zoology, “The Code regulates the names of taxa in the family group, genus group, and species group” (ICZN, Article 1.2.2). Exclusion of the higher taxa from the scope of the Code seems to me a mistake, although that is a subject for another discussion (see Rasnitsyn, 1982, 1986b, 1989a, 1991, 1996, 2002; Rasnitsyn and Quicke, 2002).

(3) “To avoid ambiguity, the use of the same name for different taxa must not occur and is prohibited. This is the Principle of Homonymy” (ICZN, Principle (5)). In other words, identical names of different taxa must not be used as valid names. The scope of the principle of homonymy is arbitrarily restricted so as not to concern (a) the species group names belonging to different genera, (b) homonymy with (and between) higher taxa

and (c) homonymy between taxa belonging to animals and to plants.

(4) The principle of priority, as formulated in the ICZN (Article 23.1). "The valid name of a taxon is the oldest available name applied to it, unless that name has been invalidated or another name is given precedence by any provision of the Code or by any ruling of the Commission."

(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, 25–35).

(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 the Code ("The Commission is empowered … under conditions specified in Article 81 to suspend the application in a particular case of any provision of the Code except those in the present and next succeeding Chapter"; ICZN, Article 78.1).

2.4.2. Taxonomy Dependent Principles

There are three taxonomy dependent principles.

(7) 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 device of name-bearing types allows names to be applied to taxa without infringing upon taxonomic judgment. Every name within the scope of the Code (except for the names of "collective groups" and of taxa above the family group) is permanently attached to a name-bearing type" (ICZN, Principle (3)). In other words, a taxon can be introduced into the system ultimately only by 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 volume (all or the most important/stable of its subtaxa). This approach is employed, for instance, by Kluge (1999, 2000). It seems apparent that this approach can be productively applied only to the groups with well elaborated, stable system; otherwise, the definition of the taxon name by volume would result in ephemeral nature of taxa and highly unstable nomenclature.

Another possibility is 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, for instance, a multidimensional matrix with each cell corresponding to a particular combination of characters and, thus, harboring a separate taxon. A version of this is an identification table sometimes used by taxonomists, a rectangular matrix with the upper row of characters and the 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, since 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 that with the taxa identified by ranked characters, as in the standard identification key, with characters being more highly ranked the earlier they enter the key. It is quite useful, although it is not so good as the general system because of the evident arbitrariness of the character rankings. Nevertheless, in somewhat modified form (that a few highest rank characters are enough to shape the system), this approach is popular among taxonomists since Linnaeus (1751), who has based his system of plants primarily on the characters of fructification. This proposal was formulated most explicitly by Lubischew (1923, 1966). He called to search for a few highest-rank characters (parameters) which should determine the distribution of all other characters, like the nuclear charge determines the features of atoms and the position of respective element in the Mendeleev's system. This should result in discovering the parametric system which is able to forecast all the important characters of the taxa involved from these key characters (parameters). The task proposed by Lubischew seemed hopeless as applied to taxonomy, and Lubischew himself failed to resolve it. A solution has been found, however, 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.

This 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, their relationships. The relationship, thus, becomes the Lubischew's 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.

The challenge has been meet. De Queiroz and Gauthier (1990, p. 307) appreciate that, in cladistic taxonomy, "names are synonymous if they refer to clades stemming from the same ancestor," Understanding and developing this basic statement has resulted in the launch of the PhyloCode project (Cantino and de Queiroz, 2004), with a main intention of attaching a taxonomic name as a label to either a (hypothetical) ancestor of a clade or (a collection of its) synapomorphy(ies) (cf. the above distinction of Hennigian and Brothers' cladistics, Section 2.3.1). I am not aware of any wide application of this approach to cladistic taxonomic practice. In general, I am afraid this will not be easy to persuade the practicing taxonomists to attach a taxonomic name to either a hypothetical ancestor or a synapomorphy and to abandon the rank system, as the

PhyloCode proposes. There is still less chance that the proposal to abandon the species notion being adopted, as some PhyloCode proponents propose (Pleijel and Rouse, 2003); the current draft version of the PhyloCode does not consider yet the species name. The current version proposes to use PhyloCode names in parallel with the traditional (ranked) names; I cannot imagine this system unless one of these two nomenclatures bears only auxiliary (clarifying) function and so is not mandatory. I doubt if the PhyloCode proponents pursue this role for cladistic nomenclature.

Now, I am leaving this exotic problem to return to alternative ways of the taxon typification. A category as a group defined by the characters of its members has the individual as the logical alternative. The proposition to consider the taxon as individual (Ghiselin, 1974, 1987, and bibliography therein) is, thus, quite natural. Being an individual, a taxon must be introducible 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 as more than one of them might be able to inherit the taxon name. This makes a difference between the ostensive definition of an individual (direct indication of its member/part) and 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 is a very special kind of individual, if at all (see, e.g., comments following 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 as to be true for species due to their divergence being suppressed by gene flow (Mayr's biological species concept). The model is limited in its scope, since "The biological species concept has validity in what I have called its 'nondimensional situation,' that is, where populations are actually in contact with each other" (Mayr, 1988, pp. 301–302).

The phylogenetic lineage was hypothesized as well to have sufficient integrity to consider the lineage and the respective taxon as an individual (Ghiselin, 1981). There is a problem here too, for all the ancestor–descendant transitions are equally integrating. I am equally related to my father and to my son, and so is a species to both its ancestral and descendent species. The only difference results from the asymmetrical distribution of common history; I share it with my father and not with my son. This is a precise description of the essence of a cladistic system. It displays very clearly what a special case of individual is a cladistic taxon; it can be born, can exist, and can die, but can never give birth to another taxon. The only available to it is to segregate its internal contents into subclades (subtaxa). I can see here an exaggerated, all-depressing role of history: nothing in the world, not a single evolutionary invention, how brilliant and influential in the subsequent history of a clade it could be, is comparable in its taxonomic meaning with the common history. The past history is everything, the future one is next to nothing—this is apparently almost a true representation of the cladistic view of the system.

However, the category-individual dichotomy does not necessarily exhaust the existing options. Indeed, a taxon possesses features of both the category and the individual; as a category it possesses characters, as its diagnosis witnesses, 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, similar to an individual, a taxon has parts (populations in relation to species), and, which is more important, it can develop (evolve) and yet not lose its individuality. While evolving, a taxon retains its wholeness in time, in the multidimensional space of its characters, and to an extent in geographical space. Because of this wholeness, a taxon is appreciable after its name, as an individual is. In possessing features of both category and individual, the taxon is a notion intermediate between these two, or rather it fills the gap between them, so that the category and the individual are two extremes of a single spectrum.

As a result, a taxon in the above sense is neither a true category nor a true individual. It is most similar to a cloud whose spatiotemporal wholeness is actual, although far from being complete. A taxon seems to be best defined as a continuum in agreement with its phyletic usage. The phyletic approach is well suited to the task introducing and handling taxa using types; it is the continuum which can be introduced into a system ultimately using a type. Indeed, unlike an individual, the possibility of identifying a continuum depends on similarity rather than integrity, and unlike a category, 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 category is a cell 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, resulting in the existence of gaps delimiting it from other continua, and by the characters of its diagnosis. Both criteria are not fixed, however, being easily changeable in the course of both evolution and knowledge acquisition, so that at any particular moment, it may not be possible for them to delimit the taxon. That is why the taxon is ultimately identifiable via its name attached as a label to its nomenclatural type.

The same result can be achieved through a different and shorter way of reasoning. Indeed, the aim of any classification is to cover all the diversity to be classified by a system of taxa which should neither overlap each other, nor leave 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, p. 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, since 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 to define individual in a sophisticated manner, as cladists do. In contrast, the taxon-continuum perfectly meets the demands of the classification procedure, because the only legitimate way to define a continuum is to trace and to rank borderlines between it and other taxa.

In addition to the type concept, there are two more taxonomy dependent principles of nomenclature. They are also an implication of the continual nature of a taxon.

(8) The principle of hierarchy (appreciated as such by neither ICZN nor ICBN). Being continua, taxa cannot be grouped in any other way than in the next more inclusive continua (higher taxa). These higher taxa must be fully inclusive, that is, they must include subordinate continua as a whole, not in part. Equally, a taxon-continuum, even as a whole, cannot be a member of two or more higher taxa, because otherwise they would overlap and, consequently, would not obey the definition of the continuum. As a result, the system takes a fully hierarchic form.

(9) The principle of excluded synonymy: "Each taxonomic group with a particular circumscription, position, and rank can bear only one correct name" (ICBN, Principle IV; I was not able to find an appropriate formulation of this principle in ICZN). Indeed, if a taxon can be a member of only a single higher taxon, it has no justification to have more than a single name, the extra ones being destined for invalidation because of synonymy.

2.4.3. Reasons for Refusing to Follow the Principles of Nomenclature

In the case of taxonomy independent principles, these reasons are necessarily subjective in the sense that there is no taxonomically justified reason to do so. Therefore, these cases are not discussed here. The problems with the taxonomy dependent principles seem more important and deserve special consideration. Being scrutinized elsewhere (Rasnitsyn, 1986b), they will only be treated in a cursory fashion here.

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

Taxonomy performed in violation of one or another taxonomy dependent principle of nomenclature is called *parataxonomy.* The least disturbing case of the *parataxon* 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. Otherwise, a taxon incertae sedis is to be treated precisely like an orthotaxon, and particularly it is a subject of synonymization whenever its synonymy is detected with either another taxon incertae sedis, or an orthotaxon. Therefore, the acting codes do not consider taxa incertae sedis in any detail even if they mention them (ICZN, Article 67.2.5 and Glossary; ICBN does not mention taxa incertae sedis, although its previous editions considered them under the name *form genus* defined as a genus attributed to a higher taxon but not to a particular family).

Another kind of parataxon was proposed under the name *formal taxon* (Rasnitsyn, 1986b) intended to cover the past botanical *organ genus* and similar cases including zoological *ichnotaxon* (parataxon dealing with fossil traces and other works of extinct animals). However, a better name has been meanwhile proposed in the ICBN, the *morphotaxon*, which is employed herein. The morphotaxon is treated as if it is an orthotaxon, but only in the framework of a special system, which is parallel to the general system and completely independent of it, except for the principle of homonymy. These are, for example, taxa in the systems created to classify isolated fossil leaves, 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. Morphotaxa differ from orthotaxa only in that any of them is possibly (sometimes even certainly) a synonym of an orthotaxon, and yet they should not be synonymized with the latter even if the synonymy is apparent.

Morphotaxa are sometimes claimed to violate not only the principle of excluded synonymy, but also the type concept. Provisions of past zoological codes to detypify ichnotaxa are fortunately deleted from the current ICZN. Nevertheless, it is worth mentioning proposals to detypify morphotaxa in order to defend them against the persistent drive of some taxonomists to synonymize morphotaxa, however, arbitrary such synonymy might be. As an example I refer to the case of *Laberius* Kieffer (see Rasnitsyn, 1986b, for more detail), where the genus 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, pp. 47–81). Detypification does prevent ungrounded synonymy. Yet it prevents any synonymy, thus being perhaps a case of where 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 safer defense against their arbitrary synonymization.

The last and poorest kind of parataxon is the *collective taxon.* It is a parataxon, usually of generic rank, which 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 digenean helminthes […], is now used as a collective-group name for trematode larvae that cannot be placed with certainty in known genera; *Cercaria* is used in this way irrespective of any taxonomic treatment of it in synonymy" (ICZN, Article 67.14. Example). The last somewhat obscure phrase "irrespective of any taxonomic treatment of it in synonymy" apparently means that the name *Cercaria* cannot be a synonym while it is used as the name of a collective group.

The collective taxon is also stated there to be detypified (ICZN, Principle (3)), 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 eventually be typified in zoology, as has been done in botany. Another example is the collective genus *Carabilarva* Ponomarenko, 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.

The above considerations allow a different and apparently clearer interpretation of the collective taxon. As we see, a collective genus is equivalent in its scope to a respective higher taxon (an order in the case of *Cercaria*, a superfamily in case of *Carabilarva*, etc.). This means that species of these collective genera are attributed to respective higher taxa omitting all interpolating taxa including (ortho)genus. Apparently, they are simply species incertae sedis. However, it is impossible under basic code provisions to use a species name (epithet in ICBN) not combined with the generic name. This makes necessary introduction of a special name (the name of collective taxon) that would embrace these orphan species. Formally it is a genus name but with the scope equal to a respective higher taxon. This equivalency extends naturally to typification of the taxa involved with the result that they share one and the same type. As in the case of other taxa incertae sedis, species in collective groups are supposed to be taxonomically distinct from any other species both within and beyond that genus, and deserve synonymization whenever their synonymy is detected. Equally, whenever a taxonomic position of such orphan species is reasonably clarified, it deserves transfer into the respective orthogenus.

The last kind of parataxon to be mentioned here is the satellite taxon, the concept introduced by Meyen (1987b) to denote taxa of obscure position that are ascribed to an orthotaxon with purely informative aim (in order not to lose it among innumerable little known groups of obscure position). For instance, *Araucarioxylon* Kraus is a satellite genus of gymnosperm plants. This kind of parataxa seems to be very useful in paleontological studies and possibly outside.

It might be also of interest to compare the approaches of the acting zoological and botanical codes to the problems of parataxonomy. I was able to select three aspects particularly worth consideration.

(1) ICBN treats all taxa of fossil plants as parataxa in that "For purposes of priority, names of fossil taxa (diatoms excepted) compete only with names based on a fossil type representing the same part, life-history stage, or preservational state" (ICBN, Article 11.7). Indeed, "The generic name *Metasequoia* Miki (1941) was based on the fossil type of *M. disticha* (Heer) Miki. After discovery of the nonfossil species *M. glyptostroboides* Hu et W.C. Cheng, conservation of *Metasequoia* Hu et W.C. Cheng (1948) as based on the nonfossil type was approved. Otherwise, any new generic name based on *M. glyptostroboides* would have had to be treated as having priority over *Metasequoia* Miki" (ICBN, Article 11.7, Ex. 29). In general, botanists tend to distinguish kinds of their material that are differently affected by parataxonomy, rather than rely on the distinction between para- and orthotaxa as such. For instance, diatom algae (Bacillariophyta) are totally excluded from the nomenclatural provisions for fossil plants, because their taxonomic position is based on the skeleton features irrespective of being extant or extinct. Unlike the above botanical approach, the ICZN considers a group as a parataxon according to an explicit statement about its nature (an ichnotaxon, a parataxon of detached beetle elytra, etc.) irrespective of it being fossil or extant.

(2) In ICBN (Preface), "for nomenclatural purposes, botanical fossils are now considered to belong in the first place to morphotaxa: taxa at definite ranks that

comprise only particular parts, life stages, or preservational states but not the whole organism (Art. 1.2). … recognition and naming of "biological" fossil taxa, in the sense of evolutionary units consisting of whole organisms, is not dealt with in the *Code*, which gives full latitude to those interested in such basically hypothetical concepts to use for them the names that are best suited for the purpose." Conversely, ICZN makes no formal distinction between fossils and living animals considered as a whole organism, even if it is only represented by a part of an animal.

(3) As mentioned above, no provisions for collective groups are found in ICBN unlike ICZN.

(4) Symmetrically, unlike ICBN, no morphotaxa are considered in the ICZN, except for ichnotaxa.

3. CONCLUSIONS

Current problems of evolutionary theory are, in my opinion, rooted in a lack of sufficient improvement of its methodological basis. I mean distinction between two main approaches which might be termed *elementarist* (reducing a complex whole to elements) and *holistic* (reducing it to features of the whole).

In evolutionary biology, the elementarist (commonly termed reductionist) approach results in the population genetic (synthetic) paradigm, which appreciates the evolutionary process as the dynamics of allele frequencies in populations, affected by selective and stochastic factors. As a result, the evolutionary process is expected to follow selective pressure as closely as the stochastic parameters permit. Therefore, the evolutionary process is expected to be even and predictable to the extent permitted by the selective and stochastic parameters. Biodiversity resulting from the above process is possible to segregate efficiently into a system of nonoverlapping taxa only using divergence and extinction events to delimit taxa. The taxonomy adequate for this evolutionary model is the cladistic one because it delimits taxa strictly through the divergence points using synapomorphies.

The alternative holistic approach reduces a system capable of evolution of the whole and, particularly, of the epigenotype (i.e., the entire developmental machinery). A complex system that secures development efficiently is deeply interconnected and therefore appears a strict compromise between the contradictory needs of optimization of different adaptive systems. As a result, the epigenotype is capable of its total rearrangement rather than partial modification. This makes evolution saltatory rather than gradual and leaves little space for prediction of results of evolution because of low correlation between selective pressure and evolutionary response. The resulting biodiversity is full of discontinuities in character variation. Therefore, the best way to translate these results into the system is to trace the discontinuities (hiatuses), as the phyletic taxonomy does.

The available body of observations suggests epigenetic and phyletic approach to be adequate. However, there is another and apparently more important aspect of the present analysis. I mean refinement of distinction between the two basic evolution paradigms, elementaristic (population genetic) and holistic (epigenetic), because the present confusion of these alternative approaches seems to be the main cause of current problems in the field considered.

The refinement of the basic ontological paradigms makes it possible to refine the methodology, as follows.

Phylogenetic inference, like any scientific work, relies on (1) observations (including experiments), (2) search for analogies, (3) development of hypotheses about the underlying patterns and mechanisms, (4) attempts to falsify these hypotheses (mostly through their implications), and (5) assessing the 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, which are divided into two groups involved in either group analysis or character analysis. 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 divided into those relevant to the study of differences, and those used in the analysis of similarities. The former subgroup covers the presumptions that help us to polarize transformation series, that is, 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 versus independently acquired similarity. These are, first of all, the presumption of parsimony, and the presumption of weighted similarity.

There are phylogenetic methods that avoid scrutinizing evolutionary trends of particular characters; instead they rely on sophisticated automatic procedures aimed to reconstruct cladograms in maximally objective and reproducible ways. These are computer cladistics and molecular phylogeny. Computer cladistics is old enough to show its claimed high superiority over the traditional (manual) methods; this superiority is still problematic at best. Molecular phylogeny is much younger, its results are promising for short time intervals (genealogy of lower ranked taxa) but it gives contradictory results in the longer run. It looks premature to assess perspectives of the molecular methods in any final form.

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 major rival taxonomic approaches, pheneticism relies solely upon available characters as such and, thus, appears to be too myopic (purely empirical). Another extremity represents the cladistic approach, which hypothesizes that the overall results of the evolutionary process deeply if not perfectly depend on the genealogy of a group, that is, on its divergence pattern. We are aware of no biological processes that might secure this tight dependence. Equally, the cladistic systems have failed to display an undoubted superiority over the results of alternative approaches. This attests cladistics as too hypothetical (relying too deeply on a hypothesis still lacking serious support).

The third altermative, the phyletic approach, is intermediate in a sense. Its ultimate goal is a system that reflects a comprehensive balance of similarities and dissimilarities, while relationships are considered to be an important heuristic method to approach this goal. Phyletics defines a taxon as a monophyletic continuum, where discontinuities (gaps) are used to delimit taxa, while monophyly is considered as a means to assess whether the resulting taxon is correctly delimited, or the system deserves reinvestigation.

Taxonomic nomenclature is claimed herein to be built on the basis of nine principles, six of which are purely conventional in the sense that they are independent of a taxonomic concept employed, and three others are taxonomy dependent principles. Among the taxonomy dependent principles, the most important is the type concept, which is the only one that more or less stabilizes the names of taxa designed as a monophyletic continuum. Two other taxonomy dependent principles, those of hierarchy and of synonymy, may not be followed in cases of taxonomically deficient material. Taxonomy of the taxonomically deficient material, using an incomplete set of principles of nomenclature, forms a special field called parataxonomy. The main kinds of parataxa are taxon incertae sedis, morphotaxa (including, among others, ichnotaxa), and collective groups which are in fact an equivalent of a higher taxon but with the name of genus, created artificially to house species incertae sedis attributable to the respective higher taxa. A subsidiary kind of parataxon is a satellite taxon, which is ascribed to a higher taxon for information purposes only. Parataxa are deficient compared to orthotaxa in that they violate the taxonomy dependent principles of hierarchy and excluded synonymy, but not the type principle.

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