

Cladistics in Palaeontology: Problems and Constraints

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Cladistics was originally developed as a method of analysis of the present-day diversity pattern, and some problems are arising when it is applied to the palaeontological record. The most important difficulties are connected with 1. the different time scales (phylogenetic scale in cladistics, geological or physical scales in palaeontology where neither paraphyletic taxa nor chronotaxa can be excluded accurately); and 2. the different basic levels for establishment of terminal branches (the single present-day level in cladistics and numerous successive levels in palaeontology). Both modified versions of cladistics and complementary methods have to be developed to describe fossil biodiversity in an adequate manner.

Key words: cladistics, phylogenetic hypotheses, palaeontology

This is not an attempt of a consistent and exhaustive analysis of the problems arising when cladistic methods are used in palaeontology. I would like to accentuate here only some points which are often ignored and which, in my view, are confusing.

First of all, a few words on the philosophy of science. The basis of phylogenetic systematics seems to be simple and logical. Biology after Darwin is an historical science *par excellence*, unlike, say, physics. It means that the characteristics of objects are considered as originated in the course of continuous evolutionary transformations and determined not only by the nearest preceding stage but by the entire evolutionary sequence. This suggests in particular that biodiversity may be ordinate in accordance with evolutionary history. Any biological object has its own unique history which makes it unique in itself; this allows discrimination between objects. The objects multiply and diverge in time so that any different objects have a common interval in their history because once they were the same object. This permits establishing relationships between objects.

This approach would be excellent, indeed, if we could observe evolution. However, it can not be observed directly; it may be only reconstructed in a speculative way on the basis of its resulting pattern. Any reconstruction of a unique process is *an ad hoc* hypothesis. This kind of hypotheses, generally regarded as not being respectable in physical sciences, is unavoidable in any historical discipline including modern biology. An attempt to reproduce consistently the logic and methodology of physics in

biology seems to be worthless until the biological paradigm remains evolution-oriented. Though the term "evolution" is used in physical sciences as well, it is taken in a different sense. The essential prerequisites of evolutionary hypotheses in biology are the axioms of uniqueness, irreproducibility, and irreversibility of evolutionary history; if these preconditions were not obeyed, the basic concept of monophyly would become senseless. No of astronomers consider similar stars as having originated from a common ancestor; these stars are believed to have originated from similar precursors in a similar way. Evolution of stars, rocks, relief, etc., is not unique but reproducible; this is the main difference between the evolution concepts in biology and in other natural sciences. The evolutionary uniqueness of biological objects pose some difficulties because the general methodology of modern science is oriented to reproducible events. When certain methodological frameworks in biology are substantiated with an appellation to this physicalistic paradigm they may fall outside biology; that is why we have to prove each of them accurately from the biological point of view.

The universal scientific method is reduction, which is a choice of a few aspects of reality which are conventionally considered as significant and a creation of models based on them while all other aspects are neglected. There are no universally tenable reductions, and the choice of one or another sort of them depends on the challenge. We never can take all aspects into account but we may make our choice optimal for particular classes of problems. Any kind

of models has its own limits of applicability. To expand an approach outside its original field and at the same time to avoid incorrect generalisation of the basic model we need some, and sometimes rather radical, modifications of the framework of modelling.

Cladistics have been developed originally as a method of analysis of the taxonomic pattern in phylogenetic or, more exactly, the genealogical aspect. In a few decades it has become the dominating methodology in phylogenetics as well as in taxonomy. Other biological disciplines attempt to adopt the same approach with more or less success. In fact, palaeontology is one of the newly exploited fields of cladistics since the latter deals primarily with living taxa; the phenomena, which can be discovered only in the fossil record, were largely ignored in the basic concept of cladistics. Even now in cladistic analysis fossils are usually either taken as equivalent to the modern taxa or omitted. Being a palaeontologist, I'll not consider the latter solution; and the former one is inaccurate. If cladistic methods are applied to fossils, much accuracy is necessary to avoid confusing interpretations, and the basic model will have to be modified. Numerous technical difficulties also exist.

There are two very serious fundamental problems. One originated from the different time scales used. Cladistics constructs its own time scale which may be called the phylogenetic one; this scale is based on the succession of cladogenetic events, that is on the subsequent phylogenetic branching (divergence). When no such events occur (or they are unknown), the time interval is taken as zero; the lines between the nodes of a cladogram if they are shown at a time scale as illustrated at Fig. 1,a, are in fact misleading because the time interval between two subsequent branching events is of no importance for cladistics. This allows us to consider each two sister groups as a simple fork of a tree: the both are originating at the same phylogenetic time point. Palaeontology deals either with geological or with physical (so called "absolute") time scales. We don't know any mechanism that can synchronise any of those scales to arrive at the time of acquiring apomorphies in two diverging populations. To the contrary, it seems to be obvious that a time lag should exist (Fig. 1,b). When we construct a phylogenetic hypothesis based on the present-day diversity pattern we may well ignore this lag. The question is, however, either the same approach is appropriate at geological and/or physical time scales. The likely answer is "no" for two reasons.

Firstly, the basic units of taxonomy, the species, may be long-living. At least, this is true for morphologically recognisable species. About a half of the Pliocene insects known are assigned to present-day species (e.g., OKE, 1957; BEER, 1967; WAGNER, 1967, 1968; HEIE, 1968, 1995; WEIDNER, 1968; GERSDORF, 1969, 1971, 1976; HEIE & FREDRICH, 1971; HOPKINS et al., 1971; MATTHEWS, 1974, 1977; KRUGER, 1979; KISELYOV, 1981; BENNIKE & BÖCHER, 1990; MATTHEWS & al., 1990). Of course, some identifications may be in doubt. For example, NEL & PAICHELER (1993) in their revision of fossil calopterygid damselflies wrote that the placement of a Pliocene Japanese fossil to the living species *Calopteryx atrata* SELYS by ESAKI & ASAHINA (1957) is possible but not certain. On the other hand, some species described as extinct have been synonymized subsequently with modern ones, like one of the two Pliocene Alaskan species of the staphylinid genus *Micropeplus* described by MATTHEWS in 1970 (COOPE, 1994). Besides morphology, the species constancy is supported in some cases by finds of plant galls indicating biochemical and physiological stability of the gall-inducing species (e.g. MARTY, 1894; STEINBACH, 1967; STRAUS, 1967, 1977; HEIE, 1968; KRUGER, 1979). There are few records of living insect species from older deposits (e.g. BOGACHEV, 1940; MASNER, 1969; DOYEN, POINAR, 1994; PETERS, 1994); however, this may well be an artefact of an experts' care in interpretation. Not infrequently a palaeontologist writes something like "the fossil can not be distinguished from the living species *B-us c-us* and I designate it as a *B-us* species". There are also some evidence for a long-time existence of extinct species. For example, some insect species are common for the Purbeck Limestone Group (Berriasian) and the Wealden Supergroup (mainly Hauterivian to Barremian) of England (CORAM & JARZEMBOWSKI, 1999; Dr. A.G. PONOMARENKO, pers. comm.); the physical time gap between the richest fossiliferous Purbeck and Wealden layers is 15 Ma. There are roach (VRSANSKY, 1997) and mycetophilid (BLAGODEROV, 1998) species common for Baissa in Siberia and Bon-Tsagan in Mongolia which correspond roughly in age to the English Purbeck and Weald, respectively. I, myself, have failed in two cases to find any differences between the Oligocenous weevils from Aix-en-Provence, France and Upper Miocenous weevils from Agrigenti, Sicily (ZHERIKHIN, 1992); the physical time interval is about 20 Ma. And the insects seem not to be the

most conservative organisms. SELNICK (1931), a great authority in mite taxonomy, has identified as still living ones a number of oribatids from the Baltic amber; the physical time gap is about 40 Ma. Most living insect species recorded from the Baltic amber are shown to be either fakes (PALMER, 1993) or misidentified (RÖSCHMANN, 1998) but some cases still remain in doubt (like the chironomid *Buchonomyia thienemarmi* FITTKAU mentioned from the Baltic amber by MURRAY, 1976)

If about 50% of living insect species exist since the Pliocene, it is improbable that none of them gave rise to any different species during at least 5 million years. Among the insects few possible cases of coexistence of the ancestral and the derived species in time are described (PETERS, 1994) but in other organisms with more complete fossil record this situation is better documented (e.g., NEVESSKAYA & al., 1986; NEHM & GEARY, 1994). If so, the ancestral species become paraphyletic and should be split into two (or more, if there were more than one cladistic event) species in a cladistic system; but such a splitting in absence of any detectable differences is senseless and inoperable. And if we accept paraphyletic taxa at the species level there are no more logical bases to reject them at higher taxonomic levels. Thus, firstly, the paraphyletic taxa can not be rejected when we deal with fossils, and, secondly, an estimation of the minimal geological or physical age of a taxon based on fossil finds of its sister group is inaccurate. Such fossil finds do not mean necessarily that the sister taxon existed during the same time interval, it may well be younger.

Another point is that not all evolutionary events observable on a physical time scale are divergent. In cladistics phyletic evolution within a lineage is ignored, and all apomorphies accumulated for a more or less long interval of physical time between two cladistic events are attributed to the same taxon (Fig. 1,c). This is of no importance when only present-day diversity pattern is analysed. In palaeontology such a procedure is confusing because phyletic evolution is documented by the fossil record, and this aspect of evolution may not be ignored, for example, in stratigraphy. Thus palaeontology needs in distinguishing of taxa lacking sister groups which is impossible in cladistics. Cladistic criticism of the chronospecies concept (e.g. WILLMANN, 1997) is based on the presumed impossibility of dividing a gradual phyletic line into species and on the biological species concept postulating the reproductive isolation as the only species criteria so that the

existence of chronospecies can not be demonstrated. Both points seem to be invalid. The acquiring of apomorphies may be used in phyletic lines to discriminate between chronospecies as well as in the case of divergence. Speciation time is likely much shorter than the time of species existence according to the well-known punctuated equilibrium hypothesis (ELDREDGE & GOULD, 1972), and the phyletic evolution is not gradual. The biological species concept is of a limited value in taxonomic practice: we do not use different taxonomic approaches for sexual and asexual species, we rarely prove our species concept with crossing, we rarely have problems with allopatric species never crossing in nature, etc. If the identity of a species had to be argued with crossing, we could not assign to the same species not only the present-day and Pliocene populations but also the population from which the LINNE'S or FABRICIUS' type specimen have been taken. If species exist in time, we have no a priori base to limit the physical time interval of their possible existence and should classify them in accordance with the available features (mostly morphology); if not, it is impossible to assign to one species any generations not overlapping in time independently from the time lag between them.

Hence the phylogenetic time scale is inadequate for important classes of palaeontological problems, and palaeontology badly needs methods allowing the description of the evolutionary process in both geological and physical time scales.

Another source of confusion is that cladistics has the single time level taken as the fixed absolute point for estimation of the rank of taxa; even when in some versions of cladistics traditional taxonomic ranks are not used, the problem of equivalent clades still exists and is resolved in the same way. The procedure is quite simple: both sister groups must have the same rank. Let us consider the results of applying this procedure to taxa at the geological time scale. There are some living species placed into the same genus. We can classify them cladistically into subgenera, species groups, and so on (Fig. 1, a). The same situation existed, say, in the Jurassic. From the point of view of a Jurassic observer, the taxa shown at the diagram 1,c, below were the species of the same genus. Most of them have disappeared in the Jurassic; only one species has given rise to a successful Cretaceous group (Fig. 1, c). This group had to be considered as a genus from the point of view of a Cretaceous observer, thus the Jurassic genus turned to be paraphyletic, and each extinct Jurassic

species or, at the best, each small species group, has been placed into a genus of its own. All but one Cretaceous species had no Cainozoic descendants. And now a Cainozoic cladist is repeating the same procedure. Nothing could be changed with either Jurassic or Cretaceous extinct species as such after their extinction; any changes in their postmortal fate depend on the fortune of a single sister clade which elevated the rank of its less fortunate sister and cousins. To do so, we make any analysis of extinction pattern senseless because the rank of disappearing taxa depends on the future success of the group and not on their relationships with other terminal branches in the time of extinction. Studies in extinction pattern are often criticised by cladists as based on paraphyletic taxa (e.g., PATTERSON & SMITH, 1987, 1989); but at the time of their extinction they were not paraphyletic because all of them were terminal. And why, if a tool is useless for an operation we are needing it for, should we use this operation instead of refusing the tool and look for a different and more suitable one?

There are many other difficulties though I believe the above-mentioned problems are the most frustrating ones. On the other hand, some problems often mentioned in literature seem to be in fact unimportant. The problem of the constitutive and the diagnostic characters provides a good example. The essence of the problem was clearly formulated by HENNIG (1981, pp. 20-21) who claimed that the taxonomic position of a fossil has to be argued with constitutive characters (the autapomorphies of the taxon) while for living organisms we may use both apomorphies and plesiomorphies as the diagnostic characters. This requirement seems to be too rigid. Any classification is a hypothesis on the relationships between the taxa; and any hypothesis have to be argued on the basis of available evidence and falsifiable. When we have failed to find any ground to classify a fossil other than its symplesiomorphic similarity with certain previously known taxon, we may suppose that it belongs to this taxon; doing this we predict in fact that when better preserved fossils (or additional synapomorphies of the taxon) will be discovered they will support our hypothesis. Such a hypothesis is falsifiable and has to be regarded as an acceptable one before the arguments against it will be obtained.

One more important question concerns the parsimony. The OCCAM'S razor is one the basic scientific principles; but, like any principle, it has to be used correctly. We may propose that evolution follows

the most economic way but this is only a hypothesis which should be tested; palaeontological record shows that it is not necessarily so. Then, we may propose that the probability of a non-economic way is low; this hypothesis again should be proved. To testify parsimony as a working hypothesis in phylogenetics we have to compare the results of phylogenetic analyses based on it with palaeontological data for a reasonably large set of taxa well represented in fossil record. Similar analysis have been never attempted. It seems that at least in one field of historical biology, namely in biogeography, the parsimony principle is inappropriate because of an inadmissibly high probability of misinterpretation, perhaps about 50% or more, as a result of numerous local extinction events. For instance, the famous "southern" or "Gondwanian" distribution pattern is very often only the pattern of survival in the Tertiary, and may not manifest the past restriction of a taxon to the Gondwanaland (ESKOV & GOLOVATCH, 1986). Even in the course of the last 100 000 years the distribution of many taxa changed quite radically more than once (in Eurasia practically from the Pacific to the Atlantic and back) (e.g. COOPE, 1994). Because of a highly complicated distributional history any models of panbiogeography, vicariance biogeography, area cladistics, etc., so popular in the last decades, are, in my view, of a very little if any real value, *if* they are based on the present-day distribution and not tested palaeontologically.

All the above does not mean that cladistics is useless for studies on fossil record. In fact, some cladistic ideas have been widely accepted in palaeontology well before Hennig: in biostratigraphy, for example, it is a usual practice when younger taxa ("apomorphies" of the assemblage) are considered as more informative for aging of sediments than older ones which may be inherited from the previous geological time interval as relicts ("plesiomorphies").

And again a few words on more philosophic topics. In the West we believe that man can successfully adapt the world to himself. The eastern view is that we should adapt ourselves to the laws of the World to be more adequate to it. To be adequate to inanimate things, physics has developed its mechanical system of models. This approach has been taken as a standard for science as general. However, to be adequate to the living world, biology has to develop an organic system of models. Any organism is adapted to an achievement of a number of challenges such as feeding, growth, development, self-

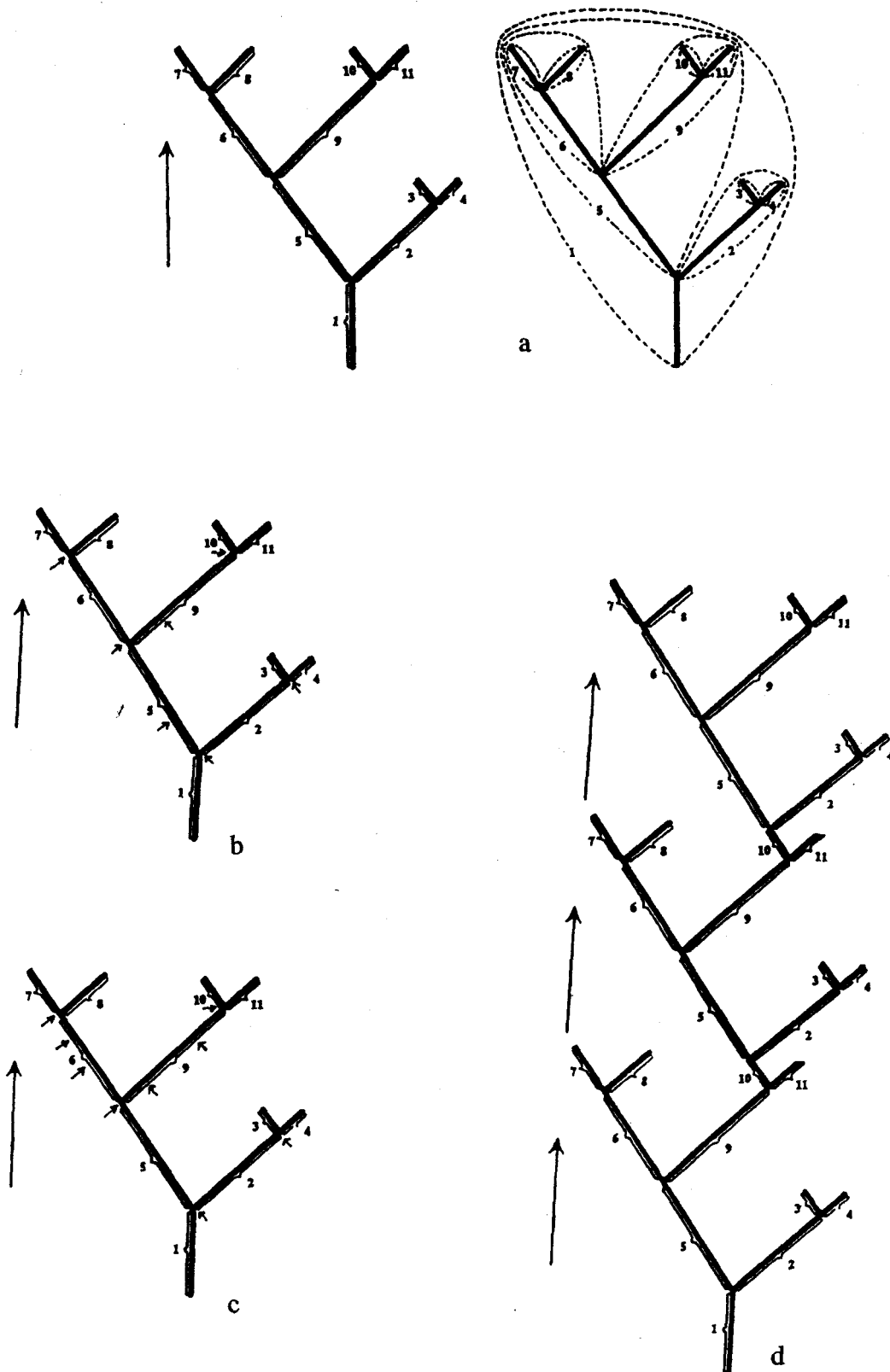


Fig. 1. Diagrammatic sketch of phylogenetic branching illustrating some problems of cladistic interpretations in palaeontology (based on Griffiths, 1974, Fig. 1, modified), a, common cladistic interpretation of observed biodiversity pattern in phylogenetic time, taxa indicated with figures, time vector with the arrow; b, acquiring of apomorphies (small arrows) indicated at physical time scale, note that it does not correspond to cladistic units; c, the same, modified to add phyletic events; d, phylogenetic branching pattern repeating at geological time scale (see comments in the text).

protection, reproduction, and so on. None of them are achieved perfectly. Any organism is a highly compromised system of adaptations to different challenges (an adaptive compromise after RASNITSYN, 1987). This is the very essence of any organic system. Like a living organism, Linnean taxonomy is perfect in nothing; however, it is good enough for everything in biology. Cladistic taxonomy is much more effective in its restricted field; however, it is much less universal. The more specialised a structure is, the less it may be used for other functions. Cladistics is no more than one of the specialised organs in the complex organism of taxonomy, and even the most simple parasite can not consist of a single organ. Cladism is so attractive mainly because of its well-based logic and well-developed formal methods. This doesn't mean that other approaches should be rejected; they should develop their own logic and methods to make them as perfect as the cladistic ones. Cladistics is not a universal lock-pick but a skilfully made opener perfectly fit to a single door only. We should try both to adapt methods of Cladistics to a wider range of problems and to develop other approaches which will be not alternative but complementary. In this connection the version of cladistics proposed by BROTHERS (1975) and gradistics recently proposed by LYUBARSKY (1998) may be mentioned as examples.

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