Temporal paralogy, cladograms, and the quality of the fossil record

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ABSTRACT

Previous attempts to quantify the adequacy between phylogenetic trees (cladograms with a temporal dimension) and the fossil record failed because of inappropriate statistics. A general explanation for this failure is based on a hierarchical perception of the temporal scale. When time is conceived as a hierarchy and not as an arrow, it can be expressed by a pectinate-shaped tree. Comparison between cladograms, based on morphological or molecular data, and time represented by a pectinate tree leads to the discovery of temporal paralogy, a phenomenon analogous to molecular, morphological, and biogeographical paralogies and already shown in these fields to bear severe difficulties.

KEY WORDS
Palaeontology,
cladistics,
temporal paralogy,
quality of the fossil record.

RÉSUMÉ

Paralogie temporelle, cladogrammes et qualité du registre fossile.

Les essais antérieurs destinés à quantifier l'adéquation entre les arbres phylogénétiques (cladogrammes avec une dimension temporelle) et le registre fossile ont échoué par l'utilisation de mesures inadéquates. Nous proposons ici une explication d'ordre général pour rendre compte de ce fait. Cette explication est fondée sur une perception hiérarchisée de l'échelle temporelle. Lorsque le temps est conçu comme une hiérarchie et non comme une flèche, il peut être représenté par un arbre pectiné. La comparaison entre des cladogrammes, qu'ils aient été établis à partir de données morphologiques ou moléculaires, nous a menés à la découverte de la paralogie temporelle, un phénomène analogue des autres instances de paralogie déjà décrites (moléculaire, morphologique et biogéographique) qui ont déjà montré des implications importantes.

MOTS CLÉS
Paléontologie,
cladistique,
paralogie temporelle,
qualité du registre fossile.

INTRODUCTION

The adequacy of the fossil record has been the source of heated debate among palaeobiologists. Is the fossil record good enough to allow for a direct reading of phylogeny in the rocks? An old debate related to this question can be found in Harper & Platnick (1978). This debate illustrates the dichotomy that divided palaeontologists in connection with the spread of phylogenetics in the 1970s: palaeontologists who choose a logical criterion to erect hypotheses of relationships (e.g., Schaefer *et al.* 1972) and palaeontologists who followed stratigraphy to demonstrate evolutionary scenarios (e.g., Harper *in* Harper & Platnick 1978; Gingerich 1979). The latter argued that the fossil record was, in certain circumstances, complete. We notice that today geochronologists themselves conclude that "the record is hopelessly incomplete" (Clarke 2003: 550). Cladists also rejected stratigraphy as informative for establishing phylogenetic relationships and use only intrinsic data to construct cladograms. Yet a question arose in the fields of cladistics. If a cladogram is interpreted as a phylogenetic tree in terms of propinquity of descent, what temporal information can be retrieved from a cladogram? A related question is: what is the connection of a given cladogram to the temporal information yielded by the fossils?

According to Hennig (1966), the founder of phylogenetic systematics (cladistics), temporal information in a cladogram (a tree, representing hierarchical relationships among taxa) is an attribute of nodes, not of branches (Fig. 1). Because nodes define a hierarchy of nested taxa, evolutionary time is also hierarchical. In this paper we show that when temporal hierarchy is formalized its shape is that of a pectinate tree. Thus, the fossil record may unambiguously document the history of life only when the shape of cladograms is also pectinate. If not, the temporal information, inherent to evolutionary narratives, is blurred. Phylogenetic trees that are not strictly pectinate imply multiple temporal hierarchies, a phenomenon comparable to molecular paralogy (Fitch 1970). In this paper we argue that the temporal information conveyed by the fossil record has been largely over-rated and, to date, all measurements of its quality are dubious if not pointless. Even more paradoxically, the improvement of the fossil record can lead to a decrease in the temporal information of the cladograms.

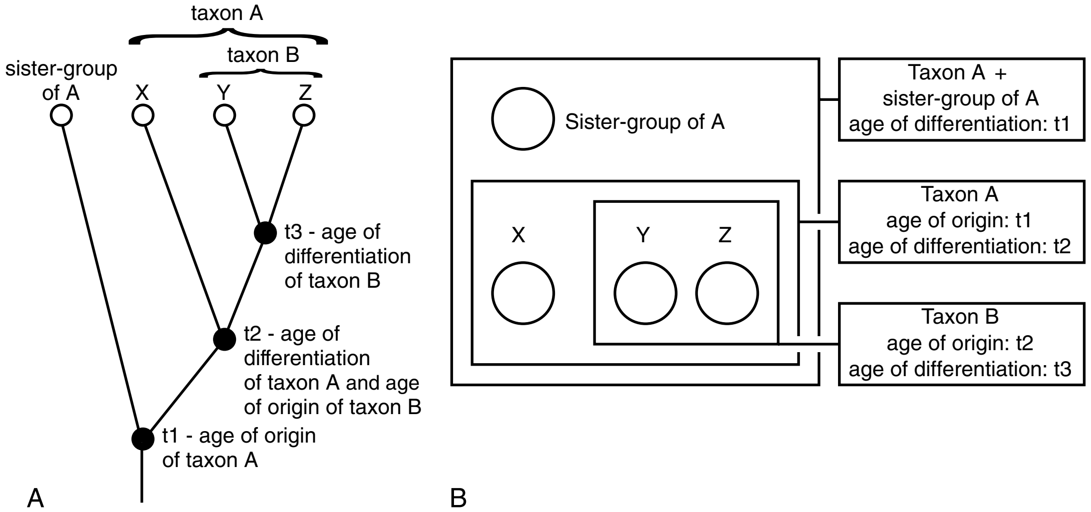

FIG. 1. — Cladogram and time; **A**, the temporal information contained in a cladogram according to Hennig (1966), modified from Hennig in Tassy (1999); **B**, same cladogram represented as a hierarchy (Venn diagram) showing that temporal information is relevant to nodes and not to branches. Phylogenetic trees usually conflate the age of origin and age of diversification.

TREES AND TIME

In the introduction to his book devoted to "Deep Time" and the information conveyed by the fossil record, Gee (1999) abruptly stated that "many of the assumptions we make about evolution, especially concerning the history of life as understood from the fossil record, are baseless. […] Once we realize that Deep Time can never support narratives of evolution, we are forced to accept that virtually everything we thought we knew about evolution is wrong. […] To see paleontology as in any way 'historical' is a mistake in that it assumes that untestable histories have scientific value. But we already know that Deep Time does not support statements based on connected narrative, so the claim that paleontology can be seen as an historical science is meaningless: if the dictates of Deep Time are followed, no science can ever be historical. […] Without cladistics, paleontology is no more of a science than the one that proclaimed that the Earth was 6,000 years old and flat […]".

We agree with Gee's views about deep time, palaeontology, and the inferred pattern of relationships retrieved by cladistic analysis. However, palaeontological data implicitly incorporate the notion of time. As systematic palaeontologists, we consider that fossils may be conceived as organisms with an extrinsic attribute represented by their age. Hence, the only direct link between time and hierarchical biological patterns is provided by the fossil record. As a consequence, the virtues of narratives about historical processes have always been considered as confusing. Dubious or irrelevant narratives about historical processes, as stated above by Gee (1999) have long been addressed: deep time, even at a small scale, always implies a statistically non-significant fossil record because of the paucity and the irregular nature of the sample (Darwin 1859; Simpson 1961).

Therefore, Gee's statement may be put in this framework, and "historical science" should be redefined, so that it becomes compatible with what we know about patterns of relationships of organisms and their parts.

Hennig (1966: 161-169) realized that the inferred age of origin of a monophyletic group is identical to that of its respective sister-group; therefore the age of clades is an attribute relevant to nodes (Tassy 1999). As a consequence, the age of a clade refers to a degree of inclusiveness (Fig. 1). Each node defines the minimum implied age of origin for a monophyletic group, and the next, less inclusive, node defines its age of diversification. The counter-intuitive consequence is that cladistic time is not directly connected to branches, branch-lengths, or other branch-dependent measurements. In a cladogram, time is distributed in a hierarchical way. In other words, time is distributed in the hierarchical framework provided by the cladogram according to the degree of inclusiveness of clades. The more inclusive a node, the older its origin is and, logically, the origin of the clades must have occurred earlier than the diversification of their parts.

The conformity between the degree of inclusiveness of a clade and its minimum age implied by the fossils can provide information about the quality of a particular fossil record. This, however, has to face the problem of comparing hierarchies and the "arrow of time" (linear data). Relatively to this topic, recent history of cladistics may be subdivided into three periods. Firstly cladograms were considered as the ultimate results of the analysis even when fossils were included. In these trees time did not appear explicitly. Secondly, cladograms were situated in the time-dimension and treated as phylogenetic trees. Thirdly, the adequacy between trees and the fossil record was measured through several indices. A considerable number of measurements has been proposed during the last decade (see Nature-debates 1998). None of them have succeeded in solving this constraint, that is, the comparison between hierarchical and linear data (Siddall 1996, 1997; Pol *et al.* 2004). Current indices are biased by the shape of trees and it has been pointed out that pectinate trees always show better fits even if the fossil record is not better than that of non pectinate trees (Siddall 1996). We propose that a hierarchical concept of time offers a solution to this problem.

TIME: THE HIERARCHY, NOT THE ARROW

The "arrow of time", used by palaeontologists, is the geological scale. It can be considered as a mathematical structure, which consists of several, ordered partitions of relative time (eras, periods, epochs, stages, etc.). Partitions are classificatory structures which have two properties: 1) each individual (each age, however defined in absolute time, e.g., 10 Ma, 72500 yrs) belongs to one temporal class (i.e. Cambrian, Cretaceous, Miocene); and 2) there is no intersection between classes. Thus, we only need to know if a temporal period is younger or older than another one.

Each geological period in the partition is defined by a temporal extension (the span between the beginning and end of a temporal class). Its beginning is identified by an event (e.g., the first appearance in the record of a given species); its end is defined by the event that defines the beginning of the following period.

Now, if one considers the event which defines the beginning of any geological period, then this partition can be interpreted, without any loss of information, as a hierarchy – a classificatory structure which differs from partitions in that the intersection between two classes is empty or one of the classes. In this temporal hierarchy, the intersection between two temporal periods is always one of these periods (Fig. 2). For instance, the intersection between Phanerozoic and Cambrian is Cambrian. Phanerozoic is a hierarchical concept relatively to Cambrian; but Precambrian is not, relatively to Cambrian. The geological events on which the definitions of the origin of the respective geological periods are based are translated into a hierarchical structure. Being a mathematical hierarchy, the temporal hierarchy may be interpreted as (is isomorphic to) a pectinate tree. Temporal hierarchy specifies that each temporal period has differentiated from a longer, more general or inclusive one. Geologists and biostratigraphers, for example, use a temporal hierarchy when they consider the Cenomanian (upper Cretaceous, 99 to 92 Ma) as a hierarchically differentiated period in the more

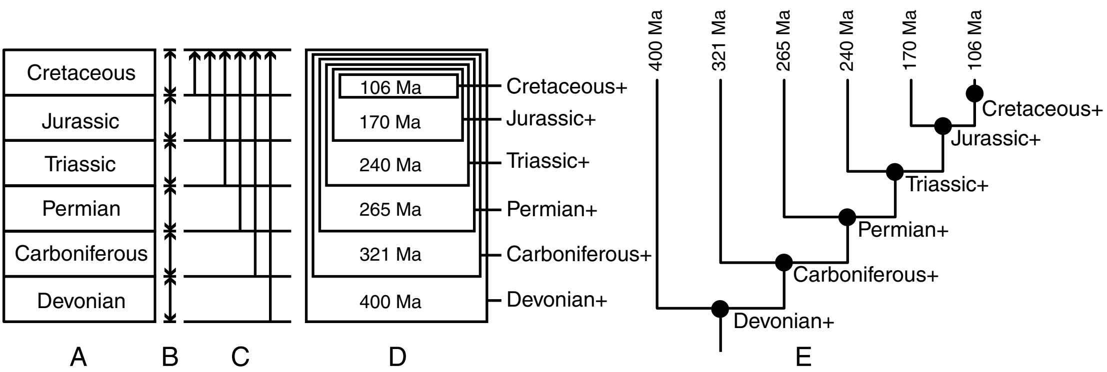

FIG. 2. — Time seen as a hierarchy; **A**, in a geological time scale geological periods are defined as an ordered partition; **B**, with linear time – "time arrow" – the same event is used to define the beginning of a period and also the end of the previous one. In order to define the temporal hierarchy, each event defines only the beginning of a period; **C**, geological periods are defined by their temporal extensions; **D**, temporal hierarchy as a Venn diagram derived from C. Particular ages are shown as individuals belonging to each class. We symbolize the new hierarchical representation of geological periods with the symbol "+" at the end of their name; **E**, temporal hierarchy represented as a tree – "time tree" –, showing that it is pectinate and that geological periods are nodes. The age of each fossil specimen, shown as a terminal, is the least inclusive temporal class that contains it.

general Cretaceous (143 to 65 Ma). When they consider Cenomanian relatively to Turonian (92 to 88 Ma) they follow the linear dimension of the arrow of time.

This hierarchical distribution of time in cladograms derived from the analysis of morphological or molecular data illustrates a phenomenon which is well known in molecular phylogenetics, called paralogy. The concept of paralogy was first proposed by Fitch (1970) from the analysis of sequences of α and β haemoglobins, which showed that haemoglobins of different organisms were more closely related than were α and β haemoglobins of the same organism, ensuing a repetition of the terminal taxa in the resulting tree. Molecular paralogy is interpreted as the result of duplication of an ancestral gene into two or more genes. Nelson & Ladiges fruitfully applied the concept of "geographical paralogy" to biogeographical data (Nelson & Ladiges 1996).

Taxa that are geographically widespread or several taxa that inhabit the same area leave artefactual duplications within areagrams (Ebach 1999). These taxa duplications are redundant (geographically paralogous). In the same way, we consider that our hierarchical interpretation of geological time is also illuminated by the concept of paralogy (Fig. 2). Temporal data associated with a cladogram can be represented by a tree where the terminals are the ages of fossil organisms and the nodes are the inferred ages of origin and differentiation of taxa. We call this representation a horogram. When a temporal period (a node) appears several times in a horogram, it defines an instance of a new class of paralogy. We term this new class of paralogy temporal paralogy. Note that the shape of the "temporal hierarchy" can only be pectinate. Thus, instances of temporal paralogy correspond to nodes that are not pectinate or, in other words, that are balanced. Balanced nodes of a horogram lead to two other nodes; we will term these nodes *paralogous*. Pectinate nodes of a horogram lead to a terminal (a particular age) and a period (a node); we term these nodes *orthologous*. Temporal paralogs are semi-independent: the age of origin of sister-groups is the same but sister-groups have their own age of differentiation *sensu* Hennig (1966; Tassy 1999), and the temporal development on each sister-lineage is independent.

This explains why measurements of fit of cladograms to stratigraphy proposed in past years (Norell & Novacek 1992; Benton & Storrs 1994; Huelsenbeck 1994; Wagner 1995) are shape-

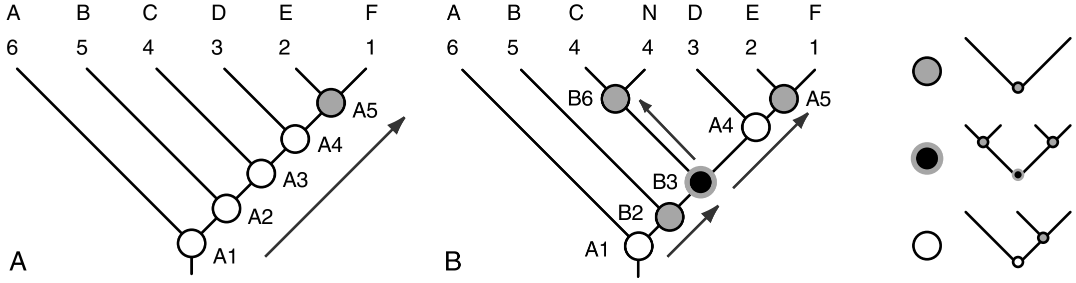

Fig. 3. — Temporal information and cladograms; **A**, maximally informative cladogram of taxa (A-F) and their ages (6-1). All nodes are orthologous, and the ages of the fossil specimens can be either consistent or not with the temporal hierarchy; **B**, the effect of a better knowledge of the fossil record by addition of the age of a supplementary taxon (N, 4) is the decrease in temporal resolution. The number of informative (orthologous) nodes decreases (white circles) as temporally ambiguous nodes appear (shown as grey circles) node leading to two terminals or a terminal and a paralogous node, the black circle corresponds a new paralogous node, indicating a temporal paralogy. The ages of sister-taxa (C, N) and (D, E, F) are temporal paralogs. Each arrow represents a semi-independent temporal hierarchy.

dependent, and thereby provide ambiguous or irrelevant results for cladograms which are not strictly pectinate. The ambiguity introduced in these measurements by more or less balanced cladograms has already been pointed out by Siddall (1996, 1997, 1998), Wills (1999) and Pol & Norell (2001). We consider the relevance of these measurements as refuted because they fail to identify instances of temporal paralogies and to formalize the effect of the shape of phylogenetic trees. A paralogous node (Fig. 3B, node B3) does not carry any information in terms of respective inclusiveness (that is, of relative age) of its two differentiated sister-groups (Fig. 3B, nodes A4 and B6). For instance, node A4 of Fig. 3B is not more or less inclusive than node B6 of the same figure and the fit of the ages of both nodes to stratigraphy is irrelevant. The question of their relative age of origin is pointless, as is the question of the fit of a balanced cladogram to stratigraphy.

The temporal information conveyed by cladograms is hence of two different kinds. Pectinate parts of horograms can be compared to the temporal hierarchy in several ways (Siddall 1996; Zaragüeta Bagils & Lelièvre 2001). Paralogous nodes support information about temporal paralogies, i.e. diversification into semi-independent temporal hierarchies, but they do not allow any other inference. Orthologous nodes (Fig. 3A, nodes A1-A4; Fig. 3B, node A1 and A4) convey chronological information. The orthology of nodes depends naturally on the taxonomic sample; they are connected to one peculiar tree. Figure 3 shows an example of such a case. Because of the improvement of the fossil record (Fig. 3B), an orthologous node (Fig. 3A, A3) becomes paralogous (Fig. 3B, B3). Hence, the node looses its chronological information. This means that the number of paralogous nodes cannot decrease, whilst the number of orthologous nodes can decrease or increase. The other two kinds of nodes (Fig. 3), i.e. nodes connecting two terminals and multifurcations, do not convey temporal information, but may become orthologous or paralogous with a richer taxonomic sampling.

Our formalization of tree shapes in relation to time shows that the quantity of temporal information conveyed by cladograms is proportional to the number of orthologous nodes.

MORE DATA, LESS INFORMATION?

We elaborate on the paradox raised above, connected to the fact that temporal information yielded by a cladogram cannot be used *per se*, to qualify a taxon in general. The addition of more terminals can reduce the proportion of orthologous nodes because of the identification of previously unrecognized temporal paralogies. Accordingly, a poor fossil record may overestimate the fit of phylogenetic hypotheses to stratigraphy

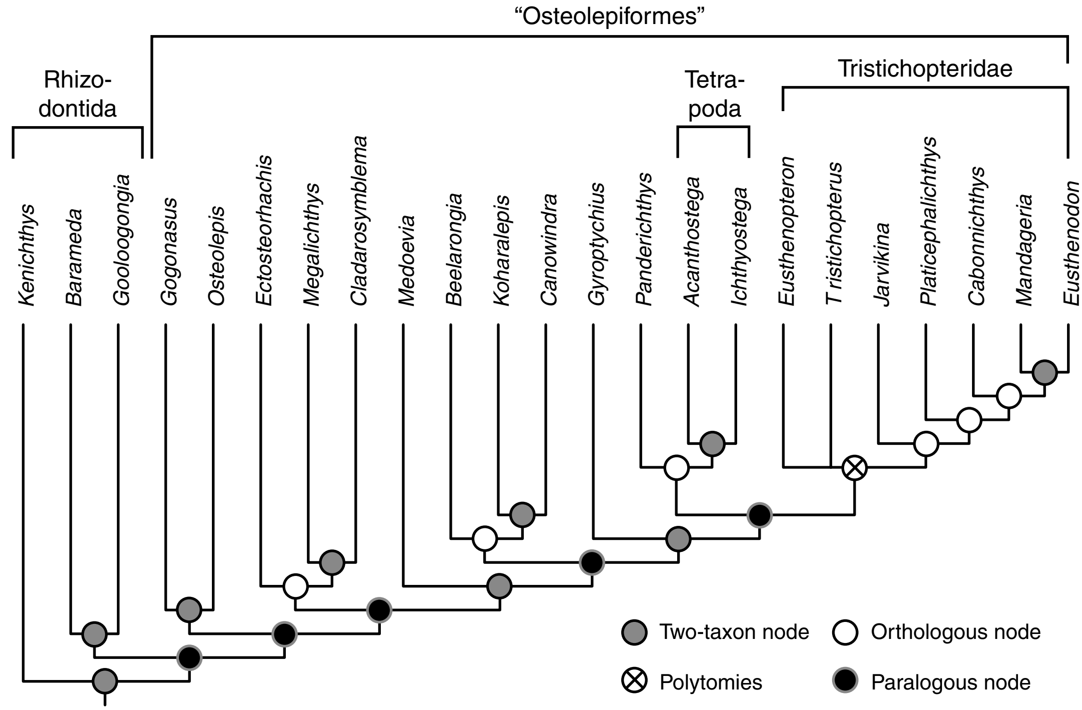

FIG. 4. — Temporal paralogy and the origin of tetrapods. The possibility of osteolepiforms being ancestors of tetrapods has been reinterpreted based on a parsimony analysis (Ahlberg & Johanson 1998). Among osteolepiforms, the Tristichopteridae appear as the closest relative to the Tetrapoda. The common ancestor of both groups is represented by a paralogous node, and according to temporal hierarchy the relative inclusiveness of each of the sister-groups cannot be decided. As a consequence, the Tetrapoda can be supposed to have occurred before the first appearance of osteolepiforms (Eifelian). There are no arguments to see osteolepiforms as possible ancestors of tetrapods, if this question has any meaning when argued from a parsimony analysis.

and a better knowledge of the fossil record can lead to a decrease in the temporal information contents of a phylogenetic hypothesis (Figs 4B; 5). A similar problem may arise if some of the terminals are groups (taxa with an implied internal hierarchy) and not particular organisms, or "species" (in the sense of the smallest recognized unit with an identified hierarchical structure). Making explicit the contents of these terminals (i.e. subdividing one terminal into two or more subterminals) changes the data (the taxonomic sample) and leads to the modification of both the shape of the cladogram and its temporal information content. Thus, one should be aware that the narratives about the relevance of the fossil record apply to one particular cladogram. Generalizations on taxa issued from one cladogram are universal only if in that cladogram terminals are organisms or "species" (smallest recognized unit or LITU-least inclusive taxonomic unit, Pleijel & Rouse 2000).

CONCLUSION

Our formalization carries some interesting consequences. One concerns the dates of origin of clades inferred from hypotheses about rates of evolution of molecular sequences according to a palaeontological calibration. These often use the first appearance in the record of a taxon as the palaeontological age of the taxon, independently of any sister-group hypothesis concerning the taxon in question. Such age estimations are erroneous (Hennig 1966). Moreover, even if a cladogram is used as the basis of the calibration, these

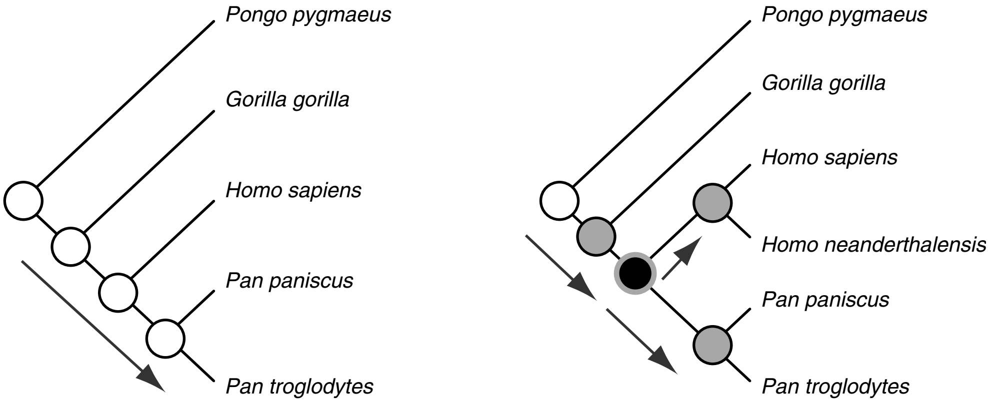

FIG. 5. — Pectinate cladogram illustrating Pongidae relationships as currently understood; **A**, all nodes are temporally informative (orthologous). The age of diversification of *Pan* is more recent than the age of origin of (*Homo*, *Pan*); **B**, the addition of a fossil taxon (*Homo neanderthalensis*) defines a paralogous node and two new arrows of time (black arrows). Consequently the fit of ages of diversification of both *Homo* and *Pan* to stratigraphy is meaningless.

techniques assume that any cladogram conveys equal temporal information about the origin of clades. As we have shown, only orthologous nodes of different ages eventually provide this information. Average temporal information supported by cladograms is thus generally largely over-rated (Figs 4; 5). Therefore, we conclude that dating ages of origin of taxa with molecular phylogenetic trees where fossils are used as calibration points, is, at best, ambiguous (e.g., Sanderson 1997; Thorne & Kishino 2002).

A second consequence concerns palaeontology. We surveyed the datasets available in the Cladestore database (Benton 2002) and found that 63.5% of the nodes conveyed by the cladograms are temporally uninformative (paralogous, two terminal nodes or polytomies). We did not find any correlation between the taxonomic sampling, in terms of number of terminals, and the temporal informative content (correlation coefficient, $R^2 = 0.29$). The concept of temporal information and the connection between trees and stratigraphy remain real epistemological problems.

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