Continuous Track Analysis: A New Phylogenetic and Biogeographic Method

John Alroy


Stable URL:
http://links.jstor.org/sici?sici=1063-5157%28199506%2944%3A2%3C152%3ACTAANP%3E2.0.CO%3B2-2

Your use of the JSTOR archive indicates your acceptance of JSTOR’s Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR’s Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

*Systematic Biology* is published by Society of Systematic Biologists. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/ssbiol.html.

*Systematic Biology*
©1995 Society of Systematic Biologists

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2002 JSTOR

http://www.jstor.org/
Thu Aug 15 17:20:24 2002
CONTINUOUS TRACK ANALYSIS: A NEW PHYLOGENETIC AND BIOGEOGRAPHIC METHOD

JOHN ALORE
Committee on Evolutionary Biology, University of Chicago, 5734 South Ellis Avenue, Chicago, Illinois 60637, USA

Abstract.—Continuous track analysis (CTA) can depict reticulate evolutionary patterns in phylogenetics and biogeography. A reticulate connection implies convergence, hybridization, or introgression in an evolutionary graph of taxa and implies dispersal in an evolutionary graph of biogeographic areas. CTA finds graphs that (1) have a minimal number of connections and (2) imply that most character states or taxa have distributions or tracks across taxa or areas (objects) that are continuous, i.e., can be traced across the connections among the objects including that state without traveling through any other objects. Continuous tracks imply either that character states in phylogenies have unique evolutionary origins or that taxa in biogeographic analyses are monophyletic. Relatively simple graphs usually cannot imply completely continuous tracks. Therefore, CTA graphs seek to minimize the number of track fragments, which are locally continuous parts of a track; tracks with more than one fragment are discontinuous. Minimizing fragments is the same as minimizing character-state transitions only if there are no reticulations. Because hypothetical ancestors do little to reduce the number of fragments, CTA tends to place known taxa or areas at internal nodes. A heuristic algorithm analogous to tree bisection–reconnection is used to find highly parsimonious CTA graphs. In phylogenetic analyses, CTA employs a special complementary binary coding convention that serendipitously solves the missing characters/missing data problem. Although the problem of ancestors “inheriting” states from hybrid descendants is irrelevant if reticulations merely represent convergence patterns, CTA includes an optional algorithm that avoids such instances by explicitly identifying ancestors and descendants. CTA was compared with standard parsimony analysis using a data set of 17 Neogene species of North American fossil hippoponine horses. CTA separates the three major clades and illustrates their convergent features with reticulations, whereas standard parsimony analysis groups the three in an unresolved polytomy. CTA also minimizes the number of hypothetical, unsampled ancestors and lineages. [Ancestors; biogeographic methods; dispersal; homology; Hippoponini; hybridization; phylogenetic methods; reticulation.]

Reticulate evolution and biogeographic dispersal are two of evolutionary biology's greatest methodological puzzles. In this paper, a new means of analyzing the patterns created by either of these superficially dissimilar processes is introduced. A unified approach is possible because both reticulating phylogenetic hypotheses and dispersal hypotheses imply more than the smallest possible number of evolutionary connections among taxa or areas. Although this fact has been noted by other authors (e.g., Nelson, 1983), the method presented here is the first to base an explicit parsimony criterion on the idea of minimizing the number of connections. The implications of this criterion are complex and require detailed discussion.

Phylogenetic reticulation has inspired relatively little debate since a symposium on the topic in 1981 (Platnick and Funk, 1983). Several different approaches to the problem were described (Humphries, 1983; Nelson, 1983; Wagner, 1983; Wannatorp, 1983), and the stage seemed set for a synthetic approach. However, even the existing methods have attracted little attention since then (but see Humphries and Funk, 1984; Funk, 1985). The only related developments are in the field of molecular systematics, where several methods are used to recognize ambiguous nodes. However, the split decomposition method of Bandelt and Dress (1992) identifies alternative taxonomic bipartitions, not reticulations, and the cladogram estimation procedure of Templeton et al. (1992) is narrowly applicable to haplotype data, makes restrictive probabilistic assumptions about the evolutionary process, and treats addi-
tional evolutionary connections as noise, not signal (see also Crandall, 1994).

All of this is particularly disappointing because so much of the recent literature has emphasized the common occurrence of interspecific hybridization in both plants (e.g., McDade, 1990) and animals (e.g., Smith, 1992). The matter has become even more urgent because an increasing amount of systematic research has focused on intraspecific relationships (e.g., Moritz et al., 1992; Templeton et al., 1992). A nonreticulate evolutionary history is the *sine qua non* of the species level under the evolutionary species concept (Simpson, 1961) and one of its necessary features under the biological species concept (Mayr, 1942). In the absence of a reasonable solution to the problem, phylogeneticists frequently have dealt with reticulation by looking for incongruences among phylogenies generated by different data sets (e.g., Patton and Smith, 1994). Unfortunately, this approach often leaves the user with better grounds for worrying about the problem but no clear historical interpretation.

A very different situation exists in biogeography, where debate over methods in general and the vicariance model in particular has been heated and continuous (e.g., Humphries and Seberg, 1989; Page, 1990). Most of the available methods lack an explicit and straightforward rule for depicting dispersal events in graphs of biogeographic relationships (e.g., Rosen, 1975; Platnick and Nelson, 1978; Brooks, 1981; Nelson and Platnick, 1981; Wiley, 1986; Page, 1987; Brooks and McLennan, 1991). This lack creates exactly the same difficulty that is raised by character incongruence in phylogenetic studies: one can acknowledge that at least some dispersal has occurred, but one cannot easily identify the individual events. The recent cladogram reconciliation method of Page (1994) does acknowledge the dispersal problem. However, this method applies strictly to analyses of two cladograms at a time, and furthermore it only makes explicit the tradition of “explaining” dispersal events by throwing out data until the “best” dispersal-free interpretation is found.

![Figure 1](image-url)  
**Figure 1.** True evolutionary tree (a) and possible cladogram (b) for seven objects.  
[ ] = known objects;  
☐ = hypothetical ancestor. Objects 2, 3, and 4 are all derived directly from object X, but 3 and 4 are convergent. Objects 4 and 6 are true ancestors, and several features of object 5 derive by reticulation (e.g., introgression or dispersal) from object 3. These patterns are misrepresented by the fully bifurcating topology of the cladogram.

Because this paper is not intended as a literature review, the rest of this section is expository. Figure 1a shows a tree that summarizes the actual evolutionary connections among a set of objects (Sober, 1988), which could be taxa in a phylogenetic analysis or areas in a biogeographic analysis. This kind of dual interpretation will be possible for most of the hypothetical examples presented in this paper. The lines (connections) in Figure 1a indicate that objects share either taxonomic characters or species (states). The tree has several unusual features that are difficult or impossible to recognize using standard methods. For example, most cladograms are computed by assuming that all internal nodes represent unknown taxa (Farris, 1970). In Figure 1a, however, the root of the tree (object 1) and all the other internal nodes except the one labeled X (square) are occupied by objects (circles) that are “known,” in the sense of having been sampled in the hypothetical study. The assumption that it is not only possible but relatively easy to sample ancestors will be justified later. The tree also is unusual because it connects multiple descendant objects to node X, which results in a polytomy. Standard cladistic methods attempt to avoid polytomies at all costs, and argu-
ments even have been made that a polytomy can only represent ignorance on the part of the observer (but see Maddison, 1989; Purvis and Garland, 1993).

The final and most important heterodoxy presented by Figure 1a is a reticulating connection (object 3 to object 5), as opposed to a simple ancestor–descendant relationship. Sober (1988) used the terms horizontal and vertical transmission to contrast these sorts of processes. In phylogenetics, vertical transmission can involve anagenesis or cladogenesis. Horizontal transmission (=reticulation) results from hybridization, introgression, or differential fixation of ancestral polymorphisms. Reticulations can be informative even when reticulate evolution does not result in perfectly intermediate hybrid forms. For example, it may be useful to show that a few characters have been "donated" from one lineage to another by introgression.

Even when there is no actual hybridization or introgression, graphic reticulations can illustrate convergence or parallel evolution that is strong enough to leave its mark on several characters but not strong enough to create spurious sister groupings. In other words, a reticulation could draw attention to the fact that two taxa on well-separated branches of a tree share many derived character states. The use of reticulations sometimes can even factor out patterns of convergence, leaving true phylogenetic relationships to be summarized by the remaining nonreticulating connections.

In biogeography, vertical transmission results either from the in situ persistence of taxa within an evolving biota or from the splitting of biotas (vicariance), and horizontal transmission results from dispersal. Dispersal can involve only one or a few taxa moving from one area into another, but it also can involve biotic homogenization on the scale of the late Pliocene Great American Interchange (Marshall et al., 1982). Such standard vicariance biogeographic methods as Brooks parsimony analysis (Brooks, 1981; Wiley, 1986; Brooks and McLennan, 1991) and component analysis (Platnick and Nelson, 1978; Nelson and Platnick, 1981) do not allow an explicit, graphical depiction of dispersal. However, the arguments that reticulations are informative in phylogenetics also hold for the extra connections that could show dispersal in biogeography. To avoid coin- ing an unnecessary new term, these connections also will be called reticulations, despite the fact that this expression has traditionally been used only in phylogenetics (e.g., Wagner, 1983).

A standard bifurcating cladogram of the kind generated by traditional methods is shown for contrast in Figure 1b. Any phylogeny or area cladogram based on this type of an analysis must be incorrect because the "true" phylogenetic pattern of Figure 1a involves known ancestors, non-bifurcative cladogenesis, and reticulation. This conflict arises because the Hennigian view of evolution (Hennig, 1966) is too restrictive to describe the real relationships in this hypothetical case. Arguments for admitting the possibility of these unusual patterns are given below. I will not address claims that Hennigian cladograms are summaries of character distributions instead of evolutionary trees (e.g., Patterson, 1982), because such an abstract approach is counterproductive. Hence, all of the graphs discussed here are treated as statements about real evolutionary patterns. Because even the best standard cladogram of the objects in the example would indicate a false phylogeny (e.g., Fig. 1b), the present concern is defining criteria that go beyond the limiting assumptions of standard cladistics.

Many phylogenetic and biogeographic methods revolve around the criterion of what is variously called cladistic parsimony, Wagner parsimony, maximum parsimony, minimum length, minimum evolution, or, hereinafter, minimum transition (MT). The main theme of this paper is that the MT criterion, which states that phylogenies should minimize the number of character-state changes (transitions) their topologies require, misses the mark because of its restrictive underlying assumptions. Instead, the goal of both phylogenetic and
biogeographic analyses should be to maximize the continuity of character or taxonomic distributions. The MT criterion is deeply entrenched, having been formulated explicitly three decades ago and advocated quite strongly since then (Edwards and Cavalli-Sforza, 1963; Camin and Sokal, 1965; Cavalli-Sforza and Edwards, 1967; Farris, 1970). The criterion is justified partly by the argument that the sharing of a state by two objects is prima facie evidence of an evolutionary connection between them (Sober, 1988), i.e., evidence that the shared state is homologous (sensu Patterson, 1982). This concern with homology is legitimate and justifies maximizing continuity. After describing algorithms for generating phylogenetic or biogeographic trees that emphasize continuity, I present applications of the method to a phylogenetic problem involving an extinct group of horses, the hipparionines. The discussion then focuses on the relationship between the current method and others and on arguments for the utility and plausibility of such controversial features as reticulations and known ancestors.

METHODS

Continuity and Reticulation

Figure 2a illustrates continuity by showing the distribution of a character state or taxon (solid circles) across a graph of 10 objects. A state's distribution is continuous whenever it can be traced across the connections among the set of all objects having that state without passing through any other objects. This type of distribution is called a continuous track. Thus, any two objects in a continuous track can be linked through a series of connected objects that all have the same state. Although the track analysis, panbiogeography, or spanning-tree methods of Page (1987) and others also make use of the term track, these methods have no other relationship to the one presented here apart from a general concern with biogeography. Looking for track continuity is important because it can test assumptions of homology. If a track is continuous, the presence of the same state in each object can be explained by vertical or horizontal transmission, as opposed to independent derivation. Hence, only states with continuous tracks can be homologous, and in the example of Figure 2a the three separate continuous tracks imply the presence of three different homologues.

Hereinafter, I use the term homology to refer to states having single evolutionary origins, even if the states would represent taxa in a biogeographic context. In this case, homology would essentially be the same as monophyly. If a taxon has a continuous track, it may have originated in one place and spread to the others, in which case it is monophyletic; if not, it must have had multiple independent origins in different areas, which means it must be polyphyletic. The argument that discontinuous tracks could result from extinction is superficial because a true evolutionary graph should include enough ancestral biotas (hypothetical or not) to fully summarize the biogeographic history of each taxon.

The problem with emphasizing conti-
nuity is that any number of reticulating connections can be added to make distributions continuous. For example, the addition of two reticulating connections to the graph (Fig. 2b) allows the state's track to be continuous and therefore requires only one assumption of homology. It always is possible to add more and more reticulating connections until every state's track is continuous, regardless of the amount of character incongruence present in the data set. Because this approach could lead to a confusing tangle of connections, a method emphasizing continuity will require a means of recognizing that not every reticulation is informative, i.e., a parsimony criterion. The correct criterion depends on counting the number of track fragments, which are isolated, locally continuous parts of a state's distribution. In Figure 2a, for example, the state is distributed across three separate fragments respectively spread across one (top), two (middle), and one (bottom) objects. The number of fragments for any state can range between one and the number of objects.

The informativeness or strength of a connection is defined as the reduction in the number of separate track fragments that it allows. For example, each of the reticulations in Figure 2b has a strength of one because each joins two fragments. The strength of other possible reticulations is zero because the derived state's distribution already is continuous, i.e., there is only one fragment. These additional connections explain nothing and should be ignored. To summarize, connections should be avoided if they do little to reduce the number of track fragments, and graphs generally should imply as much track continuity as is possible for a given number of connections. The method of continuous track analysis (CTA) creates graphs meeting this parsimony criterion.

**Finding the Best Graph**

Searching for a graph that implies the smallest number of track fragments for a given number of connections may require tremendous amounts of computation. For example, there are more than 1.8 million ways to connect just 10 objects even in the most simple type of graph, which is a linear, nonreticulating sequence. Although no known fast algorithm is guaranteed to find maximally parsimonious graphs in the sense used here, a reasonable heuristic technique is available. The connection removal-replacement (CRR) algorithm outlined below is modeled on well-known branch swapping methods such as tree bisection-reconnection (Swofford, 1991).

Computing an initial graph.—Like branch swapping, CRR operates on an initial graph generated by a “greedy” graph-building algorithm. Farris (1970) introduced a greedy algorithm, called Wagner analysis, for building cladograms, which involves adding taxa to an unrooted tree one after another following a predefined addition sequence. The current greedy algorithm requires no such sequence. Instead, the strengths of potential connections directly determine the order in which objects are added. These strengths are unusual because they can change during the course of the algorithm. The algorithm works by declaring the strongest potential connection between two objects to be present first, the second strongest next, and so on. More importantly, this procedure differs from Wagner analysis because it allows connections to reticulate and furthermore may link objects that do not belong to the original subgraph. If there is a relatively small number of connections, independent subgraphs may never be connected.

Adding connections in the order of their strengths is a straightforward concept, but correctly computing an object-by-object matrix of potential strengths is not. A detailed outline of the procedure illustrates some of the terms introduced earlier, such as track fragments and strengths, and provides the groundwork for an account of the CRR routine itself. The greedy algorithm begins with a matrix of raw potential strengths among pairs of objects. At this point, strength is defined as the number of states that each pair has in common because each state starts out having one
separate fragment per object in which it appears. Therefore, connection of any two objects that share a state would join two fragments to make one, which means that the total number of fragments eliminated must equal the number of states held in common (e.g., Fig. 3a). These raw strength values also can be thought of as a measurement of similarity in the ecological sense (e.g., Gauch, 1982).

However, iteratively defining connections by examining the matrix of raw strengths would be misleading because the strengths themselves may need to be modified. The simplest type of modification involves sets of three objects. Suppose that objects A and B are connected and B is connected to a third object C, but A and C are not yet connected. A new connection between A and C would explain nothing if the track of a state they share already is continuous, i.e., the track is present in B and in A and C (Fig. 3b). Therefore, the strength of a potential connection between A and C must discount the number of states having this kind of distribution. Such situations occur only because connections like A–C would be reticulations.

In many cases modification of strengths is somewhat more complicated. For example, the roles of A and B could be switched: perhaps A is connected to B and A is connected to another object D, but B and D are not yet connected. Distributions that span more than two connections also could create redundancy. That is, one or more states may occur throughout a chain of three or more existing connections, thereby decreasing the strength of a potential connection between the objects at the ends of the chain. The progressive weakening of connections only applies to potential reticulations, so in many analyses reticulations would be superfluous. However, if reticulations are needed the greedy algorithm will have generated a substantively different result than that of a standard minimum spanning tree analysis (Gower and Ross, 1969), which otherwise would find the same solution.

Removing and replacing connections.—CRR is conceptually very similar to the greedy algorithm that builds the initial graph. In CRR, each connection \( c_{ij} \) in the initial search graph is removed sequentially. After each removal, all of the strengths are recomputed, and the matrix of strengths is scanned for the most strongly supported potential connection \( c_{\text{max}} \) that does not involve objects \( i \) and \( j \). If \( c_{\text{max}} \) is as strong as or stronger than \( c_{ij} \), a new tree is created that replaces \( c_{ij} \) with \( c_{\text{max}} \). If additional connections in the current search matrix are as strong as \( c_{\text{max}} \), each of them is used to define a new graph. The strength of \( c_{ij} \) can be computed only after it is removed from the original graph. If graphs include \( n \) objects and \( m \) connections, a search of each graph will require the computation of \((n^2 - n)/2\) potential new connections for each original connection that is replaced, for a total of \( m \times (n^2 - n)/2 \).

The CRR algorithm is similar to tree bisection–reconnection (Swofford, 1991) because the connections of a graph are analogous to the branches of a cladogram. However, there is an important difference with respect to the amount of computation required by the two algorithms. A cladogram includes \( 2n - 2 \) branches and \( n - 1 \) internal nodes, but a CTA graph could include as few as \( n - 1 \) connections and no internal nodes. This means that there are \( 2n - 2 \) ways to bisect a cladogram, but the number of ways \( m \) to remove connections from a graph may be as small as \( n - 1 \).
There are \((2n_1 - 2) \times (2n_2 - 3)\) ways to reconnect a bisected cladogram that includes subclades of \(n_1\) and \(n_2\) taxa, as opposed to the \((n^2 - n)/2\) ways to replace an eliminated connection in a CTA graph. Therefore, searching a graph with CRR requires computing \(m \times (n^2 - n)/2\) possible connections, but searching a cladogram with tree bisection–reconnection requires computing \((2n - 2) \times (2n_1 - 2) \times (2n_2 - 3)\) possible reconnections. If \(m\) equals \(n - 1\) and \(n_1\) and \(n_2\) are nearly the same, these figures are on the order of \(n^3/2\) and \(2n^4\). In other words, CRR needs to examine only about one fourth as many new topologies as does tree bisection–reconnection because it operates on smaller graphs.

These computations assume that there is only one parsimonious optimized reconstruction of each internal node. However, if optimizations are sometimes ambiguous then assessment of the alternatives will make cladistic branch swapping even more computationally burdensome. In contrast, in a CRR search there are no hypothetical objects and therefore no similar difficulties with ambiguous optimizations. This difference could greatly accentuate the computational advantages of CRR.

Choosing the number of connections.—The philosophy of CTA could be taken to an extreme by advocating that all homoplasy be eliminated using reticulations. However, standard methods forbid reticulation and merely minimize homoplasy. Because patterns of homoplasy sometimes reflect real but isolated and uninformative evolutionary events, it is important to find a compromise solution: reticulations only should be employed when they have a relatively large amount of explanatory power. Therefore, reasonable criteria are needed for setting an upper limit on the size of the graphs to be considered, where the size of a graph is the number of connections it includes.

The two criteria used in this paper seem straightforward and robust, although there is room for improvement and a third criterion will be outlined. The first criterion is to consider only the smallest graph that links all the objects in a single network. A single network is present when it is possible to trace a path between any two objects across the existing connections. Some of the connections in a network may be reticulations, so a network is not the same as a minimal spanning tree. The total number of connections in a spanning tree is one less than the number of objects, but in a minimal single network there can be additional connections in the form of reticulations. A network will include \(n - 1\) connections for \(n\) objects plus an additional number of reticulating connections, so a network of five objects with two reticulations will include six connections.

A second approach is to plot the size of progressively larger maximally parsimonious graphs against the number of track fragments each graph implies. In a series of CRR-generated graphs that use a progressively larger number of connections, each more heavily connected graph must imply as few or fewer fragments than the last. As the number of connections increases, the differential explanatory power of each new graph (i.e., the number of fragments in the preceding graph minus the number in the current graph) should lessen. A sudden flattening in the graph size versus number of fragments curve should indicate a point after which this difference—essentially the support for additional connections—becomes trivial. Only the graph coming immediately after such a point would be used. This procedure is analogous to the scree plot method for picking the number of components to examine in a principal components analysis (e.g., Sepkoski and Miller, 1985). There is very little danger that the transition point will come before all the objects are linked in a single network.

A third method could involve topological comparisons between maximally parsimonious graphs that differ in size by the addition of a single connection. If adding a connection has little or no effect on the basic topological pattern, the additional connection may be uninformative. If a substantial perturbation results instead, the larger graph presumably expresses an important underlying pattern in the data that
fails to appear in the smaller graphs. The "similarity" between topologies could be defined as the percentage of connections in the smaller graph that are duplicated in the larger graph. A major perturbation would correspond to a low percent similarity. There are two major problems with this kind of criterion: the difficulty of computing similarity when there are numerous maximally parsimonious graphs and the fact that topological stability bears no direct relation to parsimony, however defined. However, the approach deserves to be investigated in the future.

*Goodness-of-fit statistics.*—Once an analysis is done, comparisons among alternative trees can be made with indices analogous to the consistency index (Kluge and Farris, 1969) and the retention index (Farris, 1989). These are calculated using the number of different derived states (S), the number of separate derived-state track fragments across the tree (I), and the maximum possible number of such fragments across any nonreticulating network (M). M must also equal the maximum possible number of steps sensu Kluge and Farris (1969); an appropriate method for computing this value was discussed by Archie (1989). The track continuity index equals S/I and the track retention index equals (M − I)/(M − S). (A computer program written in the language C that executes the greedy graph-building and CRR algorithms and computes these statistics may be obtained on request.)

*Additional Considerations*

Creating hypothetical ancestors.—CTA is unique because it can generate reticulating connections and ancestral nodes consisting of known objects. However, in some cases the triangle-tree rule can be used to eliminate both of these features at once from a maximally parsimonious graph. The rule is simply that a triangle created by a reticulation among three neighboring objects (Fig. 4a) always can be replaced with a Y-shaped tree (Fig. 4b) because the two topologies have exactly the same explanatory power. Each topology makes all local tracks continuous, and each includes three connections. The Y-tree does introduce a hypothetical ancestor; but this is not a difficulty because parsimony in the context of CTA only concerns character distributions and the number of connections, not the number of nodes per se.

The triangle-tree rule may seem counterintuitive because one could imagine two alternative states of the same character both being optimized at a Y-tree's nexus, which could imply the existence of an implausible, chimeralike ancestor. Many workers would be uncomfortable with explaining away such cases by allowing polymorphic ancestors. Similar cases in biogeographic analyses would be a major problem because one wishes to avoid hypothetical biotas including taxa that have never been found together (Alroy, 1992). Fortunately, these kinds of problems with optimizations never can occur: a Y-tree cannot imply that two states with mutually exclusive known distributions are both present in a hypothetical ancestor. An informal proof relies on the fact that there are only three topologically distinct distributions of states across a triangle or Y-tree. States may be found (1) in all objects, (2) in only one object, or (3) in two of three objects (e.g., characters S1, S2, and S3 in Fig. 4). States in the first class already are known to co-occur with all other states present in the three objects, and no parsimonious optimization could place a state known only in one of the three known objects at the internal node. This leaves states in the third category. Because there are

![Figure 4](image-url)
only three objects, any two states that are each found in more than one known object must co-occur in at least one of the objects.

Unfortunately, this argument cannot be extended to cases involving more than three objects: in a chain of four or more objects connected at the ends by a reticulation, there is nothing to prevent a hypothetical ancestral node replacing the reticulation from including incompatible states. However, the triangle-tree rule does provide a means of eliminating many apparent reticulations from directly connected CTA graphs. Before converting triangles to Y-trees, none of the nodes represent hypothetical objects, but after conversion the final product is a hybrid of directly connected and Wagner trees (bifurcating graphs in which internal nodes may only depict hypothetical objects).

Complementary and noncomplementary coding.—The MT criterion often is applied to biogeographic data in much the same way as it is applied to morphological characters (e.g., Brooks, 1981; Wiley, 1986; Brooks and McLennan, 1991), despite fundamental differences between these data types (Sober, 1988). Absences in biogeography are not analogous to primitive states in phylogenetics because a primitive state is potentially homologous and is only primitive in the context of a particular analysis. In a data set with additional characters and/or different taxa, the same "primitive" state may be considered derived. On the contrary, absences of taxa in areas are fundamentally different from presences. Not only is the distinction independent of character polarization, but there is no sense in which absences are ever monophyletic, whereas presences should correspond to monophyletic taxa. Therefore, the previously drawn analogy between homologous character states and monophyletic taxa does not extend to taxonomic absences.

An additional reason for treating presences and absences differently is that the presences of a taxon often are far less frequent than the absences. In an extreme case such as a biogeographic analysis of all the world’s organisms, even the most widespread species would be relatively rare. Furthermore, most species still would have relatively restricted distributions, even in a small-scale analysis. A good example is the tuatara, whose presence in New Zealand needs to be explained but whose absence either in the distant Yukon or on relatively nearby Lord Howe Island does not. Ecologists have long recognized the fact that absences are less interesting to the degree that presences are rare, and they have developed multivariate ordination techniques that take this property into account by weighting data points in proportion to row and column totals (e.g., correspondence analysis: Hill, 1973). For these reasons, analyses generating graphs need to use a criterion similar to Dollo parsimony (Le Quesne, 1974) that emphasizes presences. When CTA is applied to biogeographic problems, only the continuity of presences should be maintained. Matches between objects that involve absences should not be counted toward the strength of a possible connection between them. Thus, the algorithm should operate on the original presence-absence matrix with no modification (noncomplementary coding).

This approach is neither necessary nor desirable for character data, as argued by Farris (1977), because the distinction between primitive and derived states is relative and primitive states can be homologous. Hence, phylogenetic applications of CTA should maintain the continuity of both primitive and derived states. In practical terms, this means creating a dummy or complementary code to supplement each original character. If the original character is scored as 0 for primitive states and 1 for derived states, the complementary code is scored 1 for primitive and 0 for derived. This allows the algorithm to take the continuity of primitive states into account.

Ordered and unordered characters.—When there are only two states per character in a phylogenetic analysis, complementary coding guarantees that the tracks formed by each state are treated separately for the purpose of computing potential strengths and counting the number of track frag-
The 0 state (scored as 1) to guarantee its continuity. Therefore, in complementary coding an unordered character always has \( n \) binary codes.

The situation is much different for an ordered character, such as the one shown in Figure 5b. Standard additive binary coding creates a set of \( n - 1 \) binaries that include a nested hierarchy of 1 states. Instead of adding just one new complementary code for the original 0 state, it is now necessary to add \( n - 1 \) codes, each of which is complementary to a different one of the additive binary codes. As a result, \( 2n - 2 \) codes will be needed for each ordered character. This convention guarantees that if two taxa have neighboring states (e.g., 1 and 2), the potential strength is \( n - 2 \); if taxa have states differing by a value of 2, the potential strength is \( n - 3 \), and so on, the minimum value being \( n - n = 0 \) for taxa separated by the maximum of \( n - 1 \) states. Note that when \( n = 2 \), i.e., when a character has only two states, \( n = 2n - 2 \) and the ordered and unordered complementary coding conventions yield exactly the same codes, as they should.

**Missing data and missing characters.**—There is more than one sense in which data can be “missing” from a character matrix, and the major computational difficulties that can result have been the focus of much recent attention (e.g., Maddison, 1993). For example, if a data cell cannot be scored because of such practical difficulties as incomplete or damaged specimens, the missing cell actually could represent any of the character states. However, if a character definition simply does not apply to the organism in question, the missing data cell has a more ambiguous meaning. Maddison (1993) gave an example of trying to score tail color for taxa that have no tails. Missing characters of this kind present two main operational difficulties. Suppose that there are five adjacent objects A, B, C, D, and E in a linear graph. All the objects except C have tails. A and D have red tails, and B and E have blue tails. Because the topology already implies that A and B acquired the character “tail color” independently of D and E, the transition between
blue in B and red in D should not cost an extra step. However, if C is scored as having "missing data," standard algorithms will in fact weight this transition as if it were real.

Maddison (1993) suggested using step matrices to avoid this problem. However, step matrices are computationally demanding and require a separate analysis of the possible transitions for each character. The use of complementary coding in CTA avoids the problem from the very start by means of a simple, built-in coding convention. Taxa with missing data are treated as if they may or may not have all possible binary states, as in standard coding (Fig. 5c), whereas taxa with missing characters are treated as if they definitely have the 0 state for all of the binary codes (Fig. 5d). These coding conventions allow track fragments to be connected across taxa with missing data but not across taxa with missing characters. As a result, the number of tail color fragments (four) in the above example could not be affected by the relative positions of A and B or of D and E because none of the states of tail color could travel across C. This result holds regardless of whether track fragments or transitions are used as the measure of parsimony, which means that complementary coding is a general solution to the missing character problem that is independent of the other methods introduced in this paper.

There is an additional problem with using step matrices. If the loss or gain of tails is declared to cost a single step and tail color has four or more ordered states, hypothesizing a tail loss and then a gain requires fewer steps than a direct transformation between the most widely separated tail color states (two steps vs. three or more). Complementary coding also avoids this dangerous violation of the triangle inequality. Let us define the distance between states as the complement of the potential strength, i.e., $2n$ minus the potential strength. The $2n$ term is used because the expression's smallest possible value must be zero, i.e., when comparing a state to itself, and there are $2n$ binaries for each character. Because the number of shared track fragments for two extreme states A and Z of an ordered character is always $n - n = 0$, as discussed above, the maximal distance between normal states is $2n - 0 = 2n$. The distance between any normal state and the nonstate of missing the character completely (state X) is always $2n - n = n$ because exactly $n$ binaries will be scored as 0 for both state X and any one of the normal states, as in Figure 5d. Therefore, the total distance $A - X - Z$ is always $2n$, i.e., exactly the same as the maximal distance between normal states, and it follows that the presence of missing characters never can result in a violation of the triangle inequality as long as complementary coding is used.

Polarizing connections.—Under certain circumstances, the continuity of a track across a reticulation can defy any reasonable historical interpretation. If connections are intended to represent singular historical events in which information is passed from an ancestor to a descendant, it should not be possible for a hybrid H to pass on its states to its ancestors A and B, i.e., for states to backtrack. Therefore, a backtracking state shared by A, B, and H must actually represent two originations (or homologues), even though standard CTA counts only one.

Sometimes backtracking can be ignored. First, there may be other connections that already have created a single track fragment for the state's three occurrences. This always is true if the state is present throughout the circuit, e.g., whenever it forms a simple A-B-H triangle. It also may be true in limited circumstances involving multiple reticulations. Second, any of the connections in a circuit can be interpreted as reticulations, and any of the objects can be interpreted as hybrids. Therefore, just by examining all of the alternatives it may be possible to create a scenario that eliminates backtracking. The backtracking issue also is irrelevant in studies that are not exclusively concerned with historical relationships, such as (1) phylogenetic analyses in which reticulations account for convergence and parallelism (as in the exam-
ple described below), (2) intraspecific phylogenetic analyses in which there are reasons to believe that bidirectional gene flow connects many populations, and (3) biogeographic analyses in which there are analogous reasons to postulate bidirectional dispersal.

In any event, the CTA program has a built-in option that permits analyses of historical ancestor–descendant patterns by discounting backtracks in its graph searching routine. The algorithm requires polarizing the graphs by declaring a root and thereby determining the direction of information flow (polarity) of each connection, which in turn identifies all ancestors and descendants, including hybrids. Declaring an a priori ancestor is an unfortunate but inevitable shortcoming of the algorithm that admittedly is avoided by standard MT parsimony. Because roots and polarities have no explanatory power in a nonreticulated graph, polarized and standard CTA give the same result whenever there are no circuits involving more than three objects.

Using clades in biogeographic analyses.— Standard vicariance biogeographic techniques attempt to synthesize the biogeographic implications of several independent phylogenetic hypotheses. For example, a common approach is to generate consensus trees for cladograms that describe unrelated groups found in the same areas (e.g., Nelson and Platnick, 1981). CTA does not require phylogenetic information, but it can make use of such data in the form of the taxon-by-area matrices generated by the standard binary coding protocol of Brooks parsimony analysis (Kluge, 1988; Brooks and McLennan, 1991). This approach simply treats the nodes of every cladogram as if they were terminal taxa to be scored as present or absent in each biogeographic area. Brooks’s coding scheme is justifiable and operationally direct, but CTA demands no commitment either to Brooks’s method or to the use of phylogenetic data in the first place. Even when a data set includes species of completely uncertain phylogenetic affinities, interesting biogeographic patterns still can be derived by analyzing raw distributional data.

**Example**

This section illustrates CTA by examining the species-level phylogenetic relationships of North American hipparionine horses. In this example, the use of reticulations clarifies the phylogeny by factoring out apparent convergence, even though there is no reason to think that actual hybridization or introgression has occurred. The group in question is the tribe Hipparionini, a diverse and biogeographically widespread but completely extinct clade that is the sister group of the Equini, a second tribe that includes all living equids. Hipparionines are found in Europe, Asia, and Africa, but the group’s center of evolution was in North America, and most of the important lineages originated there during the middle Miocene. The present analysis includes the better known Miocene and Pliocene forms of North America and updates earlier work by Hulbert (1988), Hulbert and MacFadden (1991), and others. Seventeen species were scored for 56 characters of the skull, upper dentition, and lower dentition that together include 188 informative states (Appendices 1 and 2). The 20 multistate characters were treated as ordered following Hulbert (1988), and complementary binary coding was used to transform the matrix given in the table. None of the missing data were treated as missing characters. The polarized connections option was not used because the anticipated reticulations were to be interpreted as points of convergence, not as historical hybridization events.

Most of the species descriptions are based on first-hand examination of collections at the American Museum of Natural History and the Field Museum of Natural History, although figures presented by Webb (1969), MacFadden (1984), Webb and Hulbert (1986), Hulbert (1988), and Hulbert and MacFadden (1991) also were consulted. For most of the species, all of the character combinations can be demonstrated by specimens from a single quarry. "Mer-zychippus" primus was treated as the out-
group, and "M." nr. sejunctus has been identified as a primitive member of the Equini (Hulbert and MacFadden, 1991). "Hipparion" is referred to in quotes because preliminary analyses of a larger data set indicate that there were no true representatives of this genus in the New World.

A cladistic analysis using PAUP’s branch-and-bound search algorithm found six minimal-length trees of 185 steps. The strict consensus tree is shown in Figure 6. The number of derived states $S$ is 90; the maximum possible number of steps $M$ is 332, the same as the maximum number of derived-state track fragments. Each of the minimal-length trees has a consistency index of 0.486 (90/185) and a retention index of 0.607 ([332 – 185]/[332 – 90]). The strict consensus is poorly resolved with respect to the crown group of Cormohipparion, "Hipparion," Nannippus, Neohipparion, and Pseudohipparion. However, there are only three topological variations among the six trees with regard to this crown group (Fig. 7); each variation appears in two cladograms differing from each other only in the relative placement of the primitive, topologically adjacent species "H." shirleyae and M. insignis. The three crown group topologies vary in the placement of C. sphenodus, "H." tehonense, and Neohipparion. However, in every case Nannippus and Pseudohipparion form a clade and "H." forcei groups closely with C. dolichops and C. occidentale. A 50% majority rule consensus is shown in Figure 7d.

Figure 8 depicts a “cladistic” phylogeny inferred from the consensus tree by (1) as-
signing an age to each species sample using the time scale of Tedford et al. (1987), as modified by Alroy (unpublished), and (2) as in other standard cladistic analyses, assuming that the cladogram is correct, that no ancestors have been sampled because all of the species possess at least one apparent autapomorphy, and that cladogenesis is always bifurcative, destroying ancestors as it proceeds. The outgroup species, "M." primus, is by definition completely plesiomorphic. However, examination of further outgroups surely would show it to be autapomorphic in at least a few characters. Following the previous logic, therefore, "M." primus is removed from a directly ancestral position. The cladistic phylogeny includes 21 separate instances in which a hypothetical ancestral lineage (ghost taxon, sensu Norell, 1992) persists for a million years without being sampled (ghost segments).

Seventeen different sets of maximally parsimonious CTA graphs were generated with the CRR algorithm by varying the number of connections between 16 and 32 (Table 1; Fig. 9). All analyses employing fewer than 29 connections found 10 or fewer maximally parsimonious graphs. The minimal single network criterion and the scree plot criterion were used to select two graphs for examination. The graph select-
ed using the first criterion includes 277 derived-state track fragments, 16 connections, and no reticulations. The phylogeny shown in Figure 10a was derived from the graph by assuming that the graph's topology is correct and that anagenesis or bifurcative cladogenesis occurs whenever an ancestral species is older than its descendant(s). The complete lack of reticulations is not surprising because many of the species are very similar, which means that most of a species' character states will be "explained" by the first connection involving that species. The track continuity index (TCI) is 0.325 (90/277), and the track retention index (TRI) is 0.227 ([332 − 277]/[332 − 90]). The equivalent index values generated by PAUP were much higher, but the minimal single network graph includes only 16 connections, whereas the PAUP cladograms each require 32. Also, none of the relatively small CTA graphs generated the triangular sets of connections needed to create hypothetical ancestral nodes.

The plot of the number of track fragments against the number of connections in the 17 CRR analyses (Fig. 9) shows that little is gained by using more than 19 connections. The single most parsimonious graph of this size (Fig. 10b) reduces the number of derived-state track fragments to 175 (TCI = 0.514; TRI = 0.649), which is 10 fewer than the analogous number of steps required by the PAUP cladograms (MT in Fig. 9). The three circuits present in the 19-connection graph have been "broken" by designating three connections as reticulations representing strong pat-
Table 1. CTA graphs for the hipparionine data set generated by the connection removal–replacement algorithm. Separate analyses using 16–32 connections are summarized.

<table>
<thead>
<tr>
<th>No. connections</th>
<th>No. topologically distinct graphs</th>
<th>No. derived-state track fragments</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>16</td>
<td>1</td>
<td>277</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>1</td>
<td>231</td>
<td>46</td>
</tr>
<tr>
<td>18</td>
<td>2</td>
<td>198</td>
<td>33</td>
</tr>
<tr>
<td>19</td>
<td>1</td>
<td>175</td>
<td>23</td>
</tr>
<tr>
<td>20</td>
<td>2</td>
<td>166</td>
<td>9</td>
</tr>
<tr>
<td>21</td>
<td>2</td>
<td>158</td>
<td>8</td>
</tr>
<tr>
<td>22</td>
<td>4</td>
<td>151</td>
<td>7</td>
</tr>
<tr>
<td>23</td>
<td>1</td>
<td>148</td>
<td>3</td>
</tr>
<tr>
<td>24</td>
<td>6</td>
<td>141</td>
<td>7</td>
</tr>
<tr>
<td>25</td>
<td>1</td>
<td>141</td>
<td>0</td>
</tr>
<tr>
<td>26</td>
<td>10</td>
<td>137</td>
<td>4</td>
</tr>
<tr>
<td>27</td>
<td>3</td>
<td>133</td>
<td>4</td>
</tr>
<tr>
<td>28</td>
<td>6</td>
<td>131</td>
<td>2</td>
</tr>
<tr>
<td>29</td>
<td>1,000+</td>
<td>131</td>
<td>0</td>
</tr>
<tr>
<td>30</td>
<td>1,000+</td>
<td>130</td>
<td>1</td>
</tr>
<tr>
<td>31</td>
<td>1,000+</td>
<td>129</td>
<td>1</td>
</tr>
<tr>
<td>32</td>
<td>1,000+</td>
<td>129</td>
<td>0</td>
</tr>
</tbody>
</table>

a Absolute minimum is 90.

b Number of track fragments for each graph subtracted from the number of fragments for graphs with one fewer connections.

Figure 9. Relationship between number of connections and number of track fragments in the most parsimonious graphs of hipparionine relationships found by continuous track analysis (CTA) and PAUP. The CTA graphs were generated by varying the number of connections between 16 and 32 and applying the connection removal–replacement algorithm. Less parsimonious solutions would lie above this curve. MT = the six minimum transition trees generated by PAUP.

terms of convergence instead of phylogenetic relationships (dashed lines in Fig. 10b). Many alternative connections could have been designated as reticulations, but the current arrangement is unique in that it upholds the monophyly of the traditionally recognized genera *Neohipparion* and *Pseudhipparion* and of the "Hipparion"–*Cor-mohipparion–Nannippus* grouping ("Hipparion" genus group) favored by Hulbert (1988) and Hulbert and MacFadden (1991).

The 19-connection graph of Figure 10b is preferable to the two earlier alternatives at least in terms of its remarkable conservativeness. Not only does it retain several traditional groupings, but it treats *M. insignis* as the basal member of a monophyletic "Hipparion" genus group, identifies "M." coloradense as the ancestor of *Neohipparion*, and clearly separates *Pseudhipparion* from the "Hipparion" genus group. In contrast, no modern worker since Stirtion (1940) has suggested the alternative relationships shown in Figures 8 and 10a. A 19-connection polarized analysis would have produced a graph much more similar to the one generated using 16 connections. In addition to its comfortable familiarity, the 19-connection phylogeny has two objective advantages. First, the cladistic phylogeny requires 21 ghost segments, whereas the 16- and 19-connection solutions require 8 and 9, respectively. Hipparionines are among the most abundant and heavily studied of Neogene mammals, and it seems highly implausible that the basal lineages could be as poorly sampled as the cladistic results imply. Second, in the 16-connection phylogeny there are three cases of an ancestral species being a million years younger than a descendant and four other cases of ancestral and descendant species being of the same age. The 19-connection graph implies two instances in the former category and two in the latter; these figures are unaffected by alternative choices of reticulations. Thus, the 19-connection graph is strongly favored by known temporal relationships.

I attribute the relative success of the CTA results in general, and of the 19-connection phylogeny in particular, to CTA's ability to account for convergence using reticulations. For example, it is not surprising at all that each of the nonreticulating
Figure 10. Hipparrionine phylogenies based on continuous track analysis (CTA). The underlying CTA graphs were generated by connection removal–replacement. Axes and abbreviations are as in Figure 8. (a) Phylogeny based on the most parsimonious 16-connection CTA graph. No reticulations are present. (b) Phylogeny based on the most parsimonious 19-connection CTA graph. The three circuits are resolved by designating three connections as reticulations (dashed lines). This choice of reticulations maximizes the monophyly of traditionally recognized supraspecific groupings.
phylogenies spuriously groups *Pseudhipparion* and *Nannippus*. These two genera represent the only true dwarf lineages in the data set, and many characters correlate strongly with size. Stirton (1940) even chose to lump the two genera because of their convergent similarities. In Figure 10b, this convergence is accounted for by a reticulation and has no apparent impact on the placement of further connections. The placement of the other two reticulations seems to have had similar effects. *Neohipparion affine* and *Cormohipparion* convergently share features related to relatively large size and complex enamel in the lower dentitions. Describing this convergence with a reticulation allows recognition of the close relationship between *N. affine* and "M." *coloradense*. Finally, *Neohipparion trampasense* and *Nannippus peninsulatus* are both relatively small and have morphologically simplified upper dentitions. The reticulating connection between them seems not to have generated any secondary topological effects.

All of the analyses share features that conflict with some of the more innovative phylogenetic hypotheses of Webb and Hulbert (1986), Hulbert (1988), and Hulbert and MacFadden (1991). In contrast to all three of their analyses, "H." *shirleyae* is far removed from the remaining species of the genus, *Pseudhipparion* and *Neohipparion* are not sister taxa, "M." *coloradense* bears no close relation to *Pseudhipparion*, and the genera *Cormohipparion* and "Hipparion" are paraphyletic, with *Cormohipparion* ancestral to "Hipparion" and "Hipparion" ancestral to *Nannippus*. The latter relationship was proposed originally by Quinn (1955) and Webb (1969). Finally, the 19-connection phylogeny derives "M." *coloradense* and *Neohipparion* from "M." *nr. sejunctus*, a member of the Equini. This radical hypothesis is supported by distinctive features of the facial region and lower dentition that are present nowhere else in the hipparionine radiation. The possibility that *Neohipparion* is not a true hipparionine has not been suggested in print by other workers and needs further corroboration.

In summary, the numerous uninformative branches and hypothetical ancestors in the traditional cladistic analysis appear to obscure the true phylogenetic pattern. However, the reticulations employed by CTA account for strong patterns of convergence and improve apparent phylogenetic resolution as a side effect. A more detailed and extensive analysis of hipparionine phylogenetics will be presented elsewhere.

**Discussion**

**Minimal Origination or Minimal Transition?**

The preceding example shows that continuous track analysis can successfully illustrate complex empirical patterns. However, several difficult conceptual problems still need to be addressed. One concerns the logical interrelationships of homology, track continuity, and evolutionary transition. The idea of minimizing the number of fragments for any given number of connections might seem intuitively reasonable, but this approach could grossly inflate the number of state transitions across a graph, in violation of the standard MT criterion. For example, both graphs shown in Figure 2 require six transitions, one at each of the boundaries between objects that have the character state (●) and objects that do not (○). Therefore, one could argue that the two reticulations are highly uninformative. However, the boundaries between states are not truly relevant to evolutionary reconstructions: the real issue is the number of homologous states, which by definition are separate track fragments.

As stated above, homologous states stand here for monophyletic taxa in biogeography and actual character states in phylogenetics. When track fragments are minimized, origination are maximized, and because exactly one origination is hypothesized for each homologous state, when fragments are minimized, the explanatory power of hypotheses of homology is maximized. In other words, originations are the only important evolutionary transitions: any other implied transitions only show that biological information has failed to be transmitted horizontally, which does not need to be explained.
In terms of reticulating connections, phylogenetic transitions represent either the failed introgression of character states or incomplete convergence between taxa. Neither process needs to be explained in evolutionary terms. Convergent body shapes in dolphins and certain fishes may be biologically interesting, but the transition between them implied by the presence of lungs in dolphins is not interesting because our current phylogeny of the vertebrates already explains it. Similarly, a biogeographic transition across a reticulating connection is uninteresting because it only shows that a taxon has failed to disperse between the two biotas. The dispersal of cattle egrets from Africa to the New World is interesting, but the failure of the many other African birds to do so is not. In either case, the only important goal is to explain why states are shared, not why they change across reticulations.

Nevertheless, the fundamental connection between transitions and fragments validates the standard MT criterion in certain circumstances. On a nonreticulating graph, the number of transitions is one less than the number of derived plus primitive state fragments. For example, if the empty and solid circles in Figure 2a are interpreted respectively as derived and primitive states, then the six transitions between them are a direct consequence of there being a total of seven fragments. If a nonreticulating graph has one continuous track for each state, then an absolutely minimal number of transitions is required and both the MT and track continuity criteria are maximized at once. Therefore, the MT and CTA methods differ only when reticulations are needed to account for character incongruence. Even though the two methods differ substantively in these circumstances, CTA’s goal of minimizing separate hypotheses of homology agrees well with the MT criterion’s original motivation.

**Known Ancestors Are Parsimonious**

Several of the graphs discussed so far were constructed largely or entirely without hypothetical internal nodes. I call these directly connected (DC) trees to avoid con-

![Figure 11. All possible distributions of two alternative states (○, □) across three-object directly connected (a–c), Wagner (d, e), and “offset” (f) trees. Rotation of branches and/or reversal of polarities could reproduce all superficially differing trees. Distributions in trees a, b, and d–f form two track fragments; tree c creates three fragments because it does not account for the autapomorphy in the central object.](image-url)fusion with minimum spanning trees (e.g., Page, 1987), which cannot reticulate and therefore are constructed using fundamentally different criteria. The problem is to show why CTA creates graphs with few or no hypothetical internal nodes and why these graphs are biologically plausible.

Figure 11 shows several DC- and Wagner-type graphs, plus one hybrid graph. The DC trees (Figs. 11a–c) are unrooted, and each includes two connections and three nodes that represent known objects. Nonreticulating DC networks always require \( n - 1 \) connections for \( n \) objects. The Wagner trees (Figs. 11d, 11e) are rooted arbitrarily, and each includes the same three known objects plus two unknown hypothetical ancestors. Each requires four connections, following the rule that Wagner trees include \( n - 1 \) internal nodes and \( 2n - 2 \) connections for \( n \) objects.

Because Wagner trees include twice as many connections as do minimally connected evolutionary trees, one may ask what a Wagner tree’s extra connections explain (Paul, 1992). Figure 11 shows all topologically distinct distributions of two complementary states, perhaps primitive and derived morphological features. These distributions can be interpreted by assuming the most parsimonious polarity. In Fig-
ures 11a and 11d, one state is universal. None of the connections in either tree explain anything because there must be exactly one track fragment as long as the objects form a network. Therefore, the graphs each have only one homologous state, one origination, and no transitions. In the remaining trees, one object has one state and the others have a second. In Figures 11b and 11e, the state found in two objects has a continuous track across each tree. Because any state found in only one object has a continuous track, these trees are each maximally informative, requiring two homologous states, two origins (one at the root of the tree or below), and one transition within the tree. The additional connections shown in the Wagner tree explain nothing.

Only the DC graph in Figure 11c is substantively different from the other trees. It requires three fragments, three homologous states, three origins, and two state changes because the autapomorphic object is placed at an internal node, disrupting the track and implying both an acquisition and a loss of a state. Thus, the tree is less parsimonious regardless of whether one counts fragments or transitions. Addition of an extra connection in the form of either an additional internal node (i.e., a branch offsetting the autapomorphic object) or a reticulation would eliminate the extra fragments and transitions. As noted above, the triangle resulting from a reticulation could be turned into a Y-tree, resulting in the topology also generated by an offsetting branch (Fig. 11f). The Y-tree uses three branches, one fewer than the Wagner solution (Fig. 11e).

The general conclusion is that offsetting branches account only for autapomorphies, i.e., fragments that include just a single node. Furthermore, Wagner trees may use unnecessary connections even for this purpose. If a state occurs in two or more objects that form a track fragment (shaded circles in Figs. 12a, 12b), elimination of the reversal caused by the placement of the fragment in a series of exclusively internal nodes requires exactly one offset per object in the fragment. The offsets will create at least as many new transitions (two) as were eliminated from the original DC tree. Hence, even though these types of hybrid trees may use fewer connections than do Wagner trees, they are never advantageous. The only alternative optimization of Figure 12b would place the transitions at the same connections as in the directly connected graph. Similar cases in which some of the nodes in a fragment are terminal (Figs. 12c, 12d) demonstrate that the same rule applies whenever two or more of the objects in a fragment occupy internal nodes.

Because offsetting branches only account for autapomorphies, offsets are needed only when autapomorphies are common, which would be true if either homoplasy or the evolution of entirely new states were rampant. The parsimony curve of Figure 9, which compares the number of connections to the number of track fragments in the hippocarine data set, demonstrates

---

**Figure 12.** Effect of adding hypothetical ancestral nodes (□) to directly connected graphs. Distribution of primitive (○, □) and derived (●) states is indicated. As long as derived states are present in two or more adjacent objects that occupy internal nodes, the additional nodes cannot reduce the implied number of steps (bars) and track fragments.
that in a real data set standard Wagner trees do in fact make excessive use of offsetting branches. All CTA graphs that minimize the number of fragments for any one number of connections fall on the curve. However, because standard MT methods forbid reticulation and require a fixed number of connections for each object, the MT solution falls far above the curve.

**Known Ancestors Are Plausible**

Because of its tendency to eliminate hypothetical ancestors, CTA depends on the plausibility of finding real ancestors in real data sets. Some workers believe that hypotheses of ancestry are untestable and therefore useless (e.g., Engelmann and Wiley, 1977). This argument can be countered easily by noting that ancestors can be “disproved” if optimization of the most parsimonious phylogeny implies that they are autapomorphic (Szalay, 1977; Paul, 1992; Wagner and Erwin, 1995). Here I address the much more substantive claim that sampling the real ancestors of extant taxa is by definition almost impossible. I present an extreme characterization of this claim in order to make the differences between the opposing positions as clear as possible.

First, assume that hybridization has not occurred, all lineages are extant, and each has evolved independently for a substantial amount of time. If organisms have an infinite number of characters or if characters vary continuously, there must be some true autapomorphies that define every distinct lineage. It follows that a Wagner tree is the only possible representation of true history. Assuming this and also that speciation is instantaneous, the only true ancestors are forms that exist for an infinitesimal moment just before speciation. The fact that any earlier form on the same basal lineage is an ancestor, at least in a topological sense, does not mean that such a taxon should be placed at an internal node. All of the ancestor’s descendants leading up to the point of speciation must be united by synapomorphies, and such a topology would not reflect this. Parallel arguments apply to taxonomic samples of living biotas.

There are four major problems with this extreme view. First, many analyses should not be restricted to living organisms and biotas because fossils are often very informative (Donoghue et al., 1989; Huelsenbeck, 1991). Any fossil may represent the ancestral lineage of a living organism or of another fossil organism, and ancestral lineages are sampled abundantly in the fossil record (e.g., Frothero and Lazarus, 1980; Paul, 1992), as one would predict on the basis of almost any speciation model (Wagner and Erwin, 1995). The likelihood of sampling fossil ancestors is most apparent when dealing with anagenetically evolving lineages, i.e., cases in which there simply are not any true branching events.

Second, a theory of instantaneous branching events and infinite potential sets of characters is unrealistic and impractical (Remane, 1985). Speciation may be a complicated process during which interbreeding may continue for long periods of time. More importantly, the genome is not infinite and our samples of morphology and molecules are far less so. If we will never have more than a few dozen or hundred informative characters, it makes no practical difference if infinite sampling hypothetically could supply the apomorphies needed to “dislodge” a known ancestor.

A third, related argument concerns the function of phylogenetic trees. It is unlikely that any individual in a sample is a real ancestor falling exactly at a point of branching in a phylogeny. However, this is a problem only if our entire purpose is to represent the relationships of particular individuals. Most systematists are concerned with more general evolutionary patterns and accept the contrary argument that individual specimens are only of interest because they represent populations. Insisting that ancestor–descendant relationships are unknowable because cladograms only apply to individuals makes it impossible to distinguish anagenesis and cladogenesis and therefore to identify pseudoevolution due to anagenesis as Archibald (1993) attempted to do. A more reasonable approach is to argue that known morpho-
types should be used as approximations of real-world ancestors.

Finally, one or more autapomorphies are usually considered proof that a morphology is not ancestral. Hence, a fully pleiomorphic taxon may be identified as an ancestor until further evidence is gathered. In reality, the very existence of homoplasy makes it inevitable that some character states will come and go leading up to and beyond an ancestral morphology. Therefore, real ancestors always must be slightly apomorphic. A statistical method for identifying ancestral forms with tolerably small numbers of autapomorphies is a topic for future research.

CONCLUSION

This paper is not meant as an assault on competing phylogenetic and biogeographic methods. In many cases other methods may be more appropriate than continuous track analysis. For example, when a data set only includes living organisms and there is no reason to think that hybridization has occurred, a standard analysis using the minimal transition criterion may be adequate. One also may think that convergence patterns are not strong enough to require being accounted for with reticulations. However, it is incautious to justify use of the MT criterion by simply assuming that reticulations are uninformative and data sets usually exclude ancestral forms.

Perhaps even more importantly, most biogeographic studies are at risk if they fail to test for major dispersal events, even if the data only describe living organisms. Although standard biogeographic methods do allow “testing” for dispersal, their means of doing so are indirect and somewhat post hoc. For example, Brooks and McLennan (1991) advocated redefining biotas on the basis of preliminary Brooks parsimony analysis results. Similarly, there is no clear-cut criterion for choosing among the various “assumptions” of component analysis (Nelson and Platnick, 1981), even when using the explicit algorithms of Page (1987). In contrast, CTA indicates dispersal patterns with reticulating connections whenever the evidence is strong enough to support such hypotheses. CTA has other advantages: it differs from previous vicariance biogeographic methods in that it can serve without modification as a phylogenetic method, but it agrees importantly with them in its ability to use phylogenetic trees as data.

CTA relies on several unorthodox premises: (1) character state transitions are less important than track continuity, (2) real ancestors may be present in phylogenetic data sets, (3) absences are less important than presences in biogeographic analyses, and (4) reticulate evolution and dispersal should be recognized explicitly in evolutionary trees. Some of these claims are more fundamental than others. Even if all of them are flawed, continuous track analysis may at least serve as a starting point for the development of more rigorous and reasonable methods in phylogenetics and biogeography.

ACKNOWLEDGMENTS

I thank J. Flynn (Field Museum of Natural History) and R. Tedford (American Museum of Natural History) for providing access to specimens of Neogene horses and B. Chernoff, R. Evander, and R. Hulbert for encouraging my work on North American hippoponines. J. Harshman, G. Mikkelsen, J. Sepkoski, S. Suter, and P. Wagner graciously and efficiently reviewed the manuscript, which also benefitted from discussions at the Field Museum of Natural History, the University of Arizona, and the University of Michigan.

REFERENCES

BERNOR, R. L., H. TOBIEN, AND M. O. WOODBURN. 1990. Patterns of Old World hippoponine evolutionary diversification and biogeographic extension. Pages 263–319 in European Neogene mammal chro-


Received 10 May 1993; accepted 24 June 1994

APPENDIX 1

CHARACTER STATES FOR NORTH AMERICAN HIPPARIONINES

Cheek tooth morphological nomenclature was illustrated by MacFadden (1984) and Hulbert (1988). Characters identical to or only slightly modified from those of Hulbert (1988) are identified by his character numbers, which are listed in parentheses and prefixed with the letter H. Several other characters are based on descriptions by Hulbert and MacFadden (1991) or Bernor et al. (1990). Abbreviations: C = upper canine; c = lower canine; DOPF = dorsal preorbital fossa; i = lower incisor; M = upper molar; m = lower molar; P = upper premolar; p = lower premolar.

1. (H1) Depth of nasal notch. 0 = notch terminates over the midpoint of the C-P2 diastema; 1 = notch retracted, dorsal to P2 or just anterior to P2; 2 = notch dorsal to P3 or P4; 3 = notch dorsal to M1 or M2.

2. Buccinator fossa. 0 = shallow or absent; 1 = well developed, forms a distinct shelf.

3. Location of infraorbital foramen relative to DOPF. 0 = ventral to midline of DOPF; 1 = at anteroventral border of DOPF.

4. Location of infraorbital foramen relative to tooth row. 0 = above P3 or junction between P3 and P4; 1 = above P4 or further back.

5. (H2) Maximum depth of DOPF. 0 = fossa absent or very rudimentary; 1 = very shallow but outline still visible, <5 mm; 2 = shallow, about 5-10 mm; 3 = deep, >10 mm.

6. Development of DOPF marginal rim. 0 = rim or DOPF itself completely absent; 1 = anterior rim completely absent, dorsal and ventral rims weak or absent, posterior rim well developed; 2 = well-developed posterior, ventral, and dorsal rims.
7. Orientation of DPOF dorsal rim. 0 = horizontal, anterior end points straight ahead or toward incisors; 1 = oblique, anterior end points down to the C–P2 diastema or to the premolar row.

8. Development of DPOF posterior pocket. 0 = no posterior rim, no pocket, or shallow pocket created by posterior rim of DPOF; 1 = pocket deep, at least 5 mm.

9. (H10) Involvement of lacrimal in DPOF. 0 = lacrimal makes up rear portion of DPOF; 1 = lacrimal does not reach DPOF.

10. Preorbital bar length divided by upper tooth row length. 0 = less than 0.10; 1 = 0.10–0.20; 2 = 0.20–0.30; 3 = 0.30 or more.

11. Malar fossa. 0 = absent or clearly an extension of the DPOF; 1 = present.

12. Upper or lower tooth row length in middle wear. 0 = less than 105 mm; 1 = 105–125 mm; 2 = 125–140 mm; 3 = 140 mm or more.

13. (H71) Unworn M1 mesostyle or m1 metacanin crown height, ±2.5 mm. 0 = less than 20 mm; 1 = 25 mm; 2 = 30 mm; 3 = 35 mm; 4 = 40 mm; 5 = 45 mm; 6 = 50 mm; 7 = 55 mm; 8 = 60 mm or greater.

14. (H43) Curvature of upper cheek teeth. 0 = strongly curved, radius of curvature <40 mm; 1 = moderately curved or straight, radius of curvature >40 mm.

15. (H20) Presence of cement on deciduous premolars. 0 = no cement present; 1 = cement layer rudimentary, primarily on DP4 and dp4; 2 = thin but extensive cement coating on all deciduous cheek teeth; 3 = thick coating on all deciduous cheek teeth.

16. (H21) Presence of cement on permanent cheek teeth. 0 = thin layer of cement; 1 = moderate layer; 2 = thick layer.

17. Size and presence of DP1. 0 = large and always present; 1 = reduced and frequently absent or always absent.

18. Length of P2 divided by length of M1 or M2. 0 = greater than 1.25; 1 = less than 1.25.

19. Anterolateral border of anterocone on P2 and DP2. 0 = “pinched” by marked infolding of the enamel; 1 = straight or only very slightly concave.

20. Protocone shape, based on protocone length: width ratio (L/W). 0 = round (L/W < 1.2); 1 = oval (L/W = 1.2–1.6); 2 = elongate-oval (L/W = 1.6–2.0); 3 = elongate (L/W > 2.0).

21. Protoconal spur on P3–M2. 0 = elongate, well developed; 1 = frequently present but weakly developed; 2 = absent.

22. (H24) Protocone lingual border in P3–M2. 0 = usually convex; 1 = straight in most or all teeth; 2 = markedly concave in some teeth, never convex.

23. Width of M1 and/or M2 protocone divided by width of M1 and/or M2. 0 = less than or equal to 0.21; 1 = greater than 0.21.

24. Position of protocone and development of hypcone. 0 = protocone closer to anterior than posterior edge of cheek tooth, hypcone approximately as large as protocone and placed almost as far lingually as protocone; 1 = protocone centered between anterior and posterior edges of cheek tooth, notably larger than hypocone, and placed notably more lingually than hypocone and protoloph.

25. Timing of protocone connection to protoloph on P3–M2. 0 = immediate or during early wear; 1 = during middle wear; 2 = during later wear or never.

26. (H29) Timing of protocone connection to hypocone on M1 and M2. 0 = never; 1 = only in late wear; 2 = in early or middle wear.

27. Development of pli protoloph. 0 = protoloph absent or weak; 1 = protoloph single and persistent; 2 = protoloph persistent and multiple in early wear.

28. (H33) Development of internal fossette plications. Based on counts in early and middle wear. 0 = none, or a single nonpersistent pli is rarely present; 1 = very simple (plis usually single, often absent, prefossette loop not prominent); 2 = simple and nonpersistent (1–3 plis in early wear, only 1 by middle wear); 3 = simple and persistent (multiple plis in middle wear); 4 = moderately complex (2–5 plis); 5 = complex (3–7 plis); 6 = very complex (5–10 plis).

29. Development of pli hypoloph. Same states as character 27.

30. Development of pli caballin. 0 = pli caballin present only on P2–P4, if at all; 1 = pli caballin single, present on all teeth in early wear, nonpersistent on M1–M3, disappearing from these teeth in late wear; 2 = pli caballin always single, present, and persistent on all teeth; 3 = pli caballin bifid or multiple in early wear, at least in P2–P4, but generally in all teeth.

31. Plication at posterolingual corner of metatoth. 0 = strong, closes hypoglyph to form an enamel lake on most teeth in middle wear; 1 = strong, forms an enamel lake on some teeth in late middle wear; 2 = strong, may be multiple, rarely or never forms a lake; 3 = variably present and always single; 4 = absent, although corner is often flat or slightly pointed.

32. (H38 + H39) Timing of hypoglyph (hypocanoidal groove) obliteration on P2–M2. Hypoglyph includes enamel lakes, if formed. 0 = present to near base of crown; 1 = obliterated in late wear; 2 = obliterated in middle wear.

33. Connection of hypocone to metaloph in P3–M2. 0 = narrow, <2 mm in early wear; 1 = moderate, about as wide as the hypoglyph is deep; 2 = width greater than the hypoglyph depth by at least a 2:1 ratio.

34. Development of lingual hypocanoidal groove. 0 = deep, present in late wear; 1 = weak, absent or barely visible by middle wear.

35. Development of mesostyle. 0 = moderate, no neck; 1 = large, well-developed neck.

36. Groove on mandibular incisors. 0 = absent; 1 = present.

37. Relative position of i3 and c. 0 = in contact or
separated by <3 mm; 1 = separated by ≥2 mm and usually by about 5 mm.

38. Length of i3–p2 diastema divided by lower tooth row length. 0 = less than 0.65; 1 = 0.65 or more.

39. (H45) Size and presence of the dp1 in adults. 0 = large, usually present; 1 = reduced, frequently absent; 2 = very small, only rarely present.

40. Development of ectostyliids on dp2–dp4. 0 = always absent or very reduced; 1 = clearly visible on some or all teeth.

41. (H46) Development of protostyliids on dp3–dp4. 0 = weak, absent or present only near base of crown; 1 = moderate; 2 = very well developed.

42. (H49) Penetration of isthmus by ectoflexids on dp2–dp4. 0 = full; 1 = partial; 2 = none.

43. (H59) Paralophid plication. 0 = none; 1 = frequently present.

44. Extension of paralophid. 0 = paralophid generally extends to labial border of cheek teeth; 1 = paralophid is reduced and rarely extends labially farther than halfway across the cheek teeth.

45. (H52) Strength of protostyliids on p3–m3. 0 = weak, absent or present only near base of crown; 1 = moderate; 2 = very well developed.

46. (H54) Size of metaconid–metastylid complex. 0 = small; 1 = moderate; 2 = elongated.

47. (H55) Separation of metaconid and metastylid on p3–m3. 0 = hard to observe even in early wear; 1 = only clearly visible in early wear; 2 = persistent.

48. Shape of metastylid, especially in p2–p4. 0 = rounded; 1 = wide and subtriangular, often forming a point at the posterolingual corner.

49. Development of “cross” on p3–m3. 0 = metaconids and metastylids anteroposteriorly oriented, linguaflexids shallow, isthmus relatively long on p3–p4; 1 = metaconids and metastylids obliquely oriented, linguaflexids deep, isthmus very short even on p3–p4, i.e., isthmus, metaconids, and metastylids form a “cross.”

50. Isthmus plications, including the pli entotaxi. 0 = generally absent, but a small plication may be present on some teeth; 1 = one plication in most teeth; 2 = at least one plication on each side of the isthmus in several teeth.

51. Anterior plication on entoconids. 0 = absent, entoconids rounded; 1 = strong and persistent until late middle wear on P2–P4, but M1–M3 entoconids are always rounded; 2 = present on all cheek teeth in middle wear.

52. (H60) Pli caballinid on p2–p4. 0 = generally absent; 1 = small and usually lost by middle wear; 2 = large, present until late middle wear.

53. (H61) Pli caballinid on m1–m3. Same states as character 52.

54. Position of pli caballinid. 0 = originates from labial wall of the isthmus; 1 = originates from the junction of the isthmus and hypoconid.

55. Penetration of isthmus by ectoflexids. 0 = partial in p2, full in p3–m3; 1 = none in p2, partial in p3–p4, full in m1–m3; 2 = none in p2–p4, but full in m1–m3; 3 = none in p2–p4 and only partial in m1–m3.

56. (H65) Shape of protoconid–hypoconid labial borders. 0 = rounded; 1 = notably flattened.
APPENDIX 2. Character matrix for North American hipparionines. Dashes indicate missing data. See Appendix 1 for description of characters.

<table>
<thead>
<tr>
<th>Character</th>
<th>pri</th>
<th>nrs</th>
<th>col</th>
<th>ret</th>
<th>gra</th>
<th>shi</th>
<th>ins</th>
<th>aff</th>
<th>tra</th>
<th>goo</th>
<th>sph</th>
<th>dol</th>
<th>occ</th>
<th>teh</th>
<th>for</th>
<th>len</th>
<th>pen</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>19</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>23</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>26</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>27</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>28</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>31</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>32</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>34</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>36</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>37</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>38</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>39</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>40</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>41</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>42</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>43</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>44</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>45</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>46</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>47</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>48</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>49</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>50</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>51</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>52</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>53</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>54</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>55</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>56</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*pri = "Merychippus" primus; nrs = "M." nr. sejunctus; col = "M." coloradense; ret = Pseudhipparion retnusum; gra = P. gratum; shi = "Hippion" shirleyae; ins = M. insignis; aff = Neohipparion affinis; tra = Neohipparion transsese; goo = Cor-mohippuraner gooris; sph = C. sphenodus; dol = C. dolichops; occ = C. occidentale; teh = "H." tehonense; for = "H." foreri; len = Nannipps lenticularis; pen = Nannipps penertilusinus.