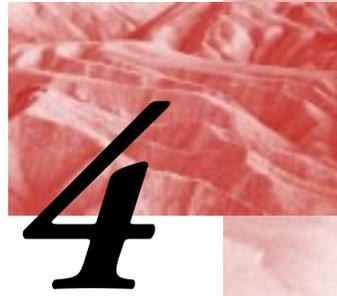


Chasing *Tyrannosaurus* and *Deinonychus* Around the Tree of Life: Classifying Dinosaurs



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We owe the word “dinosaur” and its formal version Dinosauria, meaning “fearfully great lizard,” to Sir Richard Owen. In 1842 he published a paper that described the fossil reptiles of Great Britain, and he noted that three were sufficiently different from all other reptiles to warrant a particular group name of their own: carnivorous *Megalosaurus*, herbivorous *Iguanodon*, and armored *Hylaeosaurus*.¹ In so doing, Owen began the study of classifying dinosaurs.

Classification facilitates conversation. In order to talk about anything, we have to have names and labels: words that refer to items we are discussing. This is true whether we are talking about sports teams, flavors of ice cream, emotions, or dinosaurs. Furthermore, we group these items into larger categories according to different rationales: teams by sport, league, or hometown; flavors of ice cream into fruits and non-fruits; emotions into “bad” (such as anger and hatred) versus “good” (such as happiness and love); and so forth. In other words, we look for a taxonomy (a system of names) and a scheme of classification.

Classification Schemes

Dinosaurs, as animals, are given names and are classified in the same way that all organisms are named and classified. Prior to the 1700s there was no single set of rules of taxonomy used by scientists. Instead, different cultures and different individuals in each culture organized animals, plants, fungi, and other organisms into particular schemes based on different attributes, such as the usefulness of the organism to humans, the danger it posed to humans, or its attractiveness. Carl von Linné, better known by the Latin form of his name, Linnaeus, developed the basic set of rules of biological nomenclature used by scientists since the mid-1700s. Linnaeus observed that the diversity of living things could be organized into a Natural System², based on the features

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present or absent in the physical form and on the behavior of the organisms. Linnaeus' system was universal. It could be applied to all organisms—plants, animals, fungi, and even bacteria. It was also international. The system established a set of names in Latin or Greek, or rendered into a Latinate form, to be used by scientists, regardless of their native tongue.

Nested Hierarchies

The Linnaean system was organized as a nested hierarchy—a set of categories within larger categories within larger categories, like boxes within boxes within boxes. Each named group, or taxon (plural taxa), is a unit of biological diversity. Small units, like the species *Tyrannosaurus rex*, are grouped into larger units, such as the genus *Tyrannosaurus*, which are grouped into even larger units, for example Tyrannosauridae, Theropoda, Saurischia, and Dinosauria.

Linnaeus himself wrote, at least in his early works, that he considered species to be fixed; that is, species did not change into other species. To him, the nested hierarchy was a useful descriptor of the diversity of life because it reflected the organized mind of the Creator. A century later in his 1859 masterpiece *The Origin of Species*,³ Charles Darwin recognized the underlying reason for this pattern—common descent with modification. Darwin discovered that organisms evolve in response to selection of some variations in a population relative to the other variations. His idea of evolution by Natural Selection is sometimes over-simplified as changes in a single lineage through time, but he also recognized it as responsible for larger patterns. Specifically, more than one set of variations in an ancestral population might preferentially survive relative to the rest of their kin. Over time different sets of variations (physical or behavioral attributes) would be selected for in the two different subpopulations. Eventually, these two subpopulations would be so different from each other that they would not be able to interbreed, and would therefore represent new species. Thus, Darwin recognized a mechanism by which a single common ancestral population could give rise to two or more new species, which themselves could sur-

vive and perhaps diverge into more species, or alternatively fail to survive and become extinct.

Darwin realized that this pattern of divergence of lineages through time was the reason that naturalists could uncover a nested hierarchical pattern to groups of organisms. For example, lions and tigers (*Panthera leo* and *Panthera tigris*, to give the formal names of these taxa) are more similar to each other than either is to grizzly bears (*Ursus arctos*), because lions and tigers share a more recent common ancestor with each other than they do with bears. Darwin recognized that the reason for the hierarchical nature of life was the tree-like structure of the history of life. He envisioned the stems of the tree representing common ancestors in the past whose descendants branched into different lineages, some going extinct, others surviving and perhaps developing additional branches; and he saw all evolving new and distinctive features in response to selection from the world around them. Closely related forms had diverged more recently from a common ancestral population, while distantly related forms represented branches that had split off further down the Tree of Life.

In *The Origin of Species* Darwin proposed that the Linnaean system would have to be modified to recognize that the organizing principle of taxonomy is ultimately “propinquity of descent”—that is, patterns of common ancestry. Darwin envisioned a method of classification where “more closely related to” meant “shared a more recent common ancestor with,” rather than simply “is more similar in appearance to.” Darwin recognized in *The Origin* that similarity might not always be a reliable indicator of shared ancestry. There are examples of anatomical or behavioral features evolving independently, also called convergently, in separate branches of the Tree of Life, particularly if those features were responses to similar environmental conditions. For example, animals that live in aquatic environments tend to evolve streamlined shapes, regardless of common ancestry. Therefore, he cautioned that new approaches to classification should take a look at many characters in combination, in the hope that the actual historical pattern of ancestry will show up.



The Method of Cladistics

After several attempts over the intervening decades to search for a new approach to classification that would reflect such patterns of ancestry, a German entomologist developed the organizing scheme used by most biologists today.^{4, 5} This entomologist, Willi Hennig, recognized that it would be impossible to know every single detail of the Tree of Life. Most individual animals and plants are eaten or decay before they can possibly be fossilized; indeed, many species of organisms will never be preserved in the fossil record because they did not live in environments where they would be likely to be buried, preserved, fossilized, and later discovered by paleontologists. However, Hennig recognized that the shape of the Tree of Life would reflect

primitive features, unique features, shared derived features, and convergent features. Some features are present in all the taxa being studied. Fig. 1 shows that in a set of four carnivorous dinosaurs (*Allosaurus*, *Deinonychus*, *Albertosaurus*, and *Tyrannosaurus*) all had three features in common: (1) a hinge in the middle of the lower jaw, (2) a wishbone, and (3) bipedality. Since they shared these features, then presumably the same features would be found in the common ancestor of these four dinosaurs, and hence they are considered to be primitive (or ancestral) features. Alternatively, the most recent common ancestor of *Allosaurus*, *Deinonychus*, *Albertosaurus*, and *Tyrannosaurus* may have lacked a hinged jaw, lacked a wishbone, and walked on all fours, and in which case each of these four dinosaurs evolved

Fig. 1. Four carnivorous dinosaurs, and observations of their features.

	<i>Allosaurus</i>	<i>Deinonychus</i>	<i>Albertosaurus</i>	<i>Tyrannosaurus</i>
1) Hinge in lower jaw	Yes	Yes	Yes	Yes
2) Wishbone	Yes	Yes	Yes	Yes
3) Bipedal	Yes	Yes	Yes	Yes
4) Retractable sickle claw	No	Yes	No	No
5) Backwards-pointing pubis	No	Yes	No	No
6) Number of fingers	3	3	2	2
7) Third metatarsal in foot	Unpinched	Unpinched	Pinched	Pinched
8) Astragalus (ankle bone)	Short	Tall	Tall	Tall
9) Tip of ischium	Expanded	Pointed	Pointed	Pointed

relative recency of common ancestry and this ancestry can be approximated by the distribution of features among the organisms that are available. Hennig’s method became known as cladistics (from clade, or “branch”), because it is primarily concerned with recovering the branching order of common ancestry. The method of cladistics is the search for the simplest distribution of derived features to approximate the historical branching pattern of the Tree of Life.

Different Types of Features

Hennig noted that the features found in a set of organisms fall in four general categories:

the features independently. However, that would require more evolutionary changes than the more straightforward, simpler explanation that they had all three features in common. Primitive features reveal that the taxa are related at some level, but they don’t help us resolve who is more closely related to whom.

Unique features are those found in only one of the taxa being examined. For example, among the four dinosaurs considered, two features are found only in *Deinonychus*: (4) retractable sickle claw on the foot and (5) a backward-pointing pubis (Fig. 1). These features must have evolved after the ancestor of



Deinonychus split from all the other meat-eating dinosaurs in this study. They may be helpful in recognizing *Deinonychus*, but they don't help us to determine which of the remaining three dinosaurs was the closest relative of *Deinonychus*. It should be noted that the use of "unique" or "primitive" for these features applies only to this particular analysis. For example, *Velociraptor* also had a retractable sickle claw and a backward-pointing pubis. Had it been included in the present study, these features would be shared between *Velociraptor* and *Deinonychus*, rather than limited to the latter.

The remaining features of the original set are found in more than one, but not all, of the dinosaurs being studied. These features evolved after the ancestors of the four dinosaurs in this study began to diverge from a common ancestor, and are called derived features. Hennig recognized that derived features potentially serve as clues to help discover the branching pattern of the Tree of Life, because they evolved on a lineage leading to some, but not all, of the taxa being studied. Hennig also recognized that there are two subsets of derived characters. Some features might be convergent. These convergent features would not help us discover patterns of common ancestry because they were evolved independently. The other features, though, may be shared derived features: evolutionary novelties inherited from a common ancestor. Hennig understood that by discovering the pattern of shared derived features, we might approximate the branching order of the lineages leading to the creatures we are studying.

Reconstructing the Tree of Life

Several features in this example represent derived, but not unique characters (Fig. 1). These include (6) a two-fingered (rather than three-fingered) hand, (7) a pinched third metatarsal in the foot, (8) a tall astragalus ankle bone, and (9) a pointed ischium. None of these evolutionary novelties occurs in *Allosaurus* (and indeed are lacking in meat-eaters more primitive than *Allosaurus*, such as *Torvosaurus*, *Ceratosaurus*, and *Coelophysis*). This observation suggests that the lineage leading to *Allosaurus* represents

the first of all the forms in this study to branch off from the others. Thus, the features found in *Allosaurus* represent the ancestral condition for the four taxa in this analysis. However, it is important to understand that we do not regard *Allosaurus* as the actual ancestor of any of the dinosaurs in question!

Of the remaining three, *Deinonychus*, *Albertosaurus*, and *Tyrannosaurus*, it is likely that one pair of these dinosaurs had a more recent common ancestor than either did with the third. There are in fact three possibilities for this situation:

- 1) *Deinonychus* and *Tyrannosaurus* shared a more recent common ancestor with each other than with *Albertosaurus* (Fig. 2A);
- 2) *Deinonychus* and *Albertosaurus* shared a more recent common ancestor with each other than with *Tyrannosaurus* (Fig. 2B); or
- 3) *Tyrannosaurus* and *Albertosaurus* shared a more recent common ancestor with each other than with *Deinonychus* (Fig. 2C)

We do not know ahead of time which of these three possibilities is correct, but we can construct our hypothesis based upon the evidence. The criterion for determining which pairing is most likely is simplicity. All other things being equal, we choose the simplest answer. This criterion, known more formally as parsimony, is a standard principle in science. When multiple possible explanations exist, the one that requires the fewest assumptions is likely to be more nearly correct.

The three possibilities can be represented as branching diagrams called cladograms (Fig. 2). A cladogram is the graphic representation of a hypothesis of the relationships between taxa. Unlike traditional evolutionary family tree drawings, in which the vertical lines represented the actual group of reproducing organisms through time, the lines (branches) and the nodes joining the branches are just place holders to represent common ancestry. For example, in Fig. 2C, there is a single node marked "a" that represents the shared ancestry of *Albertosaurus* and *Tyrannosaurus*. The next node towards the base of this tree, marked "b," represents that there is a common ancestor



shared by *Deinonychus* and the lineage leading to *Albertosaurus* and *Tyrannosaurus*. And finally, there is a node “c” that represents a common ancestor shared by *Allosaurus* and all remaining forms.

Choosing the Best Hypothesis

As explained, only shared derived features can actually inform us about the pattern of shared ancestral relationships. For any given set of taxa, more than one solution is possible (that is, more than one possible cladogram), each representing a different hypothesized relationship. By counting the number of evolutionary changes required to produce each of these trees, we can find the most parsimonious (simplest) solution to the distribution of features we see.

Using our example in Fig. 2A, we find that this cladogram is explained by 11 evolutionary changes: one change each for the three primitive features shared by all; one change each for the two unique *Deinonychus* features; and the remaining two features each evolving independently—once each on the line leading to *Tyrannosaurus*, and once each on the line leading to *Albertosaurus*. Similarly, the cladogram in Fig. 2B shows a similar distribution requiring 11 changes, but in this case the changes in features 8 and 9 are explained as reversals (evolving back from the derived state), having been present in the common ancestor of *Tyrannosaurus*, *Albertosaurus*, and *Deinonychus*, then reversed along the line leading just to *Deinonychus*. Finally, the cladogram in Fig. 2C requires only 9 steps, with features 6 and 7 being present in the common ancestor of *Deinonychus*, *Albertosaurus*, and *Tyrannosaurus*, and features 8 and 9 evolving only a single time—after the common ancestor of *Alberto-*

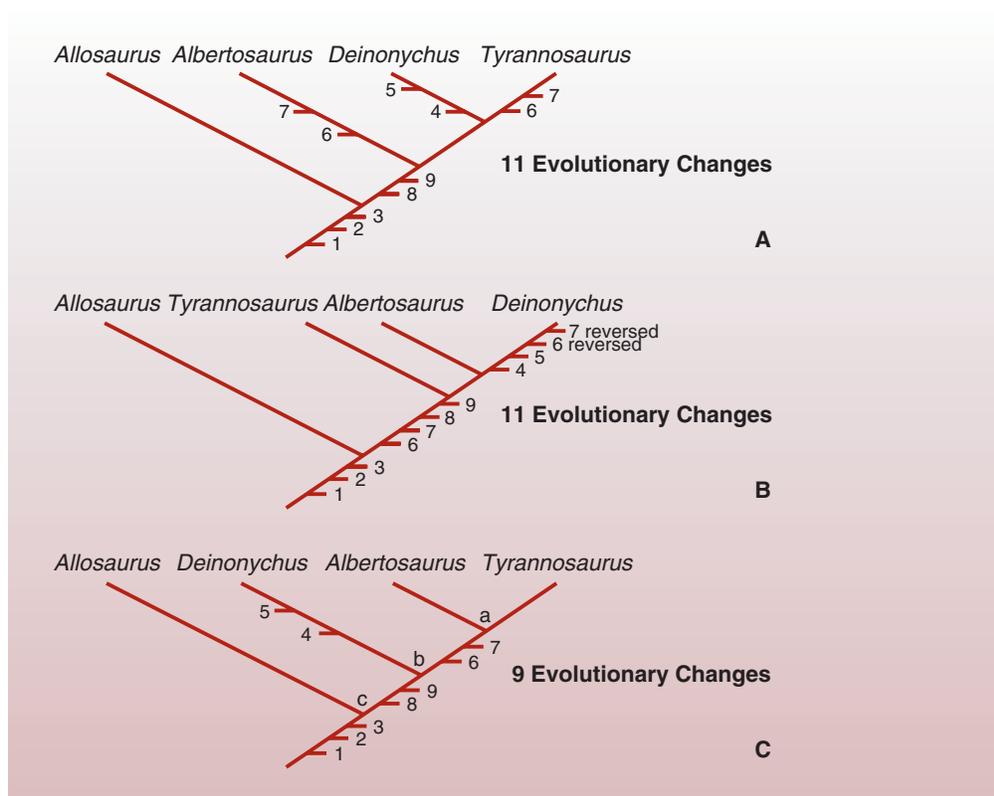


Fig. 2. The three possible different cladograms for the dinosaurs from Fig. 1, showing the distribution of derived features in each. Numbers along the branches represent the various features from Fig. 1. Note that the cladogram in 2C requires the fewest number of evolutionary changes, and so would be the one preferred in this analysis.

saurus and *Tyrannosaurus* split off from the line leading to *Deinonychus*, but before the ancestors of *Albertosaurus* and *Tyrannosaurus* split from each other. So, all other things being equal, we would choose the cladogram in Fig. 2C, with the fewest number of evolutionary changes, as representing the closest approximation to the actual historical pattern of common ancestry.

Is the cladogram in Fig. 2C the true historical pattern? We can't know for certain. It is only our best hypothesis for the pattern, given the data at hand. An advantage to the cladistic method is that its results can be subjected to further tests. For example, new taxa or new features can be added to the analysis, and if the simplest distribution of derived features in the new analysis matches the previous results, the original hypothesis is supported. If not, the original hypothesis would be rejected in light of new observations.



Advantages of the Cladistic Method

That new analyses can be run with the addition of new data gives cladistic analyses distinct advantages over the traditional method of simply connecting possible ancestors and possible descendants through time. A cladistic analysis searches for patterns of relative common ancestry, something we can be more secure about. At some level there is a common ancestor for every pair of species that ever existed. Neither *Triceratops*, nor a dog, nor a dandelion is an ancestor or descendant of the others, but we can still recognize that the first two shared a common ancestor not shared by the plant. Thus, even if some, or even many, of the individual species along the actual branches of the Tree of Life are missing, we can approximate its shape, understanding that additional data may change that approximation.

Additionally, the nature of cladistic analyses makes them relatively easy to conduct using computer programs. After a scientist has coded the observations of derived features for various taxa and entered those data into a search program, a computer can sort through millions, or even billions of trees, searching for the best—most parsimonious—results. So, more and more complex analyses, each with dozens of taxa and hundreds of features, can be conducted far faster than a human being could ever hope to achieve with a pad of paper and a pencil. Such studies are now commonplace throughout biology and paleontology, using not only the shapes of bones, but also soft tissues, DNA sequences, and even behavioral features. These studies often result in many equally simple cladograms, all of which are equally good approximations given the data available. Better approximations will be reached by running analyses as more evidence is gathered.

Cladistic Classifications

Darwin put forth the idea that a good organizing principle for classification would be patterns of common ancestry. Hennig's method of cladistic analysis allows the most likely pattern of common ancestry to be recovered and used as a basis of classification.⁶

One method, favored by many biologists (including the majority of dinosaur paleontologists), is a scheme proposed by Hennig himself, in which all taxon names represent clades (complete branches of the Tree of Life). Each named group represents an ancestor and all of its descendants. For example, on cladogram Fig. 2C, node “a” would represent the clade Tyrannosauridae containing, in this very reduced cladogram, only *Tyrannosaurus* and *Albertosaurus*. Node “b” would be the larger group Coelurosauria, containing Tyrannosauridae and *Deinonychus*; and finally node “c” would be Avetheropoda (*Allosaurus* plus the coelurosaurs). Over time, some members within a clade might become more and more transformed from the ancestral condition as new features evolved. However, they would still be considered part of the clade because they descended from that common ancestor.

So, What Are Dinosaurs? A Basic Classification

Using the methods outlined above, the position of dinosaurs within the Tree of Life (Fig. 3) and the details of the cladogram of the dinosaurs themselves (Fig. 4) have been reconstructed. Although broad consensus exists about most of the details, there are sometimes discrepancies in the exact results obtained in different studies.^{7, 8, 9, 10} These discrepancies may reflect the choice of features selected for comparison, or may simply be a reflection of lack of information about some aspects of the fossils in question.

Cladistic analyses of the tetrapods consistently show that dinosaurs are a subgroup within the archosaurian reptiles, a group that includes crocodylians among living forms, as well as many extinct creatures.¹¹ Note that calling dinosaurs “reptiles” in the cladistic sense tells us nothing about whether dinosaurs were cold-blooded or warm-blooded. Like all cladistic names, Reptilia is a group defined by common ancestry, rather than by a general grade of organization. Dinosaurs and their closest relatives, such as *Marasuchus*, are distinguished from all other reptiles by a fully upright stance of the hindlimbs and a simple ankle joint. Fur-



thermore, Dinosauria itself is distinguished by an open hip socket. Because of the incompleteness of the fossils of the immediate closest relatives of dinosaurs, there is some uncertainty as to what other features characterize the common ancestor of all dinosaurs.

Two main branches exist within Dinosauria: Ornithischia and Saurischia. The ornithischians include *Iguanodon* and *Hylaeosaurus* among the original three members of Owen's Dinosauria, as well as all the dinosaurs sharing a

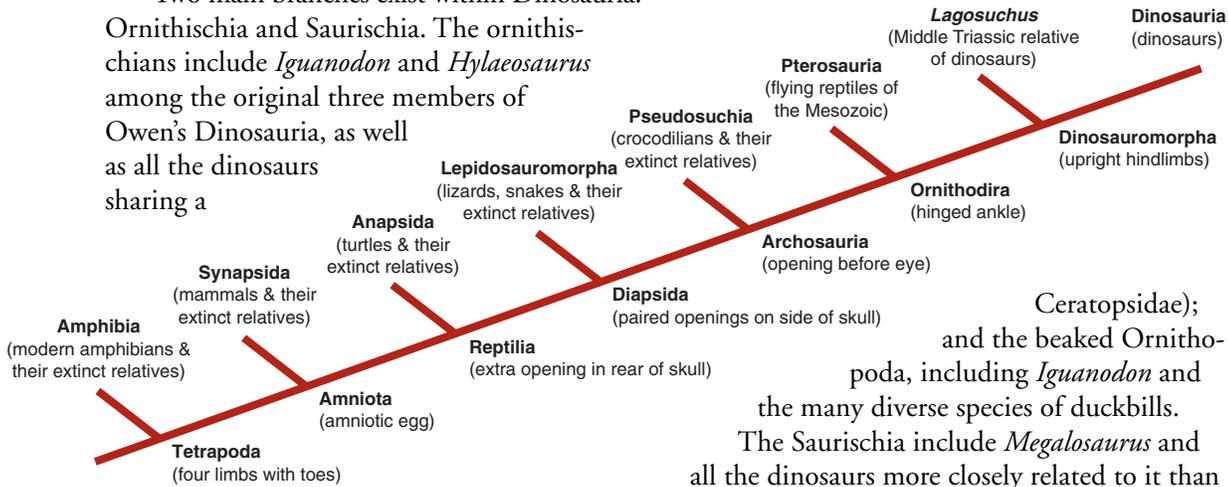


Fig. 3. A cladogram showing the position of dinosaurs among the four-limbed vertebrates.

more recent common ancestor with them than with *Megalosaurus*. At present all known ornithischians seem to have been herbivorous. In fact, they all had an extra jawbone (the prementary) which held part of a horny beak for chopping up plants. All but the most primitive had a backward-pointing pubic bone, presumably allowing for the increased gut space necessary to digest large amounts of vegetation. Major groups of ornithischians include the armored Thyreophora, comprising

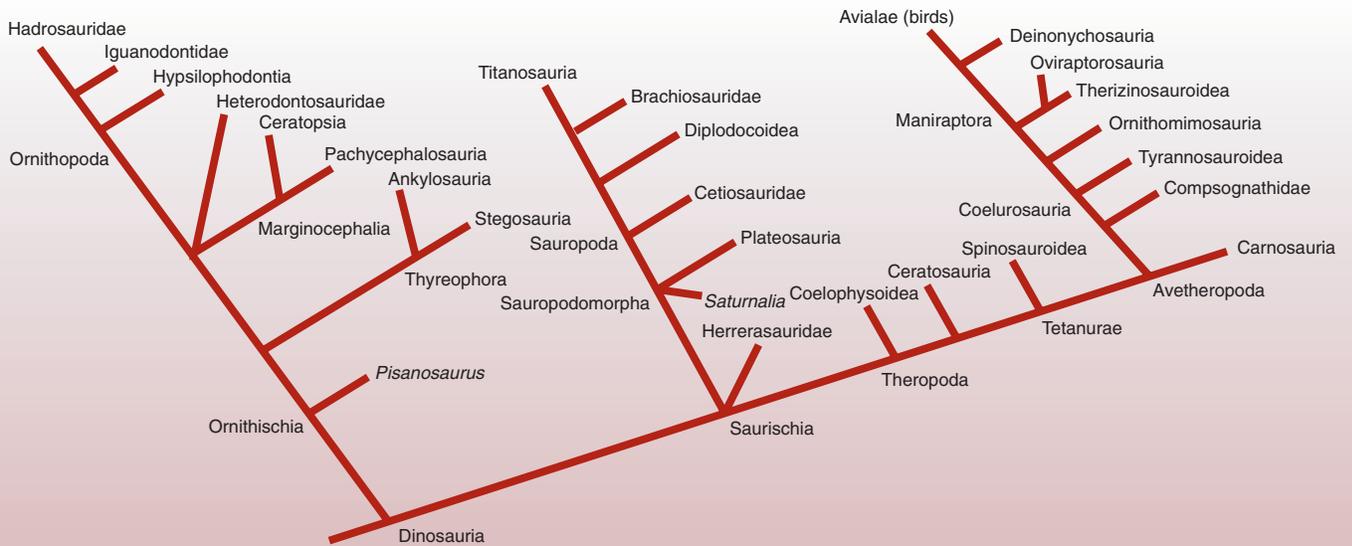
the plated Stegosauria, tank-like Ankylosauria, and their closest relatives; the ridge-headed Marginocephalia, including the dome-skulled Pachycephalosauria and the parrot-beaked Ceratopsia (most famously including *Triceratops* and the other horned

Ceratopsidae); and the beaked Ornithopoda, including *Iguanodon* and the many diverse species of duckbills.

The Saurischia include *Megalosaurus* and all the dinosaurs more closely related to it than to *Iguanodon*. One clade of saurischians is the long-necked herbivorous group Sauropodomorpha. Sauropodomorphs include primitive bipedal forms like *Saturnalia* and *Plateosaurus* as well as the gigantic quadrupedal Sauropoda (such as *Apatosaurus*, *Brachiosaurus*, and *Argentinosaurus*). True sauropods are the largest animals ever to walk the land.

Perhaps the most diverse clade of dinosaurs is the Theropoda. Theropods contain the various carnivorous dinosaurs, from tiny *Compsognathidae*;

Fig. 4. A basic cladogram of the relationships among the major groups of dinosaurs.





gnathus and *Microaptor* through giants such as *Tyrannosaurus*, *Spinosaurus*, and *Giganotosaurus*. Birds represent descendants of small carnivorous dinosaurs (see Currie, page 89). Indeed, by the principles of cladistic classification birds are members of the Dinosauria.

The methods of cladistic analysis continue to hold great promise for our understanding of the evolution of the different groups of dinosaurs. New studies continue to determine more precisely the relationships of the various

species of dinosaurs in each of the major groups. Furthermore, by using the principles of parsimony and an understanding of the shape of the Tree of Life, paleontologists are attempting to discover the pattern of evolution of various aspects of the biology and behavior of dinosaurs. Recovering the interrelationships among the dinosaurs and their position among the vertebrates is only the first step in exploring the evolution of this amazing group of reptiles.

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