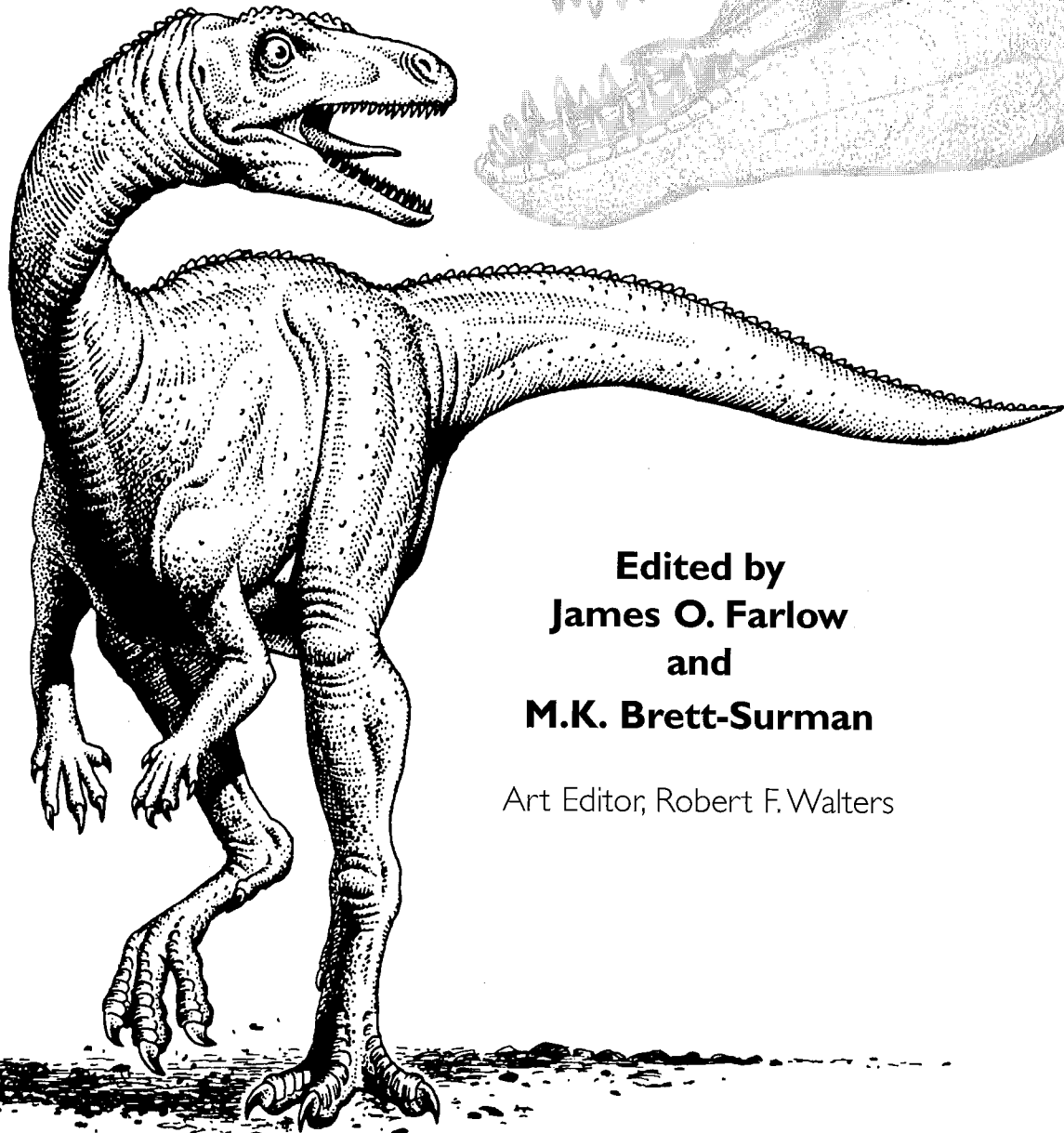


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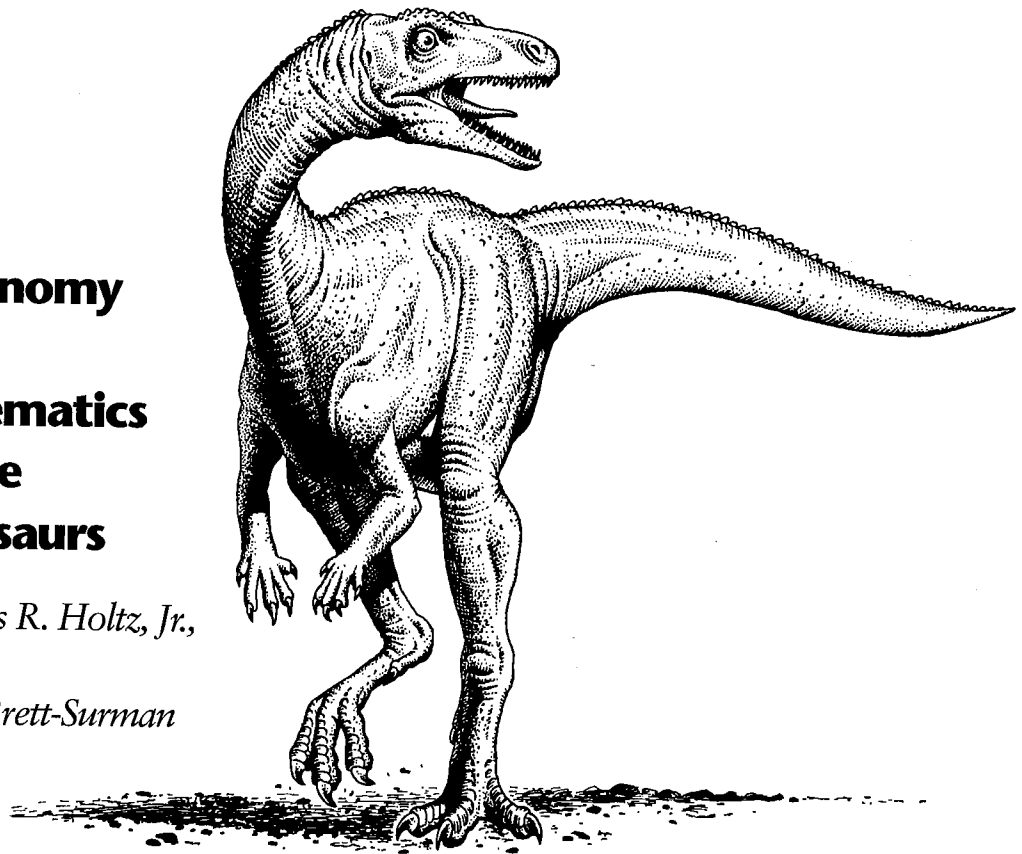


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The Taxonomy and Systematics of the Dinosaurs

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What's in a Name? Taxonomy

Taxonomy, the “naming of names,” is the scientific practice and study of labeling and ordering like groups of organisms. It should not be confused with systematics, the scientific study of the diversity of organisms within and among clades (genetically related groups of organisms). Both help us to understand the world of organisms, but each practice helps us in a different way: systematics, to understand relationships among organisms, and taxonomy, to give internationally standardized names to organisms and groups of organisms in order to increase the efficiency of communication among researchers.

All languages have common names for different plants and animals. The main problem is that all languages have *different* names for the same plants and animals! This was not a problem until natural historians started to catalogue and study the floras and faunas from around the world. It was realized by western Europeans that the animals and plants of India, eastern Asia, the Pacific Islands, and particularly the “New World” of North and South America had great economic value as sources of medicine, spices, food, and furs. Whoever was the first to find and identify new plants and animals of economic importance in these regions would have the best access to these resources. Thus it became important to identify and classify these organisms.

There was initially a great deal of confusion as the great exploring and

colonizing European countries each used their own names for the plants and animals they were discussing in the scientific literature. The only compromise that pleased all concerned was that every organism would be given a formal, official name based upon Latin or Greek, the language of the most highly educated Europeans and the Catholic church. In the seventeenth century, Caspar Bauhin (1623) and John Ray (1686–1704) invented the precursors of the later binomial (two-name) system. They introduced the concept of genus and species. It was not until the eighteenth century that these names were organized into a hierarchy of divisions (kingdom, class, order, family, genus, species) by Carl Linné (formally known as Carolus Linnaeus, a natural historian and botanist in mid-1700s Sweden) and his successors (Linné 1758).

The basic principle of Linnaean taxonomy is the nested hierarchy, in which each group is nested in a series of larger and larger, and thus more inclusive, groups. Each group is a taxon (plural *taxa*), a named group of organisms. Living taxa are recognized by their unique combinations of anatomical characters—bones, skin, hair/feathers/scales, physiology, DNA sequences, reproductive features, and so on. Extinct vertebrate taxa can be defined only by their bones and teeth.

Taxa are named in Latin or Latinized forms of other languages. Among other languages, Greek is the most common in taxonomy, but any other language (including English, Mongolian, Sanskrit, and the invented Elvish languages of J. R. R. Tolkien!) will do, as long as it has Latinized endings. All taxa, of whatever level, must be in a latinized form. Taxonomic names can be named after many things, including

- features of the anatomy: *Mammalia*, for the mammary glands;
- general appearance: *Anatotitan*, the “Titanic Duck,” for a duckbilled dinosaur;
- behavior (alleged or otherwise): *Tyrannosaurus rex*, the “King Tyrant Lizard”;
- name of their discoverer or other significant individual: *Lambeosaurus*, discovered by L. Lambe;
- the location from which it was found: *Edmontonia*, an armored dinosaur first discovered in Edmonton, Canada;
- or anything else the namer decides.

The most basic taxonomic levels, to which every living organism can be assigned, are the genus (plural *genera*) and species. The rules of nomenclature (the official naming of taxa) are based on a species. Species names are listed only along with the genus name, never by themselves. Species are, literally, more specific words than genera: species refer to a smaller total number of organisms than do genera. The international rules for naming a new species are governed by the International Code of Zoological Nomenclature (ICZN).

The exact biological and philosophical boundary where one species ends and another begins (or, more practically, whether a given specimen is assignable to a particular species) is the subject of much debate among biologists and paleontologists. Different criteria are used to define species by different scientists. Some, for example, use the degree of similarity or difference in the genetic code of a newly found organism in comparison with a catalogued specimen to include or exclude the new individual in the catalogued species. Others define the boundary of a species based on evolutionary divergence or “lineage splitting”: All individuals who had a more recent common ancestor with a catalogued specimen than with another catalogued specimen are included in the first specimen’s species.

One way many biologists determine whether two or more individuals are members of the same species is to observe the results of matings between individuals. If under natural conditions they mate and produce offspring that themselves can produce offspring, then the original two individuals are members of the same species. If the two individuals cannot mate, or do not produce living offspring, or the offspring they produce are sterile, then the two original specimens are not members of the same species. Of course, this is an impossible test with fossil individuals! For dinosaur studies, an individual is assigned to a species only if it shows a high degree of physical similarity in many parts of the skeletal anatomy to others thought to be in that species. The determination of which characteristics of the skeleton to use in classification is somewhat subjective.

A genus is defined as a group of one or more closely related species. If two members of the same genus but different species mate, they may have living offspring, but those will be sterile in almost every case (e.g., mules, the sterile offspring of the horse, *Equus caballus*, and the donkey, *Equus asinus*). Genus names are often listed by themselves. (Most people know dinosaurs only by their generic, not their specific, names; for example, people say "Triceratops," not "Triceratops horridus.") Genera are, literally, more generic than species: Genera refer to a larger number of individuals than do species. The Linnaean binomials are thus the reverse of the European style of names of individuals, in which the personal ("Christian") name comes first and the surname last. If the authors of this chapter were to write their names in analogy with a Linnaean binomial, they would be called *Holtz thomas* and *Brett-Surman michael*. The following are some examples of the names of modern animal species: humans, *Homo sapiens* (thinking person [Linnaeus was an optimist]), abbreviated *H. sapiens*; cats, *Felis cattus* (cat); dogs, *Canis familiaris* (familiar dog); moose, *Alces alces* (elk elk); and the American alligator, *Alligator mississippiensis* (Mississippi alligator). Some dinosaur species include *Tyrannosaurus rex* (king tyrant lizard), *Apatosaurus excelsus* (surpassing deceptive lizard), *Triceratops horridus* (roughened three-horned face), and *Iguanodon mantelli* ([British naturalist Gideon] Mantell's iguana tooth).

Linnaean species names are written *Genus species*, always in italics (or underlined in the case of handwriting or typescript). The species name is abbreviated *G. species*. Although it once was common practice, the trivial name is never capitalized: for example, *Tyrannosaurus Rex* (a usage seen in many popular books) is incorrect; the proper form is *Tyrannosaurus rex*. It is never proper taxonomic grammar to use a trivial nomen by itself (for the example above, *rex* or *Rex* by itself is never correct; only *Tyrannosaurus rex* or the abbreviation *T. rex* is proper).

Type Specimens, Priority, Synonymy, and Validity

Linnaean taxonomy is based on the idea of type specimens. A type is the actual individual specimen which is first given the name. Types are the "name holders" only—they are not sacred objects that represent what a species should look like. They are simply the first reference specimen to carry a new name. This specimen must be

- deposited in an accredited institution where it is available for study;
- catalogued (for example, the type specimen of the duckbilled dinosaur

Edmontosaurus annectens, in the collections of the National Museum of Natural History [Smithsonian Institution], is catalogued under number USNM 2414); and

- described in the scientific literature where its name is presented.

Additional specimens are assigned to a species (or genus or other taxon) based on how closely a taxonomist believes the new specimen is related to a type. If the specimen is very similar, showing all the features, it is probably the same taxon. However, if the specimen does not show any features that disqualify it, but it shows no features that are definitely distinctive of the taxon, it can be questionably assigned to the taxon. If the specimen shows new features, it may be a new taxon.

For example, William Buckland's first dinosaur was not like any other known reptile, so he considered it a new genus and named it *Megalosaurus*. Gideon Mantell's first dinosaur was likewise not identical to any other known reptile, so he considered it a new genus, and his specimens were made the type of *Iguanodon*.

Each species has a type specimen. Each genus, in turn, has a type species (the first species to be given that generic name).

Not all types are complete specimens. Most fossil vertebrate types are incomplete skeletal material. So it is not uncommon for two (or more) names to be proposed which later to turn out to be the same genus or even the same species! When this happens, the oldest valid name (by date of publication) has priority, and is the official name of that taxon. The younger names are considered junior synonyms and not used. For example, the name *Troodon formosus* was given to a dinosaur tooth named by Joseph Leidy in 1856. Much later, in 1932, Charles M. Sternberg named a very fragmentary skeleton of a small dinosaur *Stenonychosaurus inequalis*. More complete skeletons found after the 1960s showed that the tooth called *Troodon* and the fragments called *Stenonychosaurus* belonged to the same species. Because the former was named seventy-six years earlier, it had priority, and the small bird-like dinosaur is properly called *Troodon formosus*. For a more famous (some would say infamous) example of the use of priority, see chapter 20 of this volume for the history of the names "*Brontosaurus*" (note that invalid names are enclosed in quotation marks) and *Apatosaurus*.

Although some specimens may be named new species on valid grounds at the time, later discoveries can show that these fossils are not distinct. The names based upon these types are then considered invalid. Only those specimens with distinct features can be valid types.

For example, S. H. Haughton in 1928 referred some dinosaur bones from Africa to a new species, *Gigantosaurus dixeyi*. The type material of *Gigantosaurus* (*G. megalonyx* from England, named in 1869 by H. Seeley) turned out to have no characters distinct from other dinosaur species or genera. "*Gigantosaurus*" *dixeyi* was left without a proper generic name until Jacobs and colleagues transferred the species to a new genus, *Malawisaurus*, in 1992.

Family and Family Group Names

Biologists have long recognized that animals can be grouped together hierarchically not only into species and genera, but also into larger and larger groups. For example, lions (*Panthera leo*) and tigers (*Panthera tigris*) can be grouped with domestic cats (*Felis catus*) because of many similari-

ties, including their retractable claws. Cats can be grouped with bears and dogs because of their specialized cheek teeth. Cats, dogs, and bears can be grouped with horses, humans, and whales because they all give milk. And so on, throughout the living world.

Each of these groupings can be considered a taxon. For most taxa larger than the genus, there are no specific rules for names, other than the requirement that the names be in Latin or a Latinized form of other languages. For example, Richard Owen used three known genera (*Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*) that together were so distinct from all others that he gave them their own name, "Dinosauria" (Latinized Greek for "fearfully great lizards"). Unlike species names (which are always of the form *Genus species*), taxa from the genus and higher taxonomic levels have one-word names only: Felidae, Carnivora, Mammalia, etc. Unlike the species or genus names, taxa higher than the genus are never italicized. Other than that, there are few rules for most higher taxonomic names. One special type of taxon which does have special rules of nomenclature is the family (and the related subfamily and superfamily). A family is an assemblage of closely related genera, such as the cats (great and small), the dogs (from foxes to timber wolves), or the ostrich dinosaurs. Each family has a type genus (just as genera have type species and species have type specimens) from which that family gets its name. The family name comes from the name of the type genus (above, *Felis*, *Canis*, and *Ornithomimus*, respectively), modifying the ending according to Latin rules (generally dropping the *-is* or *-us*), and adding the suffix *-idae* (Latin for "of the family of"). Thus, the cat family is Felidae, the dog family Canidae, and the ostrich dinosaur family Ornithomimidae (remember that since a family is larger and more inclusive than a genus or species, the name is not italicized). When families are spoken of informally, their names are used in the lowercase, and the *-idae* ending becomes *-id*: above, felid, canid, and ornithomimid (see Table 8.1).

Table 8.1
Family Group Suffixes

Rank	Formal Suffix	Vernacular Suffix	Examples (Formal, Vernacular)
Superfamily	-oidea	-oid	Hadrosauroidae, hadrosauroid
Family	-idae	-id	Hadrosauridae, hadrosaurid
Subfamily	-inae	-ine	Hadrosaurinae, hadrosaurine

Traditionally, each genus belonged to a family, even if that genus was the only member of the family. However, some scientists now use families only when two or more genera are grouped together (see below).

Sometimes a family has so many genera that it becomes important to recognize groups within the family that contain more than one genus. A new taxon, the subfamily, is used for these smaller divisions. Subfamily names are formed by taking a type genus (just as in family names) and adding *-inae* instead of *-idae* to the shortened genus name. For example, Hadrosauridae, the family of duckbilled dinosaurs, contains more than

thirty distinct genera. Those closer to *Hadrosaurus*, with solid or no crests, broad bills, and very large nostrils, are grouped into the subfamily Hadrosaurinae, while those closer to *Lambeosaurus*, with hollow crests, narrow bills, and smaller nostrils, are grouped into the subfamily Lambeosaurinae. Some taxonomists split subfamilies into even smaller divisions (such as tribes, subtribes, supergenera, etc.), but this practice is not yet common in dinosaur taxonomy.

On the other hand, sometimes taxonomists want to recognize a taxon which includes a family and other closely related families or genera. The most common way to do this is to name a superfamily. Superfamilies are formed by taking a type family and changing the *-idae* ending into *-oidea*. For example, paleontologists recognize that the Allosauridae and Sinraptoridae, two families of carnivorous dinosaurs, are closely related. They are grouped together into the superfamily Allosauroidae.

Systematics

Systematics is the scientific study of the diversity of organisms within and among clades (genetically related groups of organisms). Systematics is related to taxonomy in that the former is the practice of identifying evolutionarily significant groups of organisms, while the latter is the practice of naming those evolutionarily significant groups. Traditionally, there have been two different methods of systematics employed by vertebrate paleontologists, evolutionary systematics (sometimes called evolutionary taxonomy or gradistics) and phylogenetic systematics (often called cladistics). Since the methods vary between these types of systematics, the taxonomy associated with each also varies.

Evolutionary Systematics: Grades

Evolutionary systematics ("gradistics") is an eclectic system of classification based upon morphological similarity and the Linnaean taxonomic hierarchy. Groups of organisms are recognized by their physical resemblances. In order to be considered valid, all members of a gradistic taxon must have a common ancestor which was also considered a member of that taxon (for example, the common ancestor of all lizards must be a lizard, or the common ancestor of all dinosaurs a dinosaur). However, unlike cladistics, a gradistic taxon can exclude descendant groups if the descendants share a great number of anatomical advances not shared by any other member of the larger group. In other words, only those organisms of the same grade of development are included together in a taxon, while descendants of a higher grade of development are excluded from this taxon. For example, snakes all lack legs and eyelids and have many specialized characters not shared by their ancestors (which were lizards), so the snakes (Ophidia) are excluded from the lizards (Lacertilia) under gradistic systematics. Similarly, under gradistics, birds (Aves) are excluded from their reptilian ancestors because birds possess many specialized features (toothless beaks, wishbones, feathers, warm-bloodedness, and many more) not found in turtles, lizards, snakes, crocodiles, and the like. Some taxonomists under gradistics even allow groups of animals of the same grade of organization not descended from the same common ancestor to be placed in their own taxon. Although this practice was never common, some still use this extreme version of gradistics.

Under evolutionary taxonomy, all taxa are assigned a Linnaean rank. The standard Linnaean ranks are phylum, class, order, family, genus, and species. Linnaean taxonomy is a system of nested hierarchies: in practical terms, this means that each phylum contains one or more classes, each class one or more orders, and so on. As commonly used, each species in evolutionary taxonomy must belong to a genus, family, order, class, and phylum, even if that species is the only known representative of each of those higher taxa (a case of redundant taxonomic names). For example, the ancestral bird species *Archaeopteryx lithographica* is the only known species of the Genus *Archaeopteryx*, the Family Archaeopterygidae, the Order Archaeopterygiformes, and the Subclass Sauriurae. "Archaeopterygidae," "Archaeopterygiformes," and "Sauriurae" are thus redundant taxa.

It has long been recognized that there are subgroups which are intermediate between Linnaean ranks, so various prefixes (*super-*, *sub-*, *infra-*, and many others) have been used for these intermediate ranks (superclass, subfamily, infraorder, for example). Also, some taxonomists have added additional ranks (division, cohort, etc.) which are intercalated between previous ranks. However, this ultimately resulted in a bewildering number of ranks and subranks, as shown in Table 8.2. Because the number of intercalated subranks increased to the point of being unmanageable, there has been a trend to abandon the rank concept (above the family group level) by both gradistics and cladistics.

The gradistic system of taxonomy has been very useful, in various incarnations, since the 1700s. Much of our understanding of major living groups comes from research under the evolutionary system of systematics. A taxon in gradistic systematics must have a common ancestor, but may exclude one or more groups of descendants. For example, the Superclass Tetrapoda ("four-footed ones") has long been considered to be composed of four classes: Amphibia (cold-blooded tetrapods which have no scales and must reproduce in water), Reptilia (cold-blooded tetrapods which have scales and lay their eggs on land), Aves (warm-blooded tetrapods which have scales and feathers and lay their eggs on land), and Mammalia (warm-blooded tetrapods which have hair, give milk, and either lay eggs on land or have internal eggs). Almost all cultures recognized these classes (especially birds and mammals). However, evolutionary biologists soon recognized that reptiles are descendants of extinct amphibians (as "amphibians" were traditionally conceived by Linnaean taxonomists), and that birds and mammals are descendants of different groups of "reptiles" (although mammalian ancestors are now not considered members of the Reptilia; see below).

Until the 1970s, this was the system most widely used. It is a system designed to provide a taxonomy in which like groups are placed into the same hierarchical level (such as families), and to provide "evolutionary statements" that are built into the scheme. One can look at an evolutionary classification and see which groups are most closely related, their level of organization (body plans, or grades) as reflected in their Linnaean ranking (e.g., orders within a class were assumed to be "evolutionary equals"), and sometimes a degree of anatomical complexity. Evolutionary taxonomy recognizes grades of evolution which do not reflect total genetic relationships. A good example of a grade taxon is the reptilian order "Thecodontia." This is a group of archosaurian reptiles that were all placed in the same order because they had thecodont (socket-tooth) dentition. Because they were more "advanced" than earlier reptiles, and more "primitive" than the dinosaurs, birds, pterosaurs, and crocodiles, they were put in their own group, which reflected their level (grade) of evolution rather than their particular relationships to other archosaurs. However, thecodonts were not

characterized by any unique features. Instead, they had features shared with all other archosaurs, but at the same time they lacked the specializations of the more advanced forms (dinosaurs, birds, pterosaurs, and crocodiles).

Table 8.2

Linnaean Taxonomic Ranks and the Systematics of the Duckbilled Dinosaur Species *Anatotitan copei*

See text for discussion. Note that most of these ranks are no longer used by either gradistics or cladistics.

Traditional Ranks	Additional Subordinal Ranks
Phylum Chordata	"
Class Reptilia	"
Order Ornithischia	Order Ornithischia
	Parvorder Genasauria
	Nanorder Cerapoda
	Hyporder Euornithopoda
	Suborder Ornithopoda
	Infraorder Iguanodontia
	Gigafamily Dryomorpha
	Megafamily Anklpollexia
	Grandfamily Styracosterna
	Hyperfamily Iguanodontia
	Superfamily Hadrosauroidae
Family Hadrosauridae	Family Hadrosauridae
	Subfamily Hadrosaurinae
	Tribe Edmontosaurini
Genus <i>Anatotitan</i>	Genus <i>Anatotitan</i>
Species <i>Anatotitan copei</i>	Species <i>Anatotitan copei</i>

Note: Traditional ranks are those required by standard evolutionary systematics; additional subordinal ranks are ranks below order used to more precisely describe the systematic position of the species. Parvorder Genasauria to Superfamily Hadrosauroidae from Sereno 1986; Family Hadrosauridae to Species *Anatotitan copei* from Brett-Surman 1988.

Phylogenetic Systematics: Clades

Evolutionary taxonomy (gradistics) has been correctly criticized for being too subjective and trying to put too much information into a system that tries to pigeonhole everything into a classification scheme that is a rigid artificial abstraction. To meet the need for a more objective system, one closer to the reality of evolution, with or without all the Linnaean ranks, in the 1950s entomologist Willi Hennig invented what is known as phylogenetic systematics—also known as cladistics (Hennig 1950, 1966). Cladistics has now replaced evolutionary systematics as the method used by most vertebrate paleontologists.

A method was needed to show the closeness of ancestry between two groups, because independent evidence shows that most species arise as splitting events (when two or more parts of a population of organisms, separated by some sort of barrier, follow different evolutionary pathways as a result of natural selection and genetic drift). For any three taxa, two must share a more recent common ancestor than the third. For example,

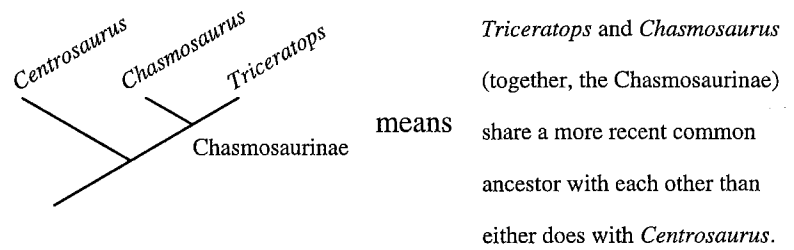


Figure 8.1. A cladogram representing the phylogenetic relationship among three horned dinosaurs.

the horned dinosaurs *Triceratops* and *Chasmosaurus* are both more closely related to each other than either is to a *Centrosaurus*. This can be shown graphically (Fig. 8.1) by a cladogram, which shows that *Triceratops* and *Chasmosaurus* are joined with each other above the level at which *Triceratops*, *Chasmosaurus*, and *Centrosaurus* are all joined.

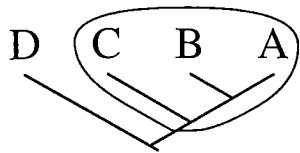
The point where two (or more) lines in a cladogram join is called a node. A node is recognized as a taxon itself—specifically the taxon containing all taxa which join at that node. In the cladogram in Figure 8.1, a node could be the Chasmosaurinae (the subfamily of horned dinosaurs with generally longer frills, longer snouts, and longer brow horns than nasal horns).

The taxon which shares a splitting event with another taxon is called the sister taxon or sister group. In the cladogram in Figure 8.1, *Chasmosaurus* is the sister taxon to *Triceratops*, *Centrosaurus* is the sister taxon to *Chasmosaurus* plus *Triceratops*, and, conversely, the group *Chasmosaurus* plus *Triceratops* is the sister taxon to *Centrosaurus*. In general practice, when scientists refer to the sister group to a particular taxon, they mean the closest that is known to science, and not just the closest on a very simplified cladogram.

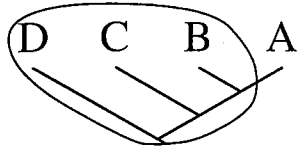
From a cladogram, we can recognize three types of groups (Fig. 8.2). Monophyletic (“single branch”) groups are composed of a single ancestor and all of its descendants. Mammals have long been recognized as a monophyletic taxon. Paraphyletic (“nearly a branch”) groups are the grades of evolutionary taxonomy: a single ancestor, but not all descendants. “Lizards” are paraphyletic if snakes are excluded from lizards. Similarly, “reptiles” are paraphyletic if birds are excluded from the Reptilia. Polyphyletic (“multiple branches”) groups have multiple ancestors, which have long been regarded as invalid by taxonomists. Grouping mammals and birds together without including “reptiles” (as a grade; see below) is a polyphyletic grouping, because mammals had a separate origin within the “reptiles” from that of birds.

Monophyletic groups are called clades (“branches”). Phylogenetic systematics seeks to find the relationships among taxa to form clades. Because our interest is in monophyletic groups, it is very important to use only smaller monophyletic groups while conducting a phylogenetic analysis.

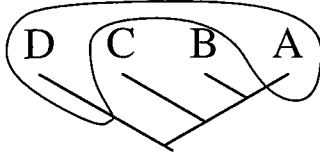
(A parenthetical note: The terms *evolutionary systematics* and *phylogenetic systematics* can be confusing at times. Scientists using the “evolutionary systematics” methodology are interested in determining phylogenies (evolutionary trees which depict ancestor-descendant relationships). Workers employing “phylogenetic systematics” are interested in the recency of common ancestry and the interrelationships of clades, without making any statements about which taxa were ancestral to other taxa. This approach accepts biological evolution as the sole reason for the existence of the branching pattern of life. The terms *gradistics* and *cladistics* more accu-



The group (A+B)+C is **monophyletic**, because it includes all descendants of the most recent common ancestor of A, B, and C.



The group (B+C)+D is **paraphyletic**, because it excludes a descendant of the most recent common ancestor of B, C, and D (namely, A).



The group A+D is **polyphyletic**, because A and D do not have a common ancestor which is not also the common ancestor of B and C.

Figure 8.2. A hypothetical cladogram portraying possible relationships among four groups of organisms. *From top to bottom*: monophyletic (an ancestor and all its descendants), paraphyletic (an ancestor but not all of its descendants), polyphyletic (no immediate common ancestor). Traditional gradistic taxonomy accepts the use of both paraphyletic and monophyletic groups, but cladistics requires that all taxa be monophyletic.

rately reflect the procedures used by these different schools of thought: Gradists sometimes accept the use of paraphyletic grades of organisms in their taxonomies, while cladists accept only the use of monophyletic clades.)

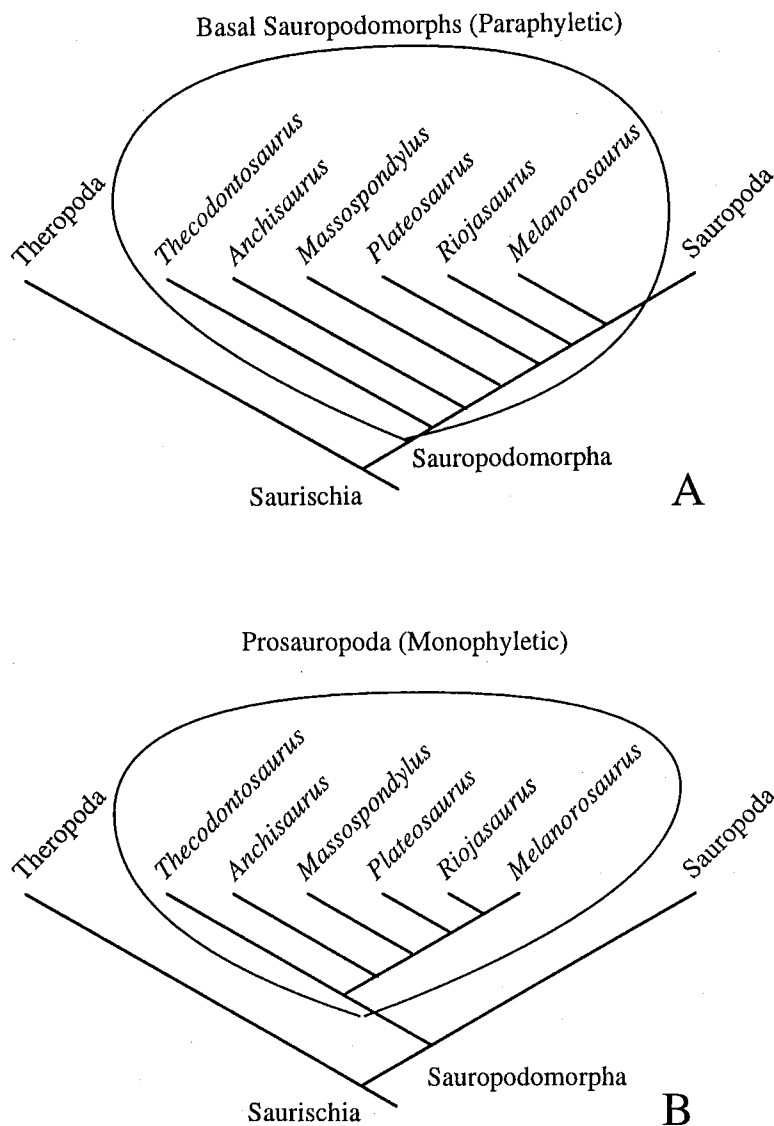
Phylogenetic Analyses

Phylogenetic analyses are the various methods used to determine the interrelationships of a group of organisms. For example, we might wish to examine the relationships of the long-necked herbivorous dinosaur group Sauropodomorpha. In particular, we wish to resolve whether the somewhat more primitive sauropodomorphs of the Late Triassic and Early Jurassic form a paraphyletic series to the giant Jurassic and Cretaceous Sauropoda, or whether these genera form their own monophyletic group, the Prosauropoda (Fig. 8.3). In the first case, some basal sauropodomorphs (for example, *Melanorosaurus* or *Riojasaurus*) are more closely related to true sauropods than are other basal sauropodomorphs (for example, *Thecodontosaurus* or *Anchisaurus*). In the second case, the Prosauropoda as a whole forms the sister group to Sauropoda.

Phylogenetic analyses are, thus, searches for clades. How is this done?

Many biologists use genetic or other biomolecular similarities between organisms to search for clades. For fossil groups (because the genes have all decayed over millions of years), the tool for finding clades is the search for shared derived characters (synapomorphies). First, scientists examine the characters of organisms, that is, their physical features (shape of the bones and their relationships to one another, presence or absence of rare structures, etc.). Then they look at how these characters are distributed among various taxa, both within and outside the groups they wish to study. They determine which characters are found in taxa both inside and outside the group of interest, which characters are found only within the group of interest but among all members of that group, and which characters occur only within subsets of the group of interest (see Chapman, chap. 10 of this volume, for more information about how organism characters are coded and analyzed in such a cladistic analysis).

Figure 8.3. Two possible cladograms for the sauropodomorph dinosaurs of the Late Triassic and Early Jurassic (see also VanHeerden, chap. 19 of this volume). (A) Some of the basal sauropodomorphs (*Riojasaurus*, *Melanorosaurus*) share a more recent common ancestor with the sauropods than they do with more primitive prosauropods. In this scheme, Sauropoda are the direct descendants of the basal sauropodomorphs, and the similarities between *Melanorosaurus* and sauropods represent shared derived characters. (B) The basal sauropodomorphs are all more closely related to each other than any is to the sauropods, making a monophyletic group (clade) Prosauropoda. In this scheme, Sauropoda is the sister taxon to Prosauropoda, and the similarities between *Melanorosaurus* and sauropods represent convergence.



Characters that are found in all the members of the group of interest (and possibly outside the group) are called primitive, and presumably were present in some common ancestor of all of the creatures in which they are now found. For example, five fingers are primitive for mammals, and hair is primitive for a primate. Therefore, the presence of five fingers cannot help us determine which mammals are most closely related to each other, nor can the presence of hair help us understand the cladistic relationships within primates. Primitive characters are considered primitive homologies.

In contrast, characters which are found in only a few groups are probably shared derived characters which evolved in some relatively recent common ancestor. For example, having five fingers is a shared derived

character of the tetrapods when compared to all vertebrates (including fishes), and hair is a shared derived character of mammals among tetrapods. Consequently the tetrapods share a common ancestor that lived more recently than the common ancestor of all vertebrates, and mammals share a common ancestor that lived more recently than the common ancestor of all tetrapods. We can therefore use the presence of a five-fingered hand to distinguish the tetrapods from other vertebrates, and hair to distinguish mammals from other tetrapods. Derived characters are advanced homologies. Shared primitive characters do not help resolve a cladogram, while shared derived characters do.

Unique derived characters (those found only within a single group), while important for understanding the biology of animals, do not help to resolve the cladistic relationships among taxa. For example, because feathers are unique to birds among modern tetrapods, they do not help us to recognize which other group of tetrapods is the sister group to birds.

Convergences are a special sort of character. Because of similar functions or behaviors, two or more groups of organisms can independently acquire very similar features. Although at first these resemblances might seem to be shared derived characters, additional evidence shows that they are convergent. For example, it might at first appear that the upright posture of some mammals and dinosaurs is a shared derived character of a mammal-dinosaur group. However, the dinosaurian skull, vertebrae, limbs, tail, and indeed most of the rest of the skeleton share more derived characters with other reptiles than with mammals. Thus the upright posture in mammals and dinosaurs is convergent.

Definition and Diagnosis

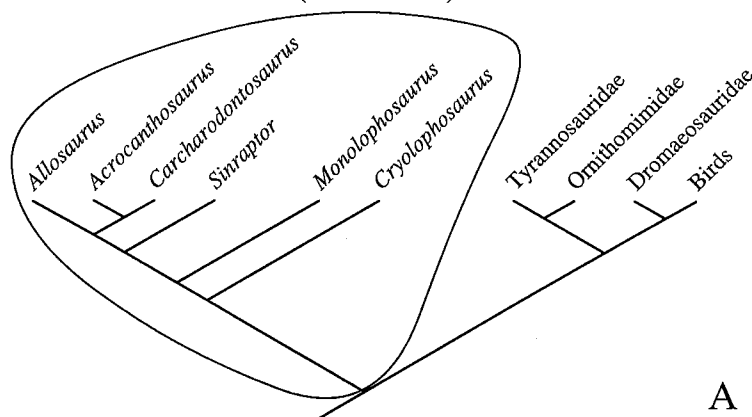
As you might imagine, there is a difference between the definition and diagnosis of different groups in the gradistic and cladistic systems of taxonomy. In the former, definition and diagnosis are for all intents and purposes identical, and are character-based. In cladistics, definitions are based on taxa and diagnoses are recognized by characters.

Under gradistics, the definition (the meaning of the taxon name) and the diagnosis (the way in which that taxon is recognized) are essentially the same. Taxa are defined by their characters (derived or primitive), so that a gradistic "Reptilia" could be defined as all amniotes (animals that reproduce by means of a specialized shelled egg, or derivatives of that style of reproduction) that have scales but lack feathers, fur, or warm-bloodedness. The diagnosis of the gradistic "Reptilia" would then be the presence of an amniotic egg and scales, and the lack of feathers, fur, and warm-bloodedness.

Similarly, under gradistics, dinosaurs would be defined as the Superorder (or Class, or Subclass, etc.) Dinosauria, that group of archosaurian reptiles with upright limbs, three or more sacral vertebrae, and perforate acetabula. The Superorder Dinosauria consists of the two orders Saurischia and Ornithischia. The Ornithischia would be considered to have had an ancestor among the Saurischia because the saurischian skeleton is the less "advanced" of the two. This information could be presented as an evolutionary tree showing when each group originated and from which clade each group arose.

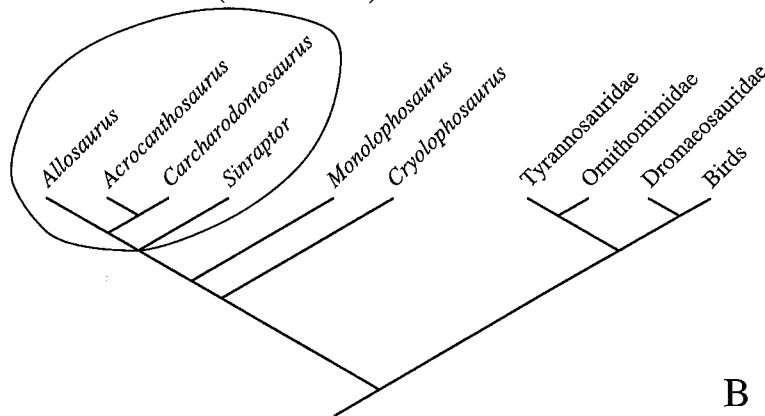
Under cladistics, the definition of a taxon is based on the relationships of two or more taxa. De Queiroz and Gauthier (1990, 1992, 1994) recognized two main kinds of phylogenetic definitions, stem-based and node-based. A third form, derived character-based, is unstable (Padian

Carnosauria (Stem-based)



A

Allosauroida (Node-based)



B

Figure 8.4. A cladogram of some carnivorous dinosaurs, showing the two main types of phylogenetic taxon definitions. (A) Carnosauria is a stem-based taxon (*Allosaurus* and all theropods closer to *Allosaurus* than to birds). (B) Allosauroida is a node-based taxon (all descendants of the most recent common ancestor of *Allosaurus* and *Sinraptor*). Thus *Cryolophosaurus* and *Monolophosaurus* are both carnosaur, but not allosauroids. *Carcharodontosaurus*, *Acrocanthosaurus*, and (by definition) *Allosaurus* and *Sinraptor* are carnosaur and allosauroids.

and May 1993; Bryant 1994; Holtz 1996), in that the character used to diagnose the clade may be found to have evolved independently more than once. On the other hand, stem-based and node-based taxon definitions will always represent natural clades, because all organisms share common ancestry to one degree or another.

Stem-based taxon definitions are of the form “Taxon X and all organisms sharing a more recent common ancestor with Taxon X than with Taxon Y” (see Fig. 8.4A). For example, the carnivorous dinosaurian taxon Carnosauria is defined as *Allosaurus* and all taxa sharing a more recent common ancestor with *Allosaurus* than with birds (Holtz and Padian 1995). Node-based definitions are of the form “the most recent common ancestor of Taxon X and Taxon Y, and all descendants of that common ancestor.” For example, Allosauroida could be defined as the most recent common ancestor of the carnosaur genera *Allosaurus* and *Sinraptor*, and all of that ancestor’s descendants.

Looking at a more inclusive group, under cladistics Dinosauria would be defined as the most recent common ancestor of Saurischia and Ornithischia, and all of that ancestor’s descendants. Note particularly that Linnaean ranks are not used, and that there is no implication as to which

group is the ancestor of the other group (in fact, they are considered sister taxa, and not ancestor and descendant).

Considering still broader, more inclusive groups, the category Reptilia is now considered a node-based taxon: the most recent common ancestor of turtles, lepidosaurs (lizards [including snakes] and the tuatara), and archosaurs (crocodiles and birds and their extinct relatives). Thus Aves (the

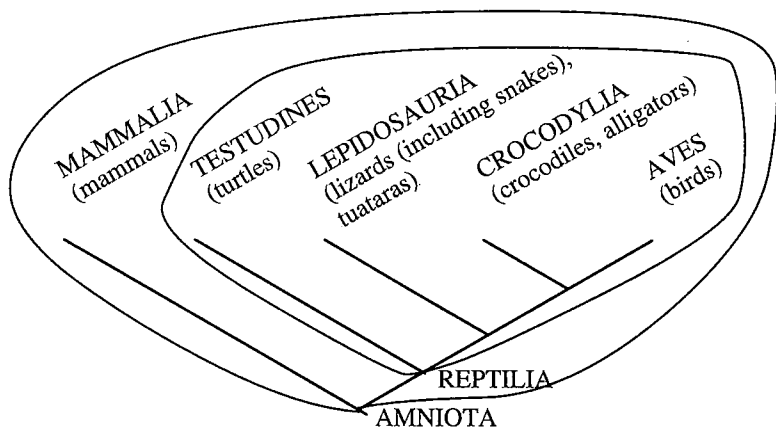


Figure 8.5. Cladogram of the living Amniota. Birds (Aves) are part of the monophyletic taxon Reptilia, but mammals (Mammalia) are not.

birds) is part of the larger monophyletic Reptilia. Mammals, however, are not part of this clade, because our ancestors diverged from the common ancestor of all reptiles (as now defined) before the turtle-lepidosaur-archosaur divergence (see Fig. 8.5). Thus under cladistics, the ancestors of mammals by definition were not reptiles (i.e., were not part of the clade Reptilia), while birds' ancestors and birds themselves are true reptiles (i.e., members of the clade Reptilia). (Some ornithologists take extreme exception to this "demotion"!)

Diagnosis of taxa under the phylogenetic taxonomic system follows definition. After the distribution of shared derived characters within a cladogram is determined, those shared derived characters which unite taxa into a stem-based or node-based taxon are used as the diagnosis of that taxon.

In the chapters that follow, the various contributing authors discuss dinosaurian relationships from both the gradistic and cladistic schools of systematics. It is informative to compare and contrast the conclusions the authors draw about the ancestors and ancestral characteristics of the dinosaur groups they study, based on the different methods they use to understand the evolutionary relationships of these wonderful ancient animals.

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