A Revision of the Parainfraclass Archosauria Cope, 1869, Excluding the Advanced Crocodylia

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Mesozoic Meanderings #2

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Preface

THERE WAS A TIME in the early 1970s when accumulating dinosaur names was one of my hobbies. In this I was assisted by the University of Toronto Computer Centre, which because I worked there as a staff programmer and graduate student gave me free access to their IBM System/360 computer. This I used to maintain and occasionally print various lists of things I was interested in; it was a convenient medium for editing my databases and producing typographically clean output.

When, in the mid-1970s, Samuel P. Welles, then at the University of California at Berkeley, delivered a public dinosaur lecture at the Royal Ontario Museum, I handed him a copy of the dinosaur list for his files. In time this fell into the hands of Michael K. Brett-Surman and Robert A. Long, then both at Berkeley as well. A letter from Long in 1976 pointed out taxa I had overlooked and, to my delight, requested references to taxa unknown to him. In 1977, Ralph E. Molnar requested a printout, and soon a multipage letter arrived from him with additions, corrections, and suggestions. At the same time, my meanderings through the Royal Ontario Museum library brought me in touch with paleontology graduate student David B. Weishampel, and we would meet from time to time thereafter to exchange information about new papers and discoveries. I also initiated correspondences with other paleontologists, who proved wonderfully generous with their knowledge.

Naturally, all this input sharply increased the quality of my list, kept me aware of impending publications, and greatly augmented my literature collection with original offprints. I also added the remaining non-crocodilian archosaurs to the dinosaur list. By 1978, Weishampel and Peter Dodson of the University of Pennsylvania sponsored my membership in the Society of Vertebrate Paleontology. (I may eventually follow one of Ralph Molnar's original suggestions and add the remaining crocodilians and the Mesozoic birds to my table, but for now the other archosaurs are handful enough.)

In the late 1970s, a freelance publishing venture (stemming from another of my computer lists) I had initiated paid off. This prompted me to terminate my computer-science doctoral candidacy at Toronto, to abandon programming computers as a career, and to become a full-time editor of my own publications. As one of my projects, in 1978 I produced *Mesozoic Meanderings* #1, a published version of the archosaur list, which for a few years I peddled at SVP annual meetings. (It sold out long ago.) After moving to San Diego in 1979, I produced several more paleontological publications, including supplements to *Mesozoic Meanderings* #1. Unfortunately for these projects, by 1981 I was locked into publishing a line of indexes to Marvel Comics, for which there was a tremendously more lucrative market, and I had neither access to a computer nor time to continue paleontological publishing. All I could do was maintain my archosaur list manually, visit the library sporadically, and reply to correspondence occasionally. By 1986, the Marvel Index project was consuming 60 or more hours per week, month after month.

Fortunately, I was able to get away every so often. I presented two talks (about uniform polyhedra and about regular four-dimensional polytopes: some of the computer work I had done as a graduate student) at a mathematics conference called "Shaping Space" at Smith College in 1984. In 1986, I attended the Dinosaur Systematics Symposium at the Tyrrell Museum in Alberta, Canada—a symposium I would not have missed for the world. It had occurred to me a few months earlier, while I was manually updating the archosaur list, that elevating the diverse archosaurian suborders to orders would bring archosaur systematics more into line with that of extant mammals and birds. Mammals and birds are each *conservatively* classified into more than 20 orders—more than 30 if the known extinct orders are counted—reflecting their worldwide distribution and body-plan diversity. Archosaurs, particularly dinosaurs, pterosaurs, and birds, filled the terrestrial world during the Mesozoic Era just as mammals and birds do today, so I wondered why there were only five archosaur orders instead of 30. Are we really ignorant of five-sixths of all the archosaurs that ever lived? Have some of the orders been masquerading as suborders? As I hope to show elsewhere in this paper, I think the answer to *both* questions is yes.

I presented my conclusions in abstract form at the Tyrrell conference. Rather to my surprise, the presentation was received with interest and engendered a post-conference discussion group on dinosaur taxonomy. It was my hope to expand the abstract into a paper for the Symposium volume (recently published as *Dinosaur Systematics: Approaches and Perspectives* by Cambridge University Press; Carpenter & Currie, eds., 1990). The Marvel Index project, however, proved too taxing to allow me to complete the paper before the deadline. I resolved that if ever time permitted, I would publish the work myself as *Mesozoic Meanderings* #2.

The Marvel Index project endured until early 1988, when I finally gave it up and returned to freelance editing and publishing. Luckily, it had paid well enough that I was able to purchase an excellent desktop publishing system, and I soon transferred my hand-compiled archosaur list back into machine-readable form. To augment my freelance income, I initiated a paleontological newsletter called *Archosaurian Articulations*, which in turn inspired Dinamation International Corporation to hire me for a while to edit a dinosaur magazine (it has not, as of this writing, been published). My workload crept upward again, eventually throwing the newsletter off its monthly schedule; *Mesozoic Meanderings* #2 remained on a distant back burner.

At long last, in the summer of 1991, a block of time opened up between editing projects, and I was actually able to prepare a version of the archosaur list for publication. Furthermore, a large audience, to whom I can market copies and perhaps recoup some of my production and research costs, will be on hand in my home city at the 1991 SVP annual meeting. In trying to keep my costs low, I have saved layout time and space by eliminating illustrations and lengthy diagnoses of the taxa. Such material would in any case have been derived largely from works already published and is abundantly available in the references listed at the end of these introductory sections.

What I have found particularly daunting in reading and trying to absorb cladistic analyses is the enormous number of what seem to be microscopically detailed anatomical features listed as phylogenetically important characters. I suppose this kind of work is necessary, but on closer scrutiny, many of the characters seem less than robust. For example (I pick a few from a fine-print figure caption in Evans, 1988): "first and fifth metacarpals shorter than second and fourth metacarpals; posterior process of dentary extends beyond coronoid; three or less (*sic*) premaxillary teeth on each side; reduction in length of metatarsals; teeth mediolaterally expanded; paroccipital process distally expanded." What I would like to know when I see such material is just how much of the relevant body part's extension, reduction, or expansion *actually counts*. For example, does "shorter" mean merely subequal, or does it mean strongly reduced? And relative to what is the "reduction in length of metatarsals" to be considered: the state in earlier or related taxa, or a different part of the animal's anatomy? All teeth, being three-dimensional objects, exhibit mediolateral expansion; how much is required for this to be considered a character state? Rather than reducing the subjectivity present in the classification process, cladistic analysis seems merely to have subdivided it into a multitude of subjective microdecisions. And in this context I would also like to understand what it would mean to the living animal in terms of its adaptability and lifestyle to have, for example, a distally expanded paroccipital process or a posterior dentary process extending beyond the coronoid. These comments may seem superficial, but I do not think I am alone in my lament (see, *e.g.*, Charig, 1982; Charig & Milner, 1990).

In constructing an archosaur phylogeny and taxonomy that make sense to me—to be described on the following pages—I have strived to understand a few well-defined archosaurian anatomical characters from functional and phyletic standpoints. Perhaps not surprisingly, I haven't been very successful in this. For example, I have neither found in the literature nor been able to contrive a compelling explanation for the appearance of the antorbital fenestra, the key archosaurian synapomorphy. It undoubtedly lightened the skull in pterosaurs, theropods, and primitive birds, but this could not have been the reason it evolved in the small, lightweight reptile that was the first archosaur. And if it was so useful as to persist in several major lineages, why did it close secondarily in such divergent groups as crocodilians and ornithischians? And what was the function of the obturator process on the ornithischian ischium? Half the known ornithischians got along without one, but it is a synapomorphy that helps to define one major lineage, the ornithopods, that persisted from at least the Middle Jurassic through the Late Cretaceous. I cannot imagine that these and other long-lasting characters arose solely for the convenience of taxonomists.

Throughout the two decades that I have been purposefully collecting information about archosaurs, I have been motivated almost entirely by curiosity. In a nutshell, I've sought answers to two very basic questions about them: "What is an archosaur?" and "What are the archosaurs?" Every so often I come to a point where I seem to have something worthwhile to say, and I prepare a document like this for anyone who is interested. The material herein is by no means the "final word" on anything, as if something like that were even possible in a field so rich with unknowns as paleontology. Rather, it is presently limited by considerations of space, time, and cost to being merely a sketch. Many of the topics discussed in the introductory sections require elaboration; some I intend to expand myself when I revive my other paleontological publication, *Mesozoic Vertebrate Life*, perhaps in time for the 1992 SVP annual meeting.

ACKNOWLEDGMENTS

My archosaur project owes a great deal to several paleontologists whose boundless enthusiasm, interest, and eagerness to exchange information have often surpassed my own. I can only hope that they keep the information coming, for without it, the archosaur table would suffer greatly. My unabashed thanks to: Michael K. Brett-Surman, Eric Buffetaut, Kenneth Carpenter, Dan Chure, Philip J. Currie, Donald Glut, John S. McIntosh, Ralph E. Molnar, Dale A. Russell, and David B. Weishampel.

Tracy Ford has been of *inestimable* help in keeping me well supplied with photocopies of references and in being a sounding-board for some of the taxonomy expressed herein. Tracy has become very good at hunting down obscure material, and I recommend his services to all interested parties.

The archosaur table has also benefited greatly from conversations and/or correspondence with the following people, who have on various occasions over the years provided me with additions, corrections, taxonomic suggestions, photographs of specimens, references, and copies of hard-to-obtain papers: Andrea Arcucci, Harley Armstrong, Donald Baird, Robert T. Bakker, Christopher Bennett, Michael J. Benton, José F. Bonaparte, William T. Blows, George Callison, Kenneth Campbell, Chao Shichin, Alan J. Charig, Sankar Chatterjee, Luis M. Chiappe, Edwin H. Colbert, Walter P. Coombs, Jr., Ruth A. Cooper of the ICZN Secretariat, Kyle Davies, Thomas Démeré, Robert K. Denton, Peter Dodson, Dong Zhiming, James O. Farlow, Peter M. Galton, David D. Gillette, He Xinlu, Rene Hernandez, John R. Horner, Nicholas Hotton III, Adrian P. Hunt, Stephen Hutt, Louis Jacobs, Sohan L. Jain, James A. Jensen, Alexander W. A. Kellner,

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Many thanks also to Carl Masthay, who aided me on a number of occasions by translating passages from Chinese and Korean papers.

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This project is supported entirely by subscriptions to *Archosaurian Articulations*, sales of *Mesozoic Meanderings* and other paleontological publications, and whatever freelance editing and writing work I can turn up. If you like what you see, let your colleagues and institution libraries know my mailing address, and I'll take it from there. Subscribers to *Archosaurian Articulations* (except libraries and other institutions) receive an automatic 20% discount off the cover price of any of my publications. Bookstores and other vendors should send inquiries about wholesale discounts to my mailing address.

Mesozoic Meanderings is published in printings of 100 copies. Once a printing sells out, the issue is returned to press—*with accumulated additions and corrections*—for another 100-copy press run. Only the first printing is signed and numbered; subsequent printings are just numbered. The introductory text does not change as much between printings as do the table and the census counts. This seems to be the most cost-effective way of keeping *Mesozoic Meanderings* perpetually in print and up to date, and I will continue this system until *Mesozoic Meanderings* #3 is ready for publication.

TECHNICAL REVIEW

Mesozoic Meanderings is a peer-reviewed publication This issue's reviewers include: **Michael K. Brett-Surman** (Smithsonian Institution), **Kenneth Carpenter** (Denver Museum of Natural History), **Daniel Chure** (Dinosaur National Monument), **Philip J. Currie** (Tyrrell Museum of Paleontology), **Ralph E. Molnar** (Queensland Museum, Australia), **John S. McIntosh** (Wesleyan University), **Dale A. Russell** (Canadian Museum of Nature), and **David B. Weishampel** (Johns Hopkins University).

Introduction

THIS PUBLICATION has several goals. Foremost of these is to present a complete and current checklist of archosaurian genera and species, classified systematically, for the convenience and use of the vertebrate paleontological community. With the exception of a now seriously outdated list that I produced in 1978 (*Mesozoic Meanderings* #1 and its supplements: Olshevsky, 1978, 1979, 1980a, and 1980b), such tables presently exist only within the contexts of broader paleontological works, such as bibliographies (*e.g.*, Chure & McIntosh, 1989), monographic texts (*e.g.*, Carroll, 1988), and multiauthored studies (*e.g.*, Weishampel, Dodson & Osmólska, eds., 1990). As such, they are not always conveniently organized, and it is not long before they become out of date. By keeping my print runs small and by maintaining it in machine-readable form as a desktop-published document, I can produce an updated checklist with each new printing.

Another goal of this publication is to present, as a framework for the checklist of genera and species, a more streamlined organization for the higher archosaurian taxa. Traditionally, the archosaurs have been partitioned into five orders: (1) the Thecodontia, a thoroughly paraphyletic assemblage of archosaurs extant almost exclusively during the Triassic Period; (2) the Crocodylia, a well-diagnosed monophyletic order that has persisted from the Triassic to the present; (3) the Pterosauria, another well-diagnosed monophyletic order, extant from at least the Late Triassic through the Late Cretaceous; (4) the Saurischia, an order I consider diphyletic, extant from at least the Late Triassic through the Late Cretaceous; and (5) the Ornithischia, another well-diagnosed monophyletic order, also extant from the Late Triassic through the Late Cretaceous. Recently, arguments have been put forward that the class Aves (extant from at least the Late Triassic [Chatterjee, 1991] to the present) arose within the theropod clade of the Saurischia (*e.g.*, Ostrom, 1976, and others), so cladistic taxonomists, such as Gauthier (1986a, 1986b, 1989), Benton & Clark (1988), and Benton (1990a) maintain that Aves should be included in Archosauria as a saurischian subgroup.

These and other systematic studies of the archosaurs absolutely mandate a revision of the traditional archosaur classification. For reasons stated in the next section (Taxonomic Considerations), however, I do not think the vertebrate paleontological community will accept and use a wholly cladistic reclassification, the only alternative that such studies have so far offered. I believe the scheme presented here merges Linnaean and cladistic philosophies in a "Simpsonian" way that reflects our present knowledge of archosaur phylogeny without sacrificing the usefulness of the hierarchic Linnaean structure. (I will know soon enough whether it satisfies traditionalists, cladists, or neither!)

Taxonomy cannot be done without a solid phylogeny, and phylogeny cannot be done without a functional understanding of the characters employed to track and unravel phylogeny from the fossil record. In particular, the phylogenetic relationship between theropod dinosaurs and birds, which has been debated at length in the literature (*cf.* Hecht, Ostrom, Viohl & Wellnhofer, eds., 1985), needs to be clarified before a reasonably correct taxonomy for those two groups can be established. Thus the third goal of this publication is to present a plausible scenario for theropod and bird origins to justify the classification I have constructed. Some aspects of this scenario are undoubtedly incorrect and stem from my imperfect knowledge of theropod and avian anatomy, as well as an outrageously poor fossil record, but I do not consider these shortcomings particularly important. What is more important is the paradigm shift that I think is required to understand bird-theropod relationships. Succinctly, it is that birds did not descend from certain theropod dinosaurs, but rather that theropod dinosaurs comprise a series of groups of flightless animals descended from a diversity of primitive gliding and flying birds. This idea is not as bizarre as it might at first seem, as I hope the scenario accompanying the discussion of the theropodomorph orders will make clear.

The final goal of this publication is to correct several nomenclatural irregularities I unearthed while recompiling the checklist. Two generic names turned out to be preoccupied and required formal changing, and several specific names needed minor respellings. Two species of Wealden theropods long (and incorrectly) referred to the genera *Megalosaurus* and *Altispinax* required new generic names. Such peculiarities surface whenever systematic checklists are assembled, and I call attention to them in a separate section below rather than simply burying them in the list.

MATERIALS AND METHODS

The master archosaur list is presently maintained as a series of documents in WordPerfect 4.2 on a Cordata AT (IBM clone) personal computer. The documents interface with a Xerox Ventura 1.0 desktop publishing system, which automatically formats them and sets them in type. They are output as camera-ready pages through a Hewlett-Packard LaserJet II printer. Additions and corrections to the master list are usually performed through the Ventura system rather than WordPerfect, although both systems allow rapid, trouble-free text editing.

Compiling and maintaining the archosaur list is primarily library work. All available archosaur compendia, such as the appropriate volumes of the *Handbuch der Paläontologie* (Steel, 1969, 1970, 1973; Wellnhofer, 1978; and Charig, Krebs, Sues & Westphal, 1976), the annual *Bibliography of Fossil Vertebrates*, the Reptilia volumes of *The Zoological Record*, the archosaur volumes of the *Fossilium Catalogus*, and various popular "dinosaur dictionaries," were used to construct the initial master list. Dan Chure, John S. McIntosh, and I cross-checked our dinosaur lists when they compiled *A Bibliography of the Dinosaurs (Exclusive of the Aves) 1677-1986* (Chure & McIntosh, 1989); David B. Weishampel and I did likewise when he was editing *The Dinosauria* (Weishampel, Dodson & Osmólska, eds., 1990). As new systematic studies are published, the results are incorporated into the list. Through personal correspondence, many workers keep me apprised of new discoveries and publications, so the actual master list contains some unpublished names. These I removed from this published version in order to avoid conflicts over nomenclatural priority. Taxa whose publication is imminent (and some whose publication is not so imminent) are indicated as "to be described." No feasible procedure can *guarantee* completeness, but the present list is certainly more complete than any archosaur list previously published, and it is almost certainly complete through the year 1988.

Readers aware of published archosaur taxa that have been omitted from my list are urged to send me references or (if possible) photocopies of the publications. Also, despite having worked on my list for nearly two decades, I have still not been able to verify spellings, authors' names, and dates of *all* the included taxa from their original sources. So I would be most interested in receiving any corrections, and I will gratefully acknowledge such improvements in subsequent printings of this list.

The present list retains much of the format of its 1978 predecessor, *Mesozoic Meanderings* #1. By adding more information about authors of synonymies, stratigraphy, localities, and type and useful referred specimens, I intend to make issue #3 substantially more comprehensive. I have already experimented with revised formats, and I do not anticipate as long a wait for *Mesozoic Meanderings* #3 as there was for #2.

HOW TO USE THIS LIST: CONVENTIONS

I generally adhere to the typographical and priority conventions set out in the third edition of *The International Code of Zoological Nomenclature* (ICZN, 1985), but I also employ certain abbreviations for brevity. These conventions are explained herewith.

Terminology

For the purposes of this discussion, a *taxon* is a set of organisms that includes their common ancestor (a "natural group" in "old-fashioned" terminology); a *clade* is a taxon that comprises *all* the descendants of the common ancestor. A taxon that is also a clade is called *monophyletic*; a taxon that is not a clade is called *paraphyletic*. Any other grouping of organisms is *polyphyletic*. In the Linnaean classification, the taxa are arranged hierarchically in levels, and each high-level taxon is completely partitioned into taxa at the next-highest level. The seven canonical levels are kingdom, phylum, class, order, family, genus, and species; in between these are often placed such noncanonical levels as tribe and cohort, as well as subfamilies, superorders, parvorders, megafamilies, and so forth. But specifying an organism's seven canonical levels (kingdom and phylum are broad enough to be understood from context and are not usually noted) completely identifies it in the Linnaean system.

Monophyletic and Paraphyletic Taxa

The current trend in taxonomy is to arrange that all named taxa be monophyletic. For reasons outlined in the next section, I do not think this is feasible, and my classification retains a number of useful paraphyletic taxa. These are signaled with the prefix para-, as in paragenus, parafamily, parasuborder, paraorder, etc. No species listed here can be identified with any degree of certainty as ancestral to any other taxon, so the term paraspecies is not needed, although it could be useful in constructing taxonomies of other groups. Formally, a paraphyletic taxon, or *parataxon*, may be defined as the difference between a clade and one or more included clades; its Linnaean rank is (usually) determined by its morphological diversity as if the deleted clades had never come into existence. Linnaean taxa without the para- prefix are monophyletic (clades). For nomenclatural purposes, parafamilies, paragenera, paraspecies, etc. should be treated exactly like families, genera, species, etc. under the ICZN. Deciding which clades to remove in creating a useful parataxon is part of the "art" of taxonomy, as is (for example) deciding when two species are distinct enough to warrant separate genera, or when two genera require separate families. One guideline I adhered to in creating the parataxa in this table was to subtract as few clades as possible, and then only when the removed clades encompassed evolutionary novelties that would compel classification at a Linnaean rank at or above that of the parent parataxon.

For example, the taxon Reptilia is a paraclass formed by the removal of the clades Aves and Mammalia, which are Linnaean classes, from the clade Amniota, which is a superclass within the infraphylum Tetrapoda. As described herein, the Archosauria is a parainfraclass within the paraclass Reptilia and parasubclass Diapsida, since it is defined as the clade Archosauria minus the clade Aves. And the parainfraclass Archosauria contains within it the parasuperorder Theropodomorpha and paraorder Theropoda, inclusively smaller parataxa defined by the removal of the clade Aves. (It should be noted in this context that Aves does not include the parafamily Archaeopterygidae, which I place in the suborder Deinonychosauria. More on that in the succeeding sections.)

Theoretically, every parataxon above the species level must contain at least one parataxon of lower rank. The fossil record, however, is too poor in most cases to identify all included taxa. As I argue in a subsequent section, a large number of families, genera, and species have yet to be discovered and identified within the Archosauria.

Genera and Species

Genera (and paragenera) are listed alphabetically within each family. Species are listed in chronological order within each genus. As a rule, the author and year of each taxon refer to the work in which the taxon was originally described. Genera and species attributed to an author within the work of another are denoted by the Latin term *vide* ("see"); the author of the taxon precedes the *vide*, the author and year of the attributing work follow it.

The type species of a genus is followed by the notation "(Type)." It is possible even for a *nomen nudum* genus (see Doubtful Names below) to have a type species, if the species is the only one named within the genus (type by monotypy) or is the first one named within the genus. Such "type" species, of course, have no formal nomenclatural standing.

Recognized species within a genus are always written with the generic name abbreviated to the initial letter; species synonyms (see below) are spelled out completely to avoid confusion. A question mark (?) preceding a species name indicates that the species is provisionally or doubtfully referred to the listed genus. Such question-marked species should be considered targets for further research and may represent as-yet-undescribed new genera. Occasionally I was able to refer such species to better genera myself (as I did, for example, with *Caudocoelus sauvagei* and *Tylocephale bexelli* in *Mesozoic Meanderings* #1). If such references create new combinations of generic and specific names, I denote them conventionally as "n. comb."

Generic and specific names enclosed in quotation marks represent published names of convenience for undescribed taxa. They should be considered *nomina nuda* (see Doubtful Names below).

Subgenera, subspecies, and varieties have occasionally been described within archosaur genera and species, but as a rule I consider the range of variation in fossil vertebrate taxa to be too poorly known to warrant such fine subdivisions. In those few instances where the subgenera seem distinctive, I have raised them to the generic level; otherwise I have listed them among the species synonyms. A subgeneric name is conventionally written in parentheses between generic and specific names; a subspecific name is conventionally written after the specific name. Varieties are denoted by "var." In older works, a generic name in parentheses following another generic name sometimes denoted a kind of informal synonymy. To avoid confusion with the formal subgeneric notation, I have separated such "double genera." Thus *Trachodon (Pteropelyx) grallipes* Lambe, 1902 is listed as both *Trachodon grallipes* Lambe, 1902 and *Pteropelyx grallipes* (Lambe, 1902).

Doubtful Names

I recognize two kinds of doubtful taxa: *nomina dubia* and *nomina nuda*. A species name presently thought to be based on material not diagnostic to the species level is noted as a *nomen dubium*. A generic name thought to be based on material not diagnostic to the generic level is similarly noted. If a genus is listed as a *nomen dubium*, then its type species is automatically a *nomen dubium* (and the notation *nomen dubium* is unnecessary), but it does not follow that all species included in a doubtful genus are themselves *nomina dubia*. Those that are not could, however, require new generic names and/or proper descriptions—a task beyond the scope of this paper. The more severe term *nomen vanum* ("empty name") sometimes seen in taxonomic studies is redundant with the term *nomen dubium* and is not employed here.

Nomina nuda are names of taxa published without descriptions. These often appear in faunal lists that refer to work in preparation, or as names of convenience for specimens to be described. Popular news articles on paleontology occasionally publish names ahead of their formal descriptions. In this list, if a taxon has been formally described, then its name is attributed to the author and year of the description; earlier usages of the name, which are all *nomina nuda*, are listed as synonyms. In cases where a name simply has no published description, the name is attributed to the earliest user as a *nomen nudum*.

Some workers (incorrectly) regard as *nomina nuda* taxa possessing inadequate descriptions instead of simply no descriptions. I consider myself incompetent to judge the adequacy of a published description, and I employ the term *nomen dubium* for such taxa. Also, although a picture might be worth a thousand words, I regard a name used solely in the caption of an illustration depicting a specimen—

the quality of the illustration or the specimen notwithstanding—a *nomen nudum*.

Synonyms and Renamings

Synonyms of genera are denoted with equals signs (=) and listed in alphabetical order following the presently accepted name of the genus. Species synonyms (also denoted with equals signs) are listed in chronological order following the presently accepted species name. Renamings of a species are listed alphabetically following the original name of the species. If the presently accepted name of a species is itself a renaming, then its first listed synonym is always its original name, followed by any other renamings. In a renaming, the author and year are those of the original name enclosed in parentheses; this notation unambiguously identifies a renaming in this list. As I was preparing this paper for publication, however, it occurred to me that it would be more useful to provide the earliest reference for each renaming, rather than just to repeat the original author and year. The ICZN provides a formal notation for doing this: the author and year of a renaming are written after the parenthesized author and year. With a few exceptions, such as among the parasuchians, I had no time to implement this convention here, but I will do so as completely as possible in *Mesozoic Meanderings* #3.

Obviously, a *nomen dubium* or a *nomen nudum* cannot enter into formal synonymy with another taxon. Nevertheless, it is often possible with some degree of reliability to pigeonhole doubtful taxa into taxa that are better established. In this list, such pigeonholing—not formal synonymy—occurs in *all* cases in which a doubtful name is listed as a synonym of another taxon (which may itself be a *nomen dubium*). My position on *nomina dubia* is not that the taxa are worthless but that we have insufficient information to assess their worth; it occasionally happens (*e.g.*, with the tooth genus *Troodon*; Currie, 1987) that new discoveries and restudies erase the "dubium" from the "nomen."

In cases where synonymizing a *nomen dubium* with another taxon could result in the alteration of a widely accepted name, however, I avoid the pigeonholing entirely and isolate the *nomen dubium*. Notes explain the situation in such cases.

Respellings and Misspellings

The original spellings of the names of genera and species are used wherever possible. The ICZN specifies, however, that an original spelling in which an adjectival specific name disagrees with its generic name in gender must be respelled correctly once the error is noticed. Similar rules also apply to other kinds of improperly formed specific names, such as honorific specific names written as singular when more than one person is to be honored. Original spellings that have been thus corrected, either here or elsewhere in the literature, are flagged with an asterisk (*). The corrected spelling immediately precedes the original spelling. Into the category of respelled names also fall names originally coined with diacritical and punctuation marks, such as diereses, hyphens, and umlauts. The ICZN (1985) rules that such names must be spelled with the marks deleted, except that German vowels with umlauts are to be respelled with an e immediately following the vowel. I have followed this rule in all cases.

Misspelled generic and specific names abound in the literature, most frequently as typographical errors, particularly in papers written in non-Latin alphabets. Compiling these is a project generally lacking in scientific interest, and I have not striven for completeness. Sometimes, however, misspellings find their way into the popular literature, so it does seem necessary to point them out. I was more prone to include bizarre misspellings than names with mundane single-character errors, and to pursue all the misspellings of names that have been misspelled in many different ways. Also, I catalogue generic-name misspellings more completely than specific-name misspellings. Occasionally a misspelled name will be the correct spelling of a different genus or species. Such cases are a potent source of confusion, and I have included them in the table whenever I have discovered them.

All spelling and typographical errors are tabulated among the legitimate renamings with the conventional notation "[*sic*]," a Latin term meaning "there," in the sense of "as written there." The same misspelling sometimes appears in more than one paper; I list only the earliest appearance of a misspelling known to me.

Preoccupied Names

Preoccupied generic names are denoted by having two attributions separated by a slash (/). The first attribution supplies the author and year of the archosaur genus, the second the author and year of the earliest use of the name. There are no preoccupied species names among the archosaurs, but every so often referring a species to a different genus creates a new combination identical to a previously created species name. In such circumstances, I separate the two attributions with "*non*." I also use this term when definitive material referred to a species is separated from it to define a new species. For example, Thulborn (1970) redescribed the species *Fabrosaurus australis* Ginsburg, 1964 using good skeletal material that Galton later (1978) removed into a new genus and species, *Lesothosaurus diagnosticus*. This is reflected in the list by showing *Fabrosaurus australis* Thulborn, 1970 *non* Ginsburg, 1964 in synonymy with *Lesothosaurus diagnosticus*.

Conserved and Obsolete Names

If a generic or specific name remains uncited by zoologists (except in faunal lists and taxonomic indexes) during the 50 years following its creation, it is considered obsolete and is known as a *nomen oblitum*. It is then no longer eligible under the rules of priority to act as a senior synonym of a later name, and it cannot preoccupy a later usage of the name for a different genus or species. Suppressing a *nomen oblitum* usually requires a special ICZN ruling, often when a well-known name is threatened with replacement by an obscure potential senior synonym. The "rescued" name is then called a *nomen conservandum*, or conserved name. Instances involving such names are suitably annotated in this list.

Families and Subfamilies

The ICZN mandates that a family-level name must be derived from an included genus. Although it is not good taxonomic practice, the genus may even be a *nomen dubium* or a junior synonym of another genus in the family, as long as the material that defines the genus is diagnostic to the family level. In cases where more than one genus in a family is a family-name eponym, rules of priority dictate that the family's name must be the eldest name formed from any included genus; the other names then become junior synonyms. As with genera, it sometimes happens that the eldest name for a family has become obsolete from disuse. In such cases, I call the eldest synonyms *nomina oblita* and conserve the best-known family names. All synonyms of family names are listed alphabetically following the accepted family name.

Because most archosaur families contain only a few genera, which seldom fall into well-defined subsets or lineages (ceratopsid genera are an exception; hadrosaurid and lambeosaurid genera may be others), I eschew categories in between family and genus. Nevertheless, archosaurian subfamilies have been defined fairly frequently. I simply list them among the synonyms of the families in which they have been included. In one case (Lewisuchidae) I thought it necessary to raise a subfamily name to the level of a full family, and I demoted a superfamily (Chaoyoungosauroidea) to a family (Chaoyoungosauridae)—a change of no consequence, since both names are still *nomina nuda*.

Attributions of family-level names are always to the first publication within a level, not necessarily to the earliest usage of the name. For example, the family Tyrannosauridae was named by Osborn (1905) to accommodate his new genus *Tyrannosaurus*. As presently constituted, the Tyrannosauridae also includes Leidy's tooth genus *Deinodon*, for which Cope (1866) erected the family Dinodontidae. Because the name Dinodontidae is based on a tooth genus, it fell out of use (even though most of the *Deinodon* type teeth definitely belong to a tyrannosaurid), and it has become a *nomen oblitum* ineligible for senior synonymy of Tyrannosauridae (though no formal ruling about this has been made to my knowledge). The spelling Dinodontidae was emended to Deinodontidae by Brown (1914), and Matthew & Brown (1922) divided the Tyrannosauridae into two subfamilies, Deinodontinae and Tyrannosaurinae. Conventionally, the two subfamilies would be attributed to Cope, 1866 and Osborn, 1905, respectively, but in this list I supply the earliest publication within a level, so I attribute them to Matthew & Brown, 1922. All these renamings and subfamilies are listed as synonyms of Tyrannosauridae Osborn, 1905.

Higher Taxa

Families, parafamilies, and higher taxa are listed in systematic order within their parent taxa. Since each taxon contains its common ancestor, the taxa can often be sorted, after cladistic analysis, by the relative positions of their ancestral nodes in the cladogram of their parent taxon. Where such sorting is ambiguous (*e.g.*, in a clade with two equivalent subclades), I list the taxon with the geologically earliest-known common ancestor first.

The families in this list are organized into higher taxa according to my own views of traditional taxonomy, cladistic analysis, and archosaur phylogeny, as outlined in the Taxonomic Considerations and Archosaur Phylogeny sections which follow. These views broadly agree with those of most other workers, because they are derived from their work; but even users who utterly disagree with my views should still find this list serviceable.

The nomenclature of taxa above the family level is not governed by the ICZN, but in those instances where a taxon has been given more than one name, I employ either the eldest name or the one in commonest use. I do not list synonyms for higher taxa, because taxa above the family level are more closely wedded to their authors' taxonomic philosophies than to the anatomical details of the included genera and species. Consequently, higher taxa tend to overlap rather than coincide, and they are not anchored to type taxa at lower levels, so synonymies among higher-level taxa are difficult to establish. In particular, cladists employ higher taxa that are clades, which fail to agree even in principle with the taxa employed by traditionalist taxonomists. I avoided using names coined specifically for clades (such as Tetanurae, Maniraptora, and Marginocephalia) unless I saw a compelling need for such taxa. There are plenty of already-available names for higher archosaur taxa in the literature.

Naturalists display considerable inertia when it comes to accepting changes in taxonomic systems that they have worked with their whole lives, and I do not expect the system constructed here to be adopted overnight. But I believe that the incrementally less cumbersome and intuitively more obvious usages advocated here, as exemplified by "paraorder Theropoda, suborder Carnosauria," will eventually supersede the more traditional usages, such as "order Saurischia, suborder Theropoda, infraorder Carnosauria."

Taxa *incertae sedis*

Sometimes lower-order taxa defy classification into higher taxa. A type specimen may be largely incomplete, or it may represent a species so different from related forms that it requires new higher taxa that the describer feels unready to create. For such problematic taxa, nomenclatural procedure provides a special category denoted by appending the Latin term *incertae sedis* ("of uncertain position") to the name of the lowest taxon in which the problematic forms are certainly classifiable. For example, theropod taxa that cannot be placed in any of the listed suborders are categorized as Theropoda *incertae sedis*; sauropod taxa not classifiable in any of the listed families are categorized as Sauropoda *incertae sedis*; ceratopsid taxa not classifiable in either of the two ceratopsid subfamilies are categorized as Ceratopsidae *incertae sedis*; and so forth. I have not always done this consistently, preferring, for example, to refer genera provisionally to established families if there is at least some chance that the referral is correct. This, I think, conveys more information about the problematic taxa than simply throwing them into an *incertae sedis* bin.

Occasionally workers will refer a taxon to the next higher taxon *incertae sedis* when they mean a provisional referral. For example, one might refer a genus to a family *incertae sedis* even though the family has not been partitioned into subfamilies. This, however, is a misuse of the *incertae sedis* notation. The *incertae sedis* category stands *in place of* the next higher category in which a taxon could be classified.

Provisional referrals in this table are always noted as such.

Ichnotaxa, Ootaxa, and Trace Fossils

Archosaur footprints, eggs, and other trace fossils can tell us an enormous amount about their makers' behavior and diversity. A large literature about trace fossils, complete with taxonomies parallelling that of the archosaurs' physical remains, has arisen, with which I have only just begun to familiarize myself. Unfortunately, synonymies and misidentifications abound in the earlier works, and I have not had the opportunity to look at the taxa comprehendingly enough to tabulate them. The best and most recent compilation of dinosaur trace taxa is in Chure & McIntosh, 1989; other entries into the literature may be found in Gillette & Lockley, eds., 1989 and Thulborn, 1990. I have started to acquire copies of trace-taxa articles for my library, and once I become familiar with the methodologies, I will also carry trace taxa in my table.

Censuses

Genera and species are counted within each family, and families, genera, and species are counted within each suborder and order. Doubtful taxa (usually *nomina dubia*) are included in the main counts but are also counted separately; *not* counted are synonyms, *nomina nuda*, and genera and species to be described. I do, however, count established species included in genera that are *nomina nuda* or to be described. Parataxa are counted along with the others.

Crocodilian taxa that have found their way into this table are counted, but the totals are not included in the census for superorder Thecodontia because the entire order Crocodilia is not listed. Taxa in the Excluded Taxa section are, of course, not counted either.

Taxonomic Considerations

WHEN I PUBLISHED my first table of archosaurian taxa, cladistic analysis of the archosaurs was in its infancy. Recognizing the onset of a "new wave," I acquired several books (Cracraft & Eldredge, eds., 1979; Eldredge & Cracraft, 1980; Schoch, 1986; and others) to guide me through its intricacies, and I soon discovered one particularly biting passage (Boucot, 1979): "After stripping away the jargon of 'morphos,' 'apos,' 'plesios,' 'syns,' 'character states,' and whatnot, I can only conclude that 'phylogenetic systematics,' or 'cladistics' (call it what you will), is nothing more or less than old-fashioned taxonomic classification so plastered over with jargon as to be unrecognizable to the casual reader."

While I don't think cladistics is *that* awful, I do view it primarily as a method of discovering whether the groupings in one's taxonomy are monophyletic or not. It can also—sometimes—identify previously unsuspected evolutionary trends, although considering the number of cladistic analyses that have been performed on various archosaur groups, the number of outright surprises seems rather small. On the whole, noncladistic and precladistic taxonomists seem to have done quite well elucidating phylogenies with just the traditional methods and, perhaps, a modicum of common sense.

The fundamental principle of phylogeny is that organisms possessing large enough suites of characters in common do so because they are descended from common ancestors, not by coincidence (*i.e.*, convergence). This is because the space of possible morphologies or molecular sequences is so immense that the chance of the same suite of characters arising within unrelated taxa is vanishingly small. Cladistic analysis at its best strives to describe such suites of characters, in order to discover which of a rather large set of possible phylogenies is most likely to be correct. As such, cladistic analysis is (among other things) a rigorous restatement of Cope's Rule ("organisms tend to evolve from generalized forms to specialized forms") and Dollo's Law ("anatomical parts lost through evolution are not restored, only replaced"). Neither of these "laws" is absolutely true, of course; they are simplified descriptions of two commonly observed evolutionary trends. Their significance lies more in their breach rather than their observance, for it is the breaches that are rare and phyletically useful.

Taxonomic papers using cladistic analysis tend to be organized alike. The reader is presented with a character matrix for the taxa under consideration. After some discussion, the paper concludes with a tree diagram, or cladogram, showing the relationships among the taxa derived from the character matrix. The important point is that there is little more information in the cladogram than already exists in the character matrix. The cladogram is simply a more comprehensible arrangement of the data in the matrix, designed to allow the creator to pick out characters that are homologous, homoplasious, reversed, and so forth. Character matrices with more than a couple of hundred entries (say, 10 taxa by 20 characters) are usually too large to analyze manually in a reasonable time, particularly when several different cladistic algorithms are being compared, so a computer generates a "most parsimonious" cladogram: one with the smallest number of violations of Cope's Rule and Dollo's Law, for example. (This, incidentally, tends to place the imprimatur of mathematical precision on the process, a phenomenon with which I, as an erstwhile computer scientist, am quite familiar. Fortunately, I am also familiar with its inverse: "garbage in, garbage out.")

There are two subtle effects that need to be mentioned with regard to the algorithms that convert character matrices into cladograms. First, not all characters should be given the same weight. I can well imagine that reversals of minor anatomical features, such as processes and rami of cranial bones, would occur more frequently and easily than reversals of major anatomical features, such as carpal or tarsal structure. Second, an organism's ecological niche tends to restrict the space of possible morphologies, making convergence and homoplasy more likely between organisms of similar size or lifestyle. For example, large carnosaurs and sauropods both exhibit hyposphene-hypantrum articulations between dorsal vertebrae, which is a size-related character, not a synapomorphy that indicates close phyletic relationship. There is no really good way to assign weights to such characters (Schoch, 1986: 116–123), and one can only hope that the balance of other characters in one's taxonomy will filter out any misleading phylogenies due to them.

Otherwise, there remains little to complain about with this methodology. It seems to me that the faults lurking in cladistics lie primarily with how characters and taxa are defined, rather than with the algorithms and procedures used to transform a character matrix into a cladogram. That is, I have less complaint with how cladograms are constructed than with how they are subdivided into taxonomies.

THE PROBLEMS OF CLADISTIC CLASSIFICATIONS

In a purely cladistic classification, all the taxa are clades, and hierarchy is determined by set inclusion rather than by an artificial system of typologically defined levels. Cladists assert, quite correctly, I might add, that clades are the only "real" phyletic sets, in the sense that they require no typological boundaries to be drawn among them. Membership in a clade is determined by descent (or, in the absence of a theory of evolution, simply by the possession of shared characters: *synapomorphies*).

The Linnaean system owes its success to the fact that extant organisms do not form a continuum of morphological types but cluster into discrete groups with well-defined suites of characters, between which transitional types can seldom be identified. The clustering pattern, amply explained by Darwinian theory, provides the natural divisions among the taxa as well as the hierarchy in which to arrange them. The name of each taxon is a convenient shorthand for the suite of characters common to the organisms classified in the taxon, and this convenience is one of the outstanding features of the Linnaean system.

When only *extant* organisms are to be named and classified, it is conceptually straightforward and even desirable to convert the Linnaean system into a cladistic system. Linnaean species are taken to be the lowest-level clades; then genera are defined as clades containing the species, families as clades containing the genera, and so on. Some Linnaean taxa, such as the paraclass Reptilia, turn out not to be clades themselves, but they can be subdivided or subsumed into taxa that are. It is easy to include common ancestors in the clades, because *they are entirely hypothetical constructs not found among the extant taxa*. The cladistic movement seeks to ensure that all Linnaean taxa are either diagnosed as clades or eliminated, in keeping with the precept that clades are the only real taxonomic entities.

The Ancestral-Taxon Problem

Both Linnaean and cladistic systems suffer when they are extended to include extinct as well as extant organisms. For example, a naturalist might discover a fossil that he or she believes is the actual ancestral form of the entire class Aves. What name is to be given to this creature's species? In the Linnaean system, the naturalist would simply bestow a binomial upon it, and probably give it its own family and order as the most primitive bird taxon. But in a cladistic system, the species would be an inadmissible paraphyletic taxon unless it included *all* birds; that is, the species itself could only be named *Aves*—or *Aves aves* if a strict binomial is required—and all later birds would have to be considered its sub-sub-...-subspecies. Some cladistic taxonomies avoid this problem by declaring the new species to be the closest possible outgroup to, or the lowest possible ingroup of, the descendant clade, but this would deny the ancestral status of the species that the naturalist wished to convey. I consider this to be untenable taxonomy: an extreme case of the Ancestral-Taxon Problem.

In the slightly modified Linnaean system used here, the hypothetical ancestral species would be given a Linnaean binomial and would be designated a paraspecies. In its role as the ancestral avian species, it would be placed at the root of its own paragenus, which would be placed in turn at the root of a parafamily and a paraorder, and ultimately at the root of the entire class. The hypothetical parent species from which the ancestral bird was descended—which, by consensus of dinosaurologists and paleornithologists, would *not* be a bird but a theropod—would itself be designated a paraspecies within a paragenus of a parafamily of the paraorder Theropoda.

Admittedly, this is an extreme case. Provably ancestral species are rarely, if ever, encountered in the fossil record, which is why cladistic taxonomies seldom face this challenge. But higher-level taxa in which hypothetical ancestral species could be classified are quite abundant, as they should be if we believe that species arise from other species.

The Stem-Group Problem

In the system used here, a parataxon is defined as the difference between a clade and one or more included clades. In a strictly cladistic taxonomy, parataxa are inadmissible, and as a result similar taxa within a clade sometimes fall into a series of outgroups converging on the clade or clades that would have been removed to make the parataxon. Sereno's (1986) cladistic classification of the Ornithischia provides a number of examples. In his Figure 6, the genera *Tenontosaurus*, *Dryosaurus*, *Camptosaurus*, *Probactrosaurus*, *Iguanodon*, and *Ouranosaurus* are shown as iguanodontian genera converging successively toward the family Hadrosauridae. Within the Iguanodontia, all five clades formed by the successive exclusion of each of the aforementioned genera are named and diagnosed: Dryomorpha for all iguanodontians except *Tenontosaurus*; Ankylopollexia for all dryomorphans except *Dryosaurus*; Styracosterna for all ankylopollexians except *Camptosaurus*; Iguanodontoidea for all styracosternans except *Probactrosaurus*; and Hadrosauroidea for all iguanodontoideans except *Iguanodon*, that is, Hadrosauridae plus *Ouranosaurus*. The families in which those genera were traditionally classified are largely scrapped. Similar series of genera are found in the Pachycephalosauria and the Ceratopsia. Taxa in such series are called stem-group taxa (Thulborn, 1984; Schoch, 1986: 25), since they connect a root node (in this case, of the clade Iguanodontia) with a crown group (in this case, Hadrosauridae). The proliferation of long sets of named, serially nested stem-group clades I call the Stem-Group Problem.

This problem has two ramifications. First, such nested higher-level taxa are of doubtful utility. We all agree that the history of life is of surpassing complexity, but it is neither necessary nor desirable for our taxonomic systems to be equally intricate. One of the great virtues of the Linnaean system is that it simplified and systematized the bewildering array of organisms that inhabit and inhabited the earth. It is difficult to imagine dinosaurologists pondering whether iguanodontian fossils they have discovered should be called dryomorphic, ankylopollexian, or styracosternal, and I can see no benefit in creating a hierarchy comprising as many nested higher-level taxa as there are genera in it. Such a classification is as inefficient as a factory with six workers and five managers.

And second, the reader is invited to consider what could happen to the above carefully constructed iguanodontian classification after a few more genera are described, or when another taxonomist (*e.g.*, Horner, 1988, 1990) proposes a different arrangement of some of the same genera! Stability of the higher taxa is a desirable trait of the Linnaean system that is not particularly evident in cladistic systems.

I avoid this kind of microtaxonomy by indicating ancestry and descent in a general way with a suitable choice of parataxa. For example, of the iguanodontian taxa under discussion, I list *Tenontosaurus* provisionally within the parafamily Hypsilophodontidae, *Dryosaurus* in the family Dryosauridae, *Camptosaurus* in the family Camptosauridae, and *Probactrosaurus*, *Iguanodon*, and *Ouranosaurus* in the parafamily Iguanodontidae. I consider it likely that the dryosaurids, camptosaurids, and iguanodontids originated among the hypsilophodontids, and virtually certain that the hadrosaurids and lambeosaurids originated among the iguanodontids, even though we cannot point to specific ancestral genera in the families (Sues & Norman [1990], however, consider the Hypsilophodontidae monophyletic, a sister group to the Iguanodontia; my idea of a hypsilophodontid is less restrictive than that). More detail than this is, in my opinion, not warranted in a taxonomy involving so few genera, and particularly not when the relationships among the taxa are still being vigorously debated (Cooper, 1985; Horner, 1988, 1990; Sues & Norman, 1990; Norman & Weishampel, 1990).

The Too-Deep-Hierarchy Problem

The Stem-Group Problem is a specific instance of a more general problem that confronts cladistic taxonomies. In the iguanodontian example above, Sereno categorizes the Iguanodontia as an infraorder and the Hadrosauridae as a family; the five serial clades in between the Iguanodontia and the Hadrosauridae are categorized at Linnaean levels in between the infraorder and the family: gigafamily Dryomorpha, megafamily Ankylopollexia, grandfamily Styracosterna, hyperfamily Iguanodontoidea, and superfamily Hadrosauroidea. Of these levels, only the superfamily is in general use by traditional taxonomists; the other levels were invented by cladists (Schoch, 1986: 259). When more iguanodontians are discovered, more levels may have to be intercalated among the giga-, mega-, grand-, hyper-, and superfamily levels. (I can imagine having to develop a taxonomy just to keep the prefixes straight: Sereno's levels are ranked differently from those listed by Schoch!) The history of life being as complicated as it is, I can even imagine the number of levels in cladistic taxonomies eventually exceeding our ability to coin names for them. I call the proliferation of hierarchic levels in cladistic taxonomies the Too-Deep-Hierarchy Problem.

To avoid the Too-Deep-Hierarchy Problem, cladistic taxonomists sometimes advocate doing away with the Linnaean hierarchic levels entirely (*e.g.*, by replacing them with numerical identifiers or by using various typographical conventions; Schoch, 1986: 255–263). The system I use here solves this problem automatically by restricting the Linnaean levels to a manageable few, and by listing included genera arbitrarily in alphabetic order. Suprageneric parataxa are listed ahead of their descendant taxa. I have tried to avoid subdividing taxa unnecessarily and using suprageneric taxa containing only one genus (this, of course, has not been possible in all cases). The most useful classification, it seems to me, is one that is conceptually simple and does not attempt to straitjacket users with its creator's philosophy or phylogeny.

The Too-Many-Clades Problem

The Too-Deep-Hierarchy Problem is a particular case of the Too-Many-Clades Problem. Most cladograms are, or strive to be, binary trees; that is, graphs in which the branch nodes lead to exactly two other nodes. This reflects the idea that in any evolutionary lineage only one new taxon breaks away at a time. Cladograms with nodes that branch to more than two other nodes are considered *unresolved*: there is not enough information to decide the order in which the taxa at the polychotomous nodes formed. A moment's reflection will show that a fully resolved cladogram with N terminal nodes *always* has N–1 branch nodes, one of which is the root; an unresolved cladogram always has fewer. This table lists over 600 archosaur genera, so a fully resolved cladogram of these genera would have at least 600 branch nodes, that is, at least 600 potentially nameable suprageneric clades. Even if half the archosaur genera are based on incomplete material that does not allow the cladogram to be fully resolved, this still leaves 300 possible clades. Since cladograms are determined objectively by shared characters, there is no reason to favor some clades with names and not others. This is undoubtedly why cladistic taxonomy has given traditional taxa unfamiliar diagnoses (such as Ornithosuchia and Pseudosuchia in Gauthier, 1986), and has afflicted us with an undesirable proliferation of named suprageneric taxa (and with taxa that have pseudo-names such as "Unnamed Taxon Including Ornithosuchidae, *Lagosuchus*, Pterosauria, Herrarasauridae* [*sic*], Ornithischia, Sauropodomorpha, and Theropoda" [Gauthier, 1986a: 151]).

In this table, I employ parataxa to sidestep the Too-Many-Clades Problem. A taxon or parataxon comprising serially listed subtaxa functions as an unresolved node in a cladogram, thus keeping the number of named suprageneric taxa manageable and allowing a variety of different interpretations of the phyletic relationships among the genera.

The Species-as-Points Problem

In cladograms, species, and supraspecific taxa whose characters are not germane to the cladistic analysis, are treated as points—the end nodes of the cladograms. But many species cannot be reduced to phyletic points, because they have speciated. That is, some of their characters were lost, others were added, and still others changed through the passage of time. The reason species can be characterized at all is that their characters change on time scales considerably longer than the lifetime of an individual researcher—or, for that matter, the span of recorded history. For all practical purposes, species change continuously and constantly, though the rate of change at any particular time may be quite rapid or very slow. The changes can involve the entire population (anagenesis) or only a reproductively isolated subpopulation (cladogenesis). Changes noticeable over the span of time required to lay down a geological stratum are considered rapid; vertebrate species do not usually change on time scales of less than a million years.

Because species and some higher taxa are represented as zero-dimensional points in a cladogram, the topology of cladograms does not lend itself readily to diagramming changes in species. For example, let A and B be two species, with A the immediate ancestor of B. There is only one possible cladogram relating A and B: the trivial cladogram showing A and B joined to a common root. But this cladogram does not specify the phyletic relationship between A and B uniquely. Species B could be ancestral to A; they could both be descended from a third species, C, omitted from the cladogram; or they need not even be closely related. All these situations result in the same cladogram, because in this case only one is possible. Increasing the number of species increases the number of possible cladograms, but it also increases the number of ways the cladograms can model the species' phylogeny incorrectly. If even the trivial two-taxon cladogram models phylogeny ambiguously, I can only imagine the number of different ways more complicated cladograms could be misinterpreted. (This is what I think has happened in theropod-bird phylogenies; the cladograms are generally correct, but the phylogenies have been improperly modeled. More on this in the Dinosaur Phylogeny section.)

It might be best to think of cladograms as relating *specimens* rather than species and higher taxa (among dinosaurs, many species of which are represented by solitary type specimens, this is not very far from reality). But all that is really needed is to acknowledge that the interesting action in a cladogram takes place on the branches joining the nodes rather than at the nodes themselves. Zero-dimensional nodes cannot change or speciate, but one-dimensional curves can. By indicating which branches represent which taxa in a cladogram, we can for all practical purposes sift out the incorrect phylogenies—or at least focus on the places in a phylogeny where our understanding is incomplete.

Species do not exist as objective entities; only populations of organisms do. Certain populations of organisms interbreed freely among themselves and not with other populations; this phenomenon leads to the concept of a biological species, and in turn to the idea that such an entity can be defined, named and studied (Otte & Endler, eds., 1989). Biological species almost always comprise individuals with similar genotypes and phenotypes; at least, they fall into a small number of such sets. This means that a named biological species can be associated with a set of typological attributes, and that these attributes can in turn be used to characterize the species. For extant species, these attributes can be morphological, behavioral, and molecular; but for fossil forms, they are almost exclusively morphological. It is the changes in these attributes that we track when we say that species change and speciate through time.

Unicellular organisms multiply by dividing, and after the act of mitosis it is impossible to decide which individual was the parent. Speciation is an analogous process, but it is almost always possible, at least theoretically, to decide which is the parent species and which is the daughter. What effects this decision is the continuity of the characters before and after the speciation event: The species that retains more of the primitive attributes is considered the parent species. According to Mayr (1942), speciation occurs when a population of organisms becomes reproductively isolated from a larger population long enough for anagenesis to render interbreeding between the populations impossible. In such a circumstance, the relative sizes of the populations may be sufficient to establish which species is the parent. But regardless of how parenthood is ultimately established, it is important to note that the parent species is a paraphyletic taxon, because it no longer includes all of its descendants.

Higher-level taxa give rise to other taxa in an exactly analogous way. A species within a supraspecific taxon may speciate, and the daughter species may again speciate, until a species appears in which enough characters have changed that it can no longer be considered part of the original supraspecific taxon. Like a parent species, the parent parataxon can continue to exist and give rise to more new taxa, some within the taxon and others perhaps outside.

Although species can be considered as being in a continuous state of anagenesis, speciation events occur rather rarely. In between such events, a species may change considerably, so that a later daughter species may be morphologically quite different from an earlier daughter species of the same parent. It is this phenomenon that leads to the morphological gaps between related taxa, and which allows us to classify species in a hierarchic system at all.

In traditional taxonomies, higher-level parataxa are defined typologically; the boundaries of a taxon are set by a consensus of the naturalists who work with it and related taxa. When a fine line must be drawn between two taxa, consensus is the only way to do it. It may sound terribly arbitrary and subjective, but it is no more arbitrary than identifying a species by its attributes and noting the appearances of new species as these attributes change.

In short, I agree with Mayr and Simpson, as cited by Schoch (1986: 262), that although a classification should be based to some degree on the hypothesized evolutionary history of the organisms, it should serve as a convenient information retrieval system about the organisms as well.

Philosophically, perhaps the worst flaw in cladistic taxonomies is this: If clades make up the only taxa, then there is ultimately no real novelty in the process of evolution. Birds and mammals are not new classes of vertebrates, they are *merely* derived archosaurs and therapsids. New phyla can no longer appear, because all the phyla that can be arose at or just after the Cambrian revolution, and all the life forms on earth ever since have fallen into subclades of these. If what determines families, orders, and classes is remoteness of ancestry rather than form and function, then humans, mammals, birds, dinosaurs, and insects are ultimately nothing more than large, highly derived, colonial microbes. While this viewpoint can be defended, I find it, and the cladistic taxonomies that spring from it, ultimately sterile. A clade, used as a taxon, becomes a prison in which groups of organisms are forever trapped, no matter how much their descendants may change from their ultimate ancestor; but a parataxon is a wellspring from which, every so often in the history of life, organisms and taxa arise that are genuinely new.

LINNAEAN TAXA AT THE ORDINAL LEVEL

There are no objective rules for classifying organisms within the Linnaean hierarchy. Although one might define a species by overall similarity to a type specimen or by the ability of the organisms in the species to interbreed, there is no algorithm to decide when two similar species belong in different genera or when they are similar enough to remain in the same genus. Nor are there algorithms for deciding when two genera belong in different families, two families in different orders, and so forth. These decisions are made *ad hoc* by naturalists acting on their personal ideas of similarity and common descent. As noted previously, this is part of the "art" of taxonomy. Successful taxonomies are those that make the most sense to their users and, as a consequence, withstand a test of time. I need not mention that this arbitrariness leads naturally to the notion that supraspecific Linnaean taxa are entirely artificial and have no objective meaning.

In particular, mammals, including extinct forms, are presently classified into 44 orders (listed in Carroll, 1988). The class Aves, which dominates aerial environments much as mammals dominate terrestrial environments, is classified into 35 orders (listed in Carroll, 1988, excluding Archaeopterygiformes), and the class Osteichthyes – which has dominated aquatic environments from at least the Silurian through the Recent – is classified into no less than 62 orders (listed in Carroll, 1988; the Camp, Welles & Green bibliography [1953] lists 70). Finally, the class Insecta, which dominates the terrestrial microfauna and comprises at least 100 times as many species as the classes Aves, Mammalia, and Osteichthyes combined, is classified into a mere 28 orders (listed in O'Toole, ed., 1986 but excluding extinct orders and certain orders of uniramians once classified as insects).

Dinosaurs were ubiquitous throughout the Mesozoic, comprising almost literally the entire continental megafauna from the Early Jurassic to the Late Cretaceous. Among terrestrial tetrapods, only the Cenozoic mammals have achieved comparable dominance. Thus it is peculiar that the traditional dinosaurian orders have not followed the pattern of the other groups enumerated above. Whereas there are some two or three score orders of birds, mammals, fish, and insects, the number of dinosaur orders is *two*. Why should this be so?

Perhaps dinosaurologists have been more conservative than mammalogists, ornithologists, ichthyologists, or entomologists, austerely classifying their objects of study into two orders despite a diversity requiring more. Conversely, it may be that students of extant forms have given their fields grandiose dimensions by splitting their taxonomies into more orders than necessary. I believe, however, that the natural sciences contain enough built-in checks that the latter alternative is untenable; the present work is an attempt to undo any effect ascribable to the former.

The situation changes somewhat when *all* reptiles are taken into consideration, not just the dinosaurs. Reptilian diversity at the ordinal level attained a maximum during the Triassic (*cf.* graphs in Padian & Clemens, 1985), when approximately 15 orders were known to be extant. But most of those orders became extinct at or just before the Triassic-Jurassic boundary, and they were seemingly not replaced by a radiation of new orders comparable to that at the beginning of the Triassic for the reptiles and the Cenozoic for the mammals. Padian and Clemens indicate a marked decline in ordinal-level diversity and origination of new orders among the reptiles from the Early Jurassic through at least the mid-Cretaceous. I believe this "decline" is at least partly artificial, the result of a tradition of maintaining the number of dinosaurian orders at two and archosaurian orders at five in spite of a real diversity reflected in an ever-widening fossil record.

Two methodologies are at work in Linnaean zoological taxonomy. Taxa at or below the family-group level are based primarily on species, descriptions of which require considerable detail. Genera and families are constructed by grouping species together. This "bottom-up" methodology is reflected in the naming process of the lower taxa, which is regulated by the ICZN: A species, when named, must be grouped into a genus, whose name becomes the first part of the species' binomial, and a family must be named after an included genus. Hundreds of new genera and species, and dozens of new families, of animals are created each year, primarily for extinct forms and small, cryptic extant forms.

Contrasting with this is the "top-down" methodology governing taxonomy at the higher levels. Kingdoms, phyla, and classes are almost always based on general descriptions emphasizing common characteristics of wide groups of organisms. The detail required to distinguish a species or genus is neither necessary nor desirable to define a phylum or a class. The discovery or definition of a new class or phylum is an infrequent and usually significant biological event; supraordinal Linnaean taxa exhibit considerable stability.

Caught in between these two methodologies are the ordinal-level taxa. Precisely at this level does the "top-down" methodology collide with the "bottom-up" methodology, which implies that defining and naming ordinal-level taxa should be a blend of both methodologies. I suggest that the requisite compromise between the methodologies is to regard each ordinal-level taxon as containing a single *morphological type* or *Bauplan* (Levinton, *et al.*, 1986) within its class. This intuitive notion is best characterized by example.

If extant mammals were classified according to the traditional methodology used for the archosaurs, there would be only six orders instead of 44: (1) a basal order for all mammals ancestral to the eutherians (corresponding roughly to the traditional "Thecodontia"); (2) an order for "primitive" eutherians, including insectivores and primates (corresponding roughly to the traditional Crocodylia); (3) an order for bats (corresponding to the Pterosauria, of course); (4) an order for carnivores (corresponding to the Saurischia); (5) an order for all ungulates, sirenians, and cetaceans (corresponding roughly to the Ornithischia); and (6) an order for rodents and lagomorphs. We can see that such an arrangement for mammals is unsatisfactory. Why then continue to apply it to the archosaurs?

Let me place the *Bauplan* idea in a dinosaurian perspective. When dinosaurologists assemble to discuss their latest discoveries, they rarely speak of saurischians and ornithischians. Instead, they focus on sauropods, theropods, ankylosaurs, stegosaurs, and so forth. Like the terms amniote and reptile, the terms saurischian and ornithischian are too general and comprise too many distinct morphological types to open a dinosaur discussion satisfactorily. This is a powerful clue to what hierarchic level, if any, the taxa Saurischia and Ornithischia should be assigned. It is the categories of interest to dinosaurologists that should lie at the ordinal level, not at the subordinal level where they have been classified for so long.

In the classification used here, I have raised many archosaurian suborders to full orders for the intuitive reasons articulated above. Each order thus comprises a single *Bauplan*. The aetosaurs were quadrupedal, heavily armored herbivores; the pseudosuchians were mainly lightly armored quadrupedal carnivores; the rhamphorhynchoids were mainly long-tailed pterosaurs; the brontosaurs were quadrupedal herbivores with elongated necks and tails; the theropods were bipedal predators; the ornithopods were mainly bipedal herbivores; and so forth. It should be pointed out that many of the archosaurian suborders were originally proposed as orders, and that suggestions to return some of them to the ordinal level appear occasionally even in the recent literature (*e.g.*, Bakker & Galton, 1974).

Of course, each order must be defined by a suite of more detailed characters to ensure that it is not a polyphyletic assemblage of similar but unrelated forms (such as aetosaurs and ankylosaurs, which were both armored quadrupedal herbivores). As cladists will agree, it is shared descent from a common ancestor – monophyly where possible, paraphyly elsewhere – that removes some of the arbitrariness and artificiality from supraspecific taxa. Discussions of the archosaurian groups along these lines are the substance of the remaining sections of this work.

NEW SUBFAMILIAL TAXA

Protognathus Renamed

The monograph on *Shunosaurus lii* by Zhang (1988) introduced a new sauropod genus and species, *Protognathus oxyodon* Zhang, 1988, whose type specimen is a dentary from the Lower Shaximiao Formation of Dashanpu, Zigong (Institute for Vertebrate Paleontology and Paleoanthropology CVOO732).

The generic name *Protognathus* is preoccupied by *Protognathus* Basilewsky, 1950, a genus of central African carabid beetles. The name *Protognathus* also appears misspelled as *Portognathus* [*sic*] in the English abstract to Zhang's paper, but this is a typographical error and cannot be considered a properly proposed replacement name for *Protognathus*. Therefore, I propose the name *Protognathosaurus* n. gen. to accommodate Zhang's species *Protognathus oxyodon*. This makes the renamed type species *Protognathosaurus oxyodon* (Zhang, 1988).

Ultrasaurus Renamed

One of the most famous recently named sauropod genera is *Ultrasaurus*, whose name appeared in print as early as 1979 as a *nomen nudum* in popular dinosaur publications. James A. Jensen applied the name to the scattered remains of an enormous sauropod that he discovered in the Dry Mesa Quarry in Colorado. He chose the name "Ultrasaurus" to signify that the dinosaur was even larger than the sauropod "Supersaurus," which he had unearthed in the same quarry in 1972 and whose name at the time was also still a *nomen nudum*. Jensen's "Supersaurus" and "Ultrasaurus" remained *nomina nuda* until 1985, when formal descriptions of the genera were published (Jensen, 1985). In the meantime, however, Korean paleontologist Haang Mook Kim had applied the name "Ultrasaurus" to fragmentary sauropod material from Korea, believing that this also represented a sauropod larger than "Supersaurus." Kim's "Ultrasaurus" remained a *nomen nudum* until 1983, when Kim formally described the genus and its type species, *Ultrasaurus tabriensis*. I have seen two versions of Kim's 1983 paper, virtually identical except that one names the type species *U. tabriensis* and the other does not (D. Chure and J. S. McIntosh, pers. comm.; R. E. Molnar, pers. comm.). It remains unclear which was published first, although the latter is probably a preprint of the former. In either case, Kim's *Ultrasaurus* did appear in print, in a properly distributed document, as a valid name with a designated type species and type specimen, some two years before Jensen's. Kim had misidentified the most diagnostic part of the type specimen, a partial humerus, as an ulna (Paul, 1988a), which led him to imagine his sauropod was larger than it really was. Furthermore, the nature of the remaining type and referred material makes Kim's name *Ultrasaurus* a *nomen dubium*. But Jensen's name is still preoccupied by Kim's, so I propose the name *Ultrasauros* n. gen. to replace it.

The ICZN recommends that a new genus-group name differ from similar names by more than just its termination or small differences in spelling (ICZN, 1985: Appendix D, section I, paragraph 3), but in the same work the ICZN regards generic names that differ by a single letter as distinct (Article 56[b]). Inasmuch as it is unlikely that Kim's genus will receive wide attention, and in view of the longstanding and continuing interest in Jensen's genus, I think that as much of Jensen's generic name should be retained as possible. It is unlikely that much confusion between the two genera will result, so the single-letter name change (suggested by Jensen, pers. comm.) to *Ultrasauros* is justifiable.

J. S. McIntosh (pers. comm.) informs me that the type specimen of *Ultrasauros macintoshi* is a dorsal vertebra, Brigham Young University 4044, whose specimen number was listed incorrectly as BYU 5000 in Jensen, 1985.

Singular Genitives Corrected

Four dinosaur species have been named in the past two decades in honor of families rather than individuals: *Tenontosaurus tilletti* Ostrom, 1970; *Sauropelta edwardsi* Ostrom, 1970; *Avaceratops lammersi* Dodson, 1986; and *Stenotholus kohleri* Giffin, Gabriel & Johnson, 1988. The ICZN (1985: Article 31[a][ii]) states that a specific name in honor of more than one person must take the genitive plural ending *-orum* or *-arum*; the former ending is to be used when there is at least one male among those honored.

Tenontosaurus tilletti Ostrom, 1970 was named after the Lloyd Tillett family of Lovell, Wyoming, and *Sauropelta edwardsi* Ostrom, 1970 was named after Nell and Tom Edwards of Bridger, Montana. *Avaceratops lammersi* Dodson, 1986 honors at least eight members of the Lammers family of Shawmut, Montana. *Stenotholus kohleri* honors Terry and Mary Kohler of Milwaukee, Wisconsin (Giffin *et al.*, 1987). *Stenotholus kohleri* was subsequently found to be a junior synonym of *Stygimoloch spinifer* (Gabriel & Berghaus, 1988), but it nevertheless remains necessary to spell the specific name correctly. In each case, the genitive singular ending *-i* is inappropriate and constitutes an incorrect original spelling of the specific name, as described in Article 32(c) of ICZN, 1985. Since at least one male is present among the honorees of each of the specific names, the ICZN mandates that the names be respelled as follows:

Tenontosaurus tillettorum Ostrom, 1970
Sauropelta edwardsorum Ostrom, 1970
Avaceratops lammersorum Dodson, 1986
Stenotholus kohlerorum Giffin, Gabriel & Johnson, 1987

Becklespinax **n. gen.**

Huene (1923) coined the genus *Altispinax* for two species of *Megalosaurus* from the Wealden of Great Britain. The older species, *Megalosaurus dunkeri*, had originally been established by Dames (1884) for a single unusual carnosaurian tooth from Hanover, Germany. The other species, *Megalosaurus oweni*, had been established by Lydekker (1889a) for a partial left metatarsus (British Museum [Natural History] R2559) originally described by Owen (1857) as belonging to the nodosaurid *Hylaeosaurus*. Huene based his name on an articulated series of three dorsal vertebrae (British Museum [Natural History] R1828) with greatly elongate neural spines that Lydekker (1888b) had catalogued, along with almost all other Wealden theropod material, in the species *Megalosaurus dunkeri*. *Altispinax* was created as a conditional name, without a type species, in case it could someday be shown that R1828 was referable to the species *Megalosaurus dunkeri*. This, however, is now impossible.

In two forthcoming papers (Olshevsky, in preparation a, b), I have disentangled the surfeit of confusion that has arisen concerning the names *Altispinax*, *Megalosaurus dunkeri*, and *Megalosaurus oweni* since they were coined. Most of the confusion stems from misidentified type and referred specimens, and some stems from outright errors in figures and figure captions that have propagated through the literature in uncritical reviews. Before I can publish these results, however, I must travel to London to examine the specimens in person, to photograph and measure them for comparative study. Based on photographs kindly supplied by Stephen Pickering, Eric Buffetaut, and Jean Le Loeuff, however, I am already convinced that R1828 and R2559 cannot possibly belong to the genus *Megalosaurus* and represent two new genera of Wealden theropods.

The tooth species *Megalosaurus dunkeri*, through one of those unfortunate mishaps alluded to above, can no longer be separated from the genus *Altispinax*; it was made its lectotype species by Kuhn (1939). The type tooth (for which I still have no specimen number, and which may, according to Stephen Pickering, have been lost from the University of Marburg collection) is unusual in having no serrations on the mesial carina. Dames regarded this as significant enough to erect a new species of *Megalosaurus*, but Lydekker considered this simply the result of wear. Then Lydekker took that unwarranted step of referring almost all the British Museum Wealden theropod material to Dames's species, instead of isolating the species and perhaps creating new taxa of his own.

In particular, Lydekker referred the three vertebrae, BMNH R1828, to *Megalosaurus dunkeri*. This specimen was discovered by noted amateur fossil collector Samuel H. Beckles, Esq., in the Lower Wealden of East Sussex sometime in the early 1850s. Owen (1855: T. XIX) figured the vertebrae at life size, and in a subsequent work (1856, oddly not the work in which the specimen was figured) described them as anterior dorsal vertebrae of *Megalosaurus*. There is little question that Owen already had the specimen in hand when he supervised the construction of the dinosaur models for the Crystal Palace. The "humpbacked" appearance of the Crystal Palace *Megalosaurus* is certainly based on R1828's elongate neural spines.

To go into all the nomenclatural problems that those specimens inspired is beyond the scope of this work. In the case of R1828, it is sufficient to note that the vertebrae are posterior dorsals, probably #8–10, and that except for the very tall neural spines, they most closely match dorsals #8–10 of the Argentine genus *Piatnitzkysaurus* (Bonaparte, 1986a) in the conformation of the apophyses and laminae and in the position of the neural spine atop the neural arch. The firm contact between the apexes of the neural spines of vertebrae #9 and 10 (and, presumably, later vertebrae in the series) is a diagnostic feature of the specimen that occurs in no other known theropod genus. It is possible that the neural spine of vertebra #8 is not broken off at the top but is naturally shorter than the spine of #9. This would constitute another very strong diagnostic feature of the genus, but it requires physical examination of the specimen before it can be confirmed. The neural spines and the vertebrae are very different from those of *Acrocanthosaurus* and *Spinosaurus*. Relative to the lengths of the centra, the neural spines of R1828 are the tallest known in the Theropoda except for *Spinosaurus aegyptiacus*. I can find little justification for referring R1828 to the genus *Acrocanthosaurus* and making it the type specimen of the species *Acrocanthosaurus altispinax* (Paul, 1988b). In view of the resemblance of R1828 to figured vertebrae of the eustreptospondylid *Piatnitzkysaurus*, I have removed the species *Acrocanthosaurus altispinax* from the allosaurid genus *Acrocanthosaurus* into a new eustreptospondylid genus, which I name *Becklespinax*, in honor of Samuel H. Beckles, the discoverer of the type specimen. The type species of the genus thus becomes *Becklespinax altispinax* (Paul, 1988).

Valdoraptor **n. gen.**

Having referred most of the Wealden theropod genera to *Megalosaurus dunkeri* (Lydekker, 1888b), Lydekker subsequently (1889a) redescribed, as a new species, *Megalosaurus oweni*, the theropod metatarsus (BMNH R2559) that Owen had originally referred to *Hylaeosaurus* (with the incorrect number R2556). Hulke (1881) had earlier noted the theropod nature of the metatarsus, but he did not refer it to any known genus, because his paper was concerned with armored dinosaurs. Unfortunately, Lydekker seems to have been misled by Owen's (1857) figure of the metatarsus (which presented a *mirror image* of the actual specimen): He misdescribed the left metatarsus as a right, and shortly thereafter (Lydekker, 1890a) referred two more metatarsals (BMNH R604d and R1525) to *Megalosaurus dunkeri*, because to him they were similar to—but not identical with—the metatarsals of *Megalosaurus oweni*. Although they had been found about 180 yards apart in the Hollington Quarry, Lydekker considered them as belonging to the *same individual*! It was not long thereafter that Lydekker (1890b) removed the British Museum Wealden theropod specimens from *Megalosaurus dunkeri* and referred them to his own species.

Huene, in a series of papers on saurischians (1926a, 1926b, 1932), misrepresented the type specimen of *Megalosaurus oweni* as four metatarsals. This error remained uncorrected in subsequent literature, surfacing in Steel, 1970 and even as recently as Molnar, 1990, both of which considered the two referred metatarsals (R604d and R1525) as cotype specimens of *Megalosaurus oweni* and overlooked the real type specimen, R2559.

I haven't the space here to provide all the details of these misidentifications, and I refer the reader to the second of my forthcoming papers on this subject (Olshevsky, in preparation b) for a more complete study. Suffice it to say that the type metatarsus of *Megalosaurus oweni* is more slenderly built and has a proportionately larger and more robust metatarsal III than a metatarsus referred to *Megalosaurus bucklandii* (Molnar, Kurzanov & Dong, 1990: Figure 6.29K). The species *Megalosaurus oweni* is therefore removed from the genus *Megalosaurus* and is made the type species of the new genus *Valdoraptor* ("Wealden robber"). The type metatarsus, R2559, shows no signs of having a proximally pinched metatarsal III, so I tentatively refer the genus to the Allosauridae, pending completion of my forthcoming paper. The proximal ends of the metatarsals are worn away, so it is difficult to ascertain their configuration from the illustrative material available to me. The type species of the genus becomes *Valdoraptor oweni* (Lydekker, 1889).

Other New Combinations in the Table

In Pterosauria (Pterodactyloidia; Pteranodontidae): *Geosternbergia sternbergi* and *Geosternbergia walkeri*, new combinations for *Pteranodon (Geosternbergia) sternbergi* and *Pteranodon (Geosternbergia) walkeri*.

In Theropodomorpha (Theropoda; Tyrannosauridae): *Tarbosaurus turpanensis*, *Tarbosaurus luanchuanensis*, and *Tarbosaurus lanpingensis*, new combinations for *Tyrannosaurus turpanensis*, *Tyrannosaurus luanchuanensis*, and *Tyrannosaurus lanpingensis*.

In Theropodomorpha (Theropoda; Troodontidae): *Saurornithoides asiamericanus* and *Troodon bakkeri*, new combinations for *Pectinodon asiamericanus* and *Pectinodon bakkeri*.

In Theropodomorpha (Theropoda *incertae sedis*): *Orthogoniosaurus rawesi*, new combination for *Massospondylus rawesi*.

In Sauropodomorpha (Brontosauria; Anchisauridae): *Anchisaurus sinensis*, new combination for *Gyposaurus sinensis*.

In Sauropodomorpha (Brontosauria; Brachiosauridae): *Giraffatitan brancai*, new combination for *Brachiosaurus (Giraffatitan) brancai*.

In Ornithischia (Ankylosauria; Nodosauridae): *Chassternbergia rugosidens*, new combination for *Edmontonia (Chassternbergia) rugosidens*.

In Ornithischia (Ornithopoda; Hadrosauridae): *Anatotitan longiceps*, new combination for *Trachodon longiceps*.

For explanations, see the notes for the individual taxa in the table.

Archosaur Phylogeny

THE ARCHOSAURS were once the most important group of terrestrial vertebrates. They dominated the Jurassic and Cretaceous faunas the way mammals have dominated Cenozoic faunas, which is one of the reasons they are so fascinating to study. Among the archosaurs are numbered the largest terrestrial predators, the largest flying creatures, and the largest land animals of all time. After the Cretaceous-Tertiary extinction event, the archosaurs were badly decimated; only 22 species in 8 genera (Ross & Garnett, eds., 1989) – all crocodilians, most endangered – remain extant. But if the cladistic viewpoint of the archosaurs is taken, then we must add 9672 extant bird species to the count (as tabulated in Sibley & Monroe, 1990).

Like the fossil records of most groups, the archosaur fossil record is generally awful. This is partly because most of the archosaurs were terrestrial animals that lived in nondepositional environments, and partly because most of the evolutionary changes among the archosaurs occurred in the small forms, which required exceptional conditions for preservation as fossils. Consequently, there are many gaps in our knowledge of their evolution. Some may say that it is through these gaps that I am driving the large truck of my phylogeny, but I think that we can still say something about what happened in those gaps. Like the "dark matter" of the universe, which makes its presence known solely by its gravitational effects, the as-yet-unknown archosaurs that have fallen through the cracks in the fossil record have sometimes left their evolutionary traces on the forms we have already discovered.

General Considerations

Among terrestrial vertebrates, evolution usually follows Cope's Rule (Stanley, 1973). That is, larger, more specialized forms evolve from smaller, generalized forms. I will avoid the question of what the terms "generalized" and "specialized" mean; but the pattern of size increase has a simple and cogent explanation. All other things being equal, larger individuals tend to dominate their smaller contemporaries, outcompeting them for resources and leaving a disproportionate number of offspring. This selection effect induces the general evolutionary trend toward size increase noticeable in the vertebrate fossil record. Counteracting this trend may be such adverse circumstances as heavy predation, wherein larger individuals simply become bigger targets less able to find concealment; and scarcity of resources, when larger individuals are less able to locate sustenance. The latter circumstance gives rise to island-endemic dwarfism, for example. Also counteracting this trend are requirements of physiological fitness: giant individuals are seldom as fit as normal-size individuals. There is a limit to how much of a size increase can be tolerated in the *Bauplan* of a particular species before the species itself must change. Finally, small vertebrates tend to attain sexual maturity faster and have larger litters than large vertebrates. This results in a faster genetic turnover among the smaller forms (Simpson's "tachytelic" evolution), which in the absence of predation can radiate rapidly into many lineages. As larger forms evolve, their evolutionary tempo slows (Simpson's "bradytelic" evolution), and the tendency to evolve wholly new *Baupläne* greatly decreases. These effects are quite evident in the evolution of the archosaurs.

DEFINING ARCHOSAURS

Defining the archosaurs as a reptilian subgroup has proved difficult. As discussed by Benton & Clark (1988) and Benton (1990a), one proposal is to make the Archosauria the smallest clade containing both the extant Crocodylia and Aves: the "crown group" definition. A second proposal is to choose a particular suite of characters that sets the archosaurs apart within the Diapsida, ensuring that the characters chosen are sufficient to include both Crocodylia and Aves. Despite being cladistic, both proposals clearly partake of a certain arbitrariness, and there is no satisfactory way to consider either method of defining the archosaurs – that is, choosing which node to call Archosauria on the diapsid cladogram – more "natural" than the other.

It is necessary to point out that two different groups are called Archosauria in the current literature: the clade Archosauria and the traditional reptilian subgroup Archosauria, which is not a clade but a parataxon, because it does not include the birds. There is certainly a need for a name for that group of animals that are archosaurs but not birds – probably more so than for the archosaurs *plus* the birds – but strict cladistics does not supply it. Having the same name for two different groups is aesthetically unacceptable, but since my nomenclature is not strictly cladistic, I refrain from coining a new name for the clade Archosauria. I have elected to use the name Archosauria for the traditional parataxon, and I will simply rely on context when it is necessary to distinguish between the two different "Archosaurias."

The archosaurs diversified to such an extent that there is no synapomorphy uniting all of them. Nevertheless, I follow Charig (1976a) and Benton (1990a) in considering the key archosaurian synapomorphy the presence of an antorbital fenestra; Benton lists seven additional synapomorphies. The antorbital fenestra became closed in later crocodilians and ornithischians, and it merged with the narial opening in later pterosaurs, but loss of the fenestra is not a radical enough reversal to warrant excluding those groups from the Archosauria.

The antorbital fenestra seems to have appeared abruptly in the Diapsida toward the end of the Permian. The earliest-known archosaurs possessed large fenestrae; only one diapsid taxon is known with what can be considered an "incipient" antorbital fenestra. But since the earliest archosaurs were undoubtedly small, lightly built animals not likely to be preserved as fossils, I take the position that the abrupt appearance of the antorbital fenestra is an illusion resulting from the lack of a fossil record. In view of the absence of forms intermediate between the archosaurs and the other diapsid reptiles, the antorbital fenestra, whatever its origin, remains the primary part of the convenient but somewhat slender morphological and fossil-record gap that defines the Archosauria.

There is, on the other hand, a truly enormous morphological and perhaps also physiological gap between the known archosaurs and their paramount descendant group, the class Aves. Chatterjee (1991: 317) lists 23 cranial apomorphies possessed by his new species *Protoavis texensis* in common with Aves that are "not found in any archosaurs," even though its postcranial anatomy differs little from what might be expected in an arboreal small theropod. Later birds, with the modifications to their postcranial anatomy that evolved as adaptations to powered flight, are much further removed from the theropod *Bauplan*. Those morphological differences necessitate subtracting the clade Aves from the clade Archosauria and defining the Archosauria as a diapsid parainfraclass. Aves may then be retained as a traditional (and monophyletic) class.

But just what constitutes the class Aves? For over a hundred years, it was simplest to define the Aves by the (in most cases presumed) presence of feathers, a strong synapomorphy uniting *Archaeopteryx* with later birds. The total absence of well-documented feathered intermediates between *Archaeopteryx* and its theropod forebears helped to provide a very sharp line of demarcation between Aves and Reptilia.

It is recognized, however, that feathers themselves evolved from reptilian scales, their earlier homologues. The featherlike structures observed in *Longisquama* (Sharov, 1970) presumably represent or are derived from a stage in that evolutionary history. Are they then to be counted as feathers, supporting reference of *Longisquama* to the class Aves? Or are they to be considered scales, supporting reference of *Longisquama* to the paraclass Reptilia? The fossil record of Mesozoic birds may be awful, but the fossil record of feathers is truly abysmal. I suggest, in view of their rarity in the fossil record and the morphological evolution they must have undergone in the early history of the archosaurs, that the presence of feathers not be used to define the class Aves. This is why I regard feathers as a plesiomorphic character retained by birds from ancestral theropods.

As long as *Archaeopteryx* was comfortably ensconced as the "oldest bird," there was no compelling reason to exclude it from the class Aves, and no compelling reason to discard feathers as an avian synapomorphy. But the discoveries of fully volant (although not yet undescribed) birds from the Early Cretaceous of China (P. C. Sereno, pers. comm.; Dong Z., pers. comm.), *Protoavis* from the Late Triassic of Texas (Chatterjee, 1991), and *Iberomesornis romerali* from the Early Cretaceous of Spain (Sanz, 1990), among others, have made it necessary to take a harder look at conventional avian phylogeny. It has begun to seem more and more as if *Archaeopteryx* was a "living fossil" in the Late Jurassic: a small, feathered, habitually volant theropod dinosaur that probably coexisted with more advanced birdlike forms better capable of powered flight.

In the archosaur phylogeny I have constructed, I imagine the commonly accepted theropod dinosaur groups as originating from various kinds of feathered gliding and flying forms. While this hypothesis seems to me to answer many questions about theropod and avian origins, it does complicate theropod-avian taxonomy. Do we classify the theropods as birds, or do we classify those aerial theropods as dinosaurs (or "dino-birds")? I have opted for the latter choice, because the skeletal anatomy, particularly the postcranial anatomy, of those "dino-birds" was evidently much more like that of what we traditionally call small theropods than that of volant birds. The class Aves, to me, begins not with *Archaeopteryx* but with those birds in which the forelimb elements had entirely lost their grasping function by fusing into a "true" wing. There is little chance that a flightless form with *grasping* forelimbs—which we would naturally call a theropod dinosaur—would have evolved at or above this stage of avian evolution. In birds descended from fully volant ancestors, the wings are usually reduced or vestigial and seldom even reacquire clawed hands (though ostriches have them).

Two avian clades originate near this point in the avian cladogram. Cracraft (1988) calls the more inclusive clade Ornithurae (Haeckel, 1886), the other Carinatae (Merrem, 1813); he does not employ Carinatae in its original sense, namely, apposed to Ratitae Merrem, 1813. The only ornithuran birds Cracraft regards as not carinate are the hesperornithiforms (other authorities, *e.g.*, Gauthier, 1986a, 1986b, and Chatterjee, 1991, include more). These were Cretaceous toothed diving birds with vestigial wings that I think perfectly exemplify flightless birds descended from fully volant, that is, carinate rather than merely ornithuran (*sensu* Cracraft), ancestors.

Cracraft lists many characters that define carinate birds, including a typically avian pectoral girdle with enlarged or keeled sternum and elongate coracoids. He also lists many ornithuran characters, such as a greatly reduced tail and a strongly opisthopubic pelvis, in which the ilia extend caudally to include numerous sacral vertebrae and the pubes extend caudally parallel to the ischia (usually fusing with them and the ilia). Evidence from new discoveries shows (Sanz, 1989; Chiappe, 1990: Figure 38), however, that the carinate wing and pectoral girdle appeared *prior* to the ornithuran pelvis. This would make the clade Ornithurae a subclade of the Carinatae (*contra* Cracraft). The tail of a flying animal like *Archaeopteryx* helped to stabilize it in flight, so that it did not need to rely on the volant ability of its wings alone to keep it aloft. Once birds were able to fly mainly or solely with their wings, that is, became unstable powered fliers, their tails were free to shorten and to become modified into the accessory flight appendages that they are in extant birds. Functionally, therefore, it makes more sense for the carinate clade to include the ornithuran clade rather than vice versa.

To summarize, the parainfraclass Archosauria is here defined to include all diapsid reptiles possessing antorbital fenestrae, together with all their descendants except the carinate birds, which are regarded as a separate class, Aves. This definition approximates the current usage of the term Archosauria among noncladistic taxonomists (*e.g.*, Charig, 1976a), and if the class Aves is not excluded, the resulting clade coincides with Archosauria as defined by Benton (1990a). This clade Archosauria includes the entire "crown-group" clade Archosauria (Benton & Clark, 1988), as well as a few primitive thecodontian groups that would otherwise be consigned to a cladistic limbo as serial archosaur outgroups (or to a more inclusive clade Archosauromorpha).

EARLY ARCHOSAURS

Efremov (1940) described *Mesenosaurus romeri*, from the Early Permian of Russia, as a pelycosaur but later (1955) referred to it as a primitive archosaur. Ivakhnenko & Kurzanov (1978) redescribed the type skull and noted a number of archosaurian characters, including a minute antorbital fenestra. A photograph of the entire skeleton appears in Ivakhnenko & Korabelnikov (1987: 183), who identify it as a primitive archosaur. Unfortunately, the illustration is too indistinct to make out anatomical details, but the limb proportions and general morphology of the specimen do not contradict an archosaur identification. Evans (1988), in a cladistic study of nonarchosaurian and problematic diapsids, concluded that *Mesenosaurus* was not an archosaur but an early diapsid offshoot. She identified the small antorbital fenestra of Ivakhnenko & Kurzanov as a lacrimal foramen. But Ivakhnenko & Kurzanov had already located the lacrimal duct at a different site on the skull, so Evans's identification of the antorbital fenestra as a lacrimal foramen is not certain. For the purposes of this list, I have provisionally accepted Ivakhnenko & Kurzanov's identification of *Mesenosaurus* as a very early archosaur.

Potentially the most interesting feature of the skull of *Mesenosaurus* is the small size of the temporal fenestra. Ivakhnenko & Kurzanov take this as evidence that archosaurs evolved the diapsid condition independently of the other diapsid reptiles. In view of the rather large number of characters shared between archosaurs and other diapsids (Benton & Clark, 1988), however, this conclusion may be premature.

Being an Early Permian reptile, *Mesenosaurus* is temporally well placed to be a basal archosaur. The earliest undoubted archosaur, however, is the Late Permian proterosuchid *Archosaurus rossicus*, recently redescribed by Sennikov (1988). It, and all later proterosuchids, were specialized archosaurs clearly part of a lineage that originated before the Late Permian (Charig, 1976b). With the exception of *Mesenosaurus*, the fossil record of that lineage is entirely nonexistent.

The proterosuchids were archosaurs specialized for a riparian lifestyle. This is curious, because most of the later archosaurs were highly adapted to terrestrial or aerial lifestyles. Only a few, such as the parasuchians, hupehsuchians, and crocodilians, remained (or became) semiaquatic or fully aquatic. Throughout this paper, I assert that the fossil record is strongly biased—*hyperbiased*—against the preservation of small, fully terrestrial vertebrates in favor of riparian and aquatic forms. This is why the proterosuchids enjoy a modest worldwide fossil record while the record of the other Permian and Early Triassic terrestrial archosaurs does not exist. This is also why I will not accept a phylogeny in which the proterosuchids are considered *ancestral* archosaurs, despite the priority of their appearance.

But in the absence of evidence to the contrary (and in the absence of any fossil record at all), the proterosuchids may be considered a side branch within a larger parataxon, the Proterosuchia, that *would* include those hypothetical ancestral archosaurs, as in Charig, 1976a. In particular, *Mesenosaurus* can provisionally be grouped therein. Along with the characteristic antorbital fenestra, the proterosuchians retained many plesiomorphic diapsid characters, such as the diapsid skull, palatal teeth, unfenestrated mandibles, "saurischian" pelves, primitive mesotarsal ankles, a significant size disparity between fore and hind limbs, a sprawling, lizardlike posture, and a long tail. Most of those characters became lost or heavily modified in later archosaurs, and the evolutionary patterns of these modifications broadly define how the archosaurs are classified and how we understand their phylogeny.

THECODONTIAN ORDERS

Over the more than thirteen decades since the Thecodontia was first recognized (Owen, 1859), it has lost its original conception and has expanded to include an ever-increasing morphological range of archosaurian taxa. Among these are the feathered glider *Longisquama*; the gliding reptile *Sharovipteryx*; various large, heavily armored, quadrupedal herbivores; some small, gracile, bipedal predators; a number of semiaquatic piscivores; and many medium-size to gigantic quadrupedal carnivores. I find it astonishing that a single order was made to accommodate reptiles with such divergent body plans while at the same time *excluding* the crocodiles. Merely comparing the wide *Bauplan* diversity encompassed within the traditional "Thecodontia" with the restricted *Bauplan* diversity of extant vertebrate orders demonstrates how necessary it has become to redefine the group.

Originally, the name "Thecodontia" was coined for reptiles whose teeth were individually socketed in their jaws. The fact that some reptiles later referred to the group had acrodont, subthecodont, or no teeth at all, and that most reptiles with thecodont dentitions (such as most dinosaurs) were excluded from the "Thecodontia," does not invalidate the name for taxonomic purposes. The complicated history of the taxon is well covered by Charig (1976b).

The major evolutionary trend among the early archosaurs in general and the "thecodontians" in particular was the development of the semi-erect and fully erect stance from the sprawling stance that characterizes the Proterosuchia. Charig (1972) documented this trend fully, correlating it with the development of the crocodile-normal (CN) and crocodile-reverse (CR) tarsi in the semi-erect forms. Both can be derived straightforwardly from the primitive mesotarsal tarsi of the Proterosuchidae (Krebs, 1963), as adaptations to keep the hind foot entirely on the ground (instead of at an angle) while the hind limb was held in a semi-erect position. Both are characterized by a large calcaneum with a caudally directed tuber. In living crocodiles, a tendon attaches to the tuber that allows the animal to raise itself off the ground while walking (Charig, 1972; Carroll, 1988: 279), and this was presumably the function of the tuber in all the early archosaurs that had it. This adaptation undoubtedly abetted the significant increase in body size and weight undergone during the evolution of the "thecodontians" in the Triassic.

In the CN ankle, a peg from the astragalus inserts into a hollow in the calcaneum at the movable joint between the two tarsal elements. In the CR ankle, the peg is reversed, going from calcaneum to astragalus. The boundary between the calcaneum and astragalus appears to be evolutionarily labile, however, so the direction of the peg may not be as phyletically significant as the simple presence of the calcaneal tuber. Indeed, the shapes of the astragalus and calcaneum are complicated (Benton, 1990: Figure 1.3), and, as in a "yin-yang" symbol, it is sometimes unclear which element had the peg and which had the hollow.

In this work, the traditional order "Thecodontia" is elevated to a parasuperorder and is in turn partitioned into several orders. These orders are restricted primarily to archosaurs thought to have possessed tarsi with calcaneal tubera. Most of these thecodontian orders had been subsumed into the traditional "Thecodontia" as suborders, though some had originally been proposed as orders. Only one of these, the aforementioned Proterosuchia, is a paraorder with descendant taxa outside the Thecodontia, which prevents the Thecodontia from being a clade. Not only can all the other thecodontian orders be derived from the Proterosuchia, but as I explain in succeeding sections, I believe the pterosaurs and dinosaurs to be independently derived from the Proterosuchia as well. Taxonomists who require monophyletic groups in their classifications should either remove the Proterosuchia from the Thecodontia as an outgroup or simply restrict it to one or both of the two included families, neither of which can plausibly be regarded as ancestral to any later archosaur groups. Restricting the Proterosuchia this way would relegate the common ancestor of the archosaurs to an as-yet-unknown group of Permian diapsids instead of an as-yet-unknown group of proterosuchians.

The parasuperorder Thecodontia must include the order Crocodylia, whose present-day representatives are actually the last surviving thecodontians. Thus constituted, the Thecodontia is nearly congruent to Gauthier's (1986a, 1986b) clade Pseudosuchia and Benton & Clark's (1988) clade Crocodylotarsi. Thecodontia is an older name than Pseudosuchia, however, and (as noted in Benton & Clark, 1988 and in Charig & Milner, 1990) it would be far more appropriate than Pseudosuchia, or "false crocodiles," for a group containing the *true* crocodiles(!). I do retain the group Pseudosuchia as a thecodontian order, but in a sense closer to that in which it has customarily been used. Crocodylotarsi is an appropriate name for the clade comprising all the thecodontians except the Proterosuchia, Ornithosuchia, and Hupehsuchia.

Besides calcaneal tubera, another character occurring in the later Thecodontia is the presence of dermal scutes. In lightly armored forms (*e.g.*, ornithosuchians), these were restricted to a double row running along and above the spine (the primitive condition), but the bodies of some later forms (aetosaurs) are almost completely encased in latitudinal rings of armor. In crocodilians, the dorsal scutes and their associated musculature help to support the body (Frey, 1988a, 1988b). This suggests a similar weight-bearing function in the other thecodontians, in addition to whatever protective role the scutes had. Dermal armor is presently unknown in the Proterosuchidae and the Erythrosuchidae (Charig & Reig, 1970), but its prevalence in the remaining thecodontian groups suggests that it originated within a closely related but as-yet-undiscovered family. Parasagittal dermal armor might even be plesiomorphic among archosaurs, since it was described in the eosuchian *Heleosaurus* (Carroll, 1976).

Some Triassic archosaurs previously classified as "thecodontians" fall outside the superorder Thecodontia as constituted here. These include the archosaurs that possessed mesotarsal tarsi advanced over the proterosuchian condition, among which were the earliest pterosaurs and dinosaurs. As usual, such "protopterosaurs" and "protodinosaurs" are almost entirely—and frustratingly—lacking from the fossil record. So not only is there a distinct morphological gap between the Thecodontia and the four mesotarsal-ankled clades (Pterosauria, Theropodomorpha plus Aves, Sauropodomorpha, and Ornithischia), there is a convenient—and profound—fossil-record gap as well.

Paraorder Proterosuchia

Broom (1906) originally created the order Proterosuchia for the single genus *Proterosuchus*, but this order was later incorporated into the "Thecodontia" as a suborder (*cf.* Charig & Sues, 1976). In view of the morphological and functional distance between the proterosuchids and the other thecodontians, I consider it best to reinstate Broom's order within the parasuperorder Thecodontia. Isolated subordinal status for the Proterosuchia was strongly advocated by Bonaparte (1984), and I have translated this into ordinal status here. In view of its ancestral position with respect to all the later thecodontians, the pterosaurs, and the dinosaurs, I consider it a paraorder. The Proterosuchia is the only group available to accommodate the small, generalized archosaurs from which all the others are descended.

As noted above, controversy surrounds the status of *Mesenosaurus romeri*. Rather than erect a separate order for this single species (which further research may indicate it requires), I have tentatively placed it and its monotypic family into the order Proterosuchia as the most primitive known archosaur. The lack of a downturned premaxilla excludes *Mesenosaurus* from the Proterosuchidae. Only further examination of the available specimens, or the discovery of more specimens, can confirm this classification.

Other than *Mesenosaurus*, the oldest archosaurs in the fossil record fall mainly into the single family Proterosuchidae. Broadly similar in their anatomy, extant worldwide (known from Australia, China, South Africa, and the Soviet Union) from the Late Permian through the Early Triassic, proterosuchids are thought to have been small to medium-size riparian piscivores (Charig & Sues, 1976). None of the known genera was directly ancestral to any later archosaurs, because they possessed a sharply downturned premaxilla, an autapomorphy not found in more advanced archosaurs (Carroll, 1988: 271) except the primitive erythrosuchid *Garjainia* (Charig, 1976b; Ivakhnenko & Korabelnikov, 1987: Figure 237; it may ultimately prove necessary to classify *Garjainia* in a monotypic family in the Proterosuchia because of this, as was done by Ochev, 1958). But smaller, more terrestrial versions of the proterosuchids, classifiable in as-yet-unknown but probably distinct families within the Proterosuchia, would have been the ultimate ancestral forms of the other thecodontians, the pterosaurs, and the dinosaurs. In fact, it is remotely possible that the proterosuchid premaxilla was retained as the downturned, kinetic premaxilla of podokesaurid and halticosaurid ceratosaurians such as *Rioarribasaurus* and *Dilophosaurus*.

Plesiomorphic proterosuchid characters inherited from earlier diapsid reptiles include palatal teeth, lack of a mandibular fenestra, presence of intercentra in the vertebral column of some included genera, primitive mesotarsal ankle—the least-derived ankle among the archosaurs—and sprawling stance; the major synapomorphy shared with other archosaurs is the antorbital fenestra. Many other anatomical features of proterosuchids are enumerated by Charig & Sues (1976). Considerations such as these place the Proterosuchidae in a small clade of its own at the base of the Archosauria (Benton & Clark, 1988).

My list organizes the Proterosuchidae mainly according to the most thorough reviews of the family by Charig & Reig, (1970), Cruickshank (1972), Charig & Sues (1976), and Thulborn (1979).

Order Ornithosuchia

In the Early Triassic, a second evolutionary lineage among the archosaurs becomes evident in the fossil record, with the appearance of the South African form *Euparkeria capensis* and related forms from the Soviet Union and China. Many authors have considered *Euparkeria* close to the ancestry of practically all the other archosaurs, including the pterosaurs and the dinosaurs (as discussed in Benton, 1990a). Gauthier (1986a), for example, declared *Euparkeria* undiagnosable independently from his clade Archosauria, which is as close as cladists come to stating that one taxon is ancestral to another. Indeed, it is difficult to dispute a close connection between the euparkeriids and the non-thecodontian archosaurs. In the phylogeny developed below, however, I maintain that the pterosaurs and dinosaurs acquired their advanced mesotarsal ankles directly from the primitive mesotarsal ankles of proterosuchians, without passing through either a CR or CN topology. So I have removed the euparkeriids from direct ancestry of the pterosaurs and dinosaurs, viewing the similarities between euparkeriids and dinosaurs as homoplasious.

Instead, I regard the euparkeriids as early members of the order Ornithosuchia, a small group comprising all the known CR-ankled archosaurs. Although the ankles of *Euparkeria* are small, poorly ossified, and difficult to study, they do seem to be CR (Parrish, 1986). Gauthier (1986a) and Benton (1990a) noted several anatomical features tending to unite *Euparkeria* with the later and more advanced family Ornithosuchidae, suggesting that the ornithosuchids are best regarded as large, advanced euparkeriids. Likewise, the imperfectly known *Erpetosuchus*, from the Late Triassic of Scotland, may be a euparkeriid descendant, because the skull shows several ornithosuchian features, such as carnivorous dentition and a deep fossa surrounding the antorbital fenestra. Unfortunately, the ankle of erpetosuchids is not known. Such considerations prompt me to divide the Ornithosuchia into the parafamily Euparkeriidae and two families Ornithosuchidae and Erpetosuchidae. The presence of calcaneal tubera and parasagittal dermal armor in the known ornithosuchians further affirms a closer alliance with thecodontians than with pterosaurs and dinosaurs (see also Bakker, 1986).

To wit, *Ornithosuchus* is frequently cited as an ancestral dinosaur and is invitingly depicted in a bipedal pose by Walker (1964). Walker even considered it, quite specifically, to be an ancestral carnosaur. The popular dinosaur literature abounds with discussions of the origin of dinosaurs among "bipedal thecodontians," with *Ornithosuchus* furnished as the model dinosaurian ancestor. But although *Ornithosuchus* was a fully erect reptile (the femoral head was medially inturned and the acetabulum was mildly perforated in some ornithosuchids), there is little evidence besides the size disparity between fore and hind limbs to substantiate bipedality. I agree with Bakker (1986) and Paul (1988b) that the ornithosuchids were quadrupedal predators better classified in the Thecodontia than ancestral to the dinosaurs.

A fully erect stance is known to have evolved more than once within the archosaurs (*e.g.*, among the rauisuchians and the dinosaurs), and the inturned femoral head and perforate acetabulum were the way this was accomplished within the Ornithosuchia; the non-dinosaurian nature of this adaptation in the group is betrayed by the CR tarsi.

Gauthier (1986a, 1986b) greatly expanded the scope of the Ornithosuchia by diagnosing it as the clade containing all the archosaurs from *Euparkeria* to birds, the complementary clade to his Pseudosuchia. Interestingly, he noted several ornithosuchian characters (listed, *e.g.*, in Benton, 1990a) as *paralleled* in various thecodontian clades. I regard these, contrarily, as still more evidence of a close relationship between the Ornithosuchia and the other thecodontians.

Ornithosuchians enjoyed a worldwide distribution (their shed teeth are sometimes classified as Triassic "carnosaur" teeth) as a minor thecodontian side branch that became extinct along with most of the other thecodontians toward the end of the Triassic. In assembling the Ornithosuchia, I mainly followed Krebs (1976); the order sorely needs a systematic restudy, particularly to resolve its relationships with the other archosaurs in more detail.

Order Pseudosuchia

The group Pseudosuchia has had a long and colorful history since it was first named in Zittel's enormous paleontological handbook (Zittel, 1887–90) – too long and colorful to be detailed here. It suffices to note that over time it had come to include practically all the thecodontians except the proterosuchids, parasuchians, and crocodilians, and as late as 1986 Gauthier (1986a, 1986b) rediagnosed it to include the crocodilians as well. Most previous authors have included the ornithosuchians in the Pseudosuchia, sometimes restricting the Pseudosuchia to include *only* those forms. Various authors also often grouped putative "ancestral dinosaurs" and "ancestral birds" with these, so when such creatures (*e.g.*, *Longisquama*, *Lagosuchus*) emerged from the fossil record, they were classifed as pseudosuchians, too. So was that primitive proterosuchian, *Mesenosaurus* (Ivakhnenko & Kurzanov, 1978)! Of all the thecodontian groups, this order is most in need of redefinition.

Like the ornithosuchians, many pseudosuchians exhibit dental and cranial morphologies strikingly similar to those of carnosaurs, which caused earlier workers to classify pseudosuchian teeth and jaws as specimens of Triassic theropods. This error resulted largely from our inadequate knowledge of pseudosuchian anatomy, and it was compounded when the shed teeth of large pseudosuchian predators were discovered in association with the remains of prosauropod prey: An entire generation of paleontologists was thus misled into considering prosauropods to be ancestral or primitive theropods (see, *e.g.*, references in Galton, 1985). Most workers now believe that the similarities between pseudosuchian and theropod teeth are entirely homoplasious.

As constituted here, the Pseudosuchia is a monophyletic order including most of the families of carnivorous quadrupedal archosaurs classified as Pseudosuchia by Krebs (1976), together with some apparently bipedal archosaurs (poposaurians) probably derived from them. Regrettably, I have had to exclude the aetosaurs, which were the original constituents of Zittel's group, because they were herbivores. Pseudosuchians, aetosaurs, parasuchians, and crocodilians (clade Crocodylotarsi of Benton & Clark, 1988) all probably acquired their CN tarsi from an as-yet-unknown proterosuchian common ancestor as part of a suite of forelimb and hindlimb adaptations associated with increased size and weight, semi-erect stance, and more rapid terrestrial locomotion. Among the pseudosuchians, Bonaparte (1982, 1984) recognized a close connection between the erythrosuchids and the rauisuchids, the latter being basically swifter, more efficient versions of the former, when he segregated them in the suborder Erythrosuchia outside the Proterosuchia. As he showed, the locomotor improvements of the semi-erect erythrosuchians culminated in the fully erect stance of the rauisuchians, convergent with but anatomically different from that of the ornithosuchians and the dinosaurs (rauisuchians possessed horizontally inclined ilia rather than vertical ilia). This apparently allowed the evolution of bipedal (but, unfortunately, not particularly well known) forms such as *Postosuchus* and *Poposaurus*, whose family, Teratosauridae (*cf.* Galton, 1985), I have placed in a new suborder, Poposauria. It is not clear whether the poposaurians derived directly from the rauisuchids or represent a parallel development from another, as-yet-undescribed rauisuchian family, but in either case they differed sufficiently from the quadrupedal rauisuchians that a new suborder is justifiable. (In this context, it should be noted that newly described long-necked, gracile rauisuchids [Sennikov, 1990] from Russia may be close to ancestral poposaurians.) Should research deny the bipedality of the poposaurians, however, then the suborder Poposauria would have to be rejected in favor of installing the Teratosauridae as a rauisuchian family.

Essentially, then, the parasuborder Erythrosuchia includes quadrupedal pseudosuchians with a semi-erect stance, the parasuborder Rauisuchia includes quadrupedal pseudosuchians with a fully erect stance, and the suborder Poposauria includes fully erect, bipedal pseudosuchians. I regard the erythosuchians as ancestral to the rauisuchians, which in turn were ancestral to the poposaurians; hence the paraphyly of the first two suborders.

Also included in the Pseudosuchia are the archaeosuchians, better known as the proterochampsians, a side branch of crocodiloid riparian predators from the Triassic of South America. Bonaparte (1971a, 1982, 1984) collected the proterochampsids in their own subgroup of the Erythrosuchia (but Archaeosuchia Sill, 1967 takes precedence over Proterochampsia Bonaparte, 1971a as the name of this taxon). They apparently form a clade distinct from (but less derived than) the erythrosuchian-rauisuchian-poposaurian clade, and they may eventually even acquire their own thecodontian order. I classify them provisionally as the most primitive pseudosuchian suborder.

An unusual armored archosaur from the Late Triassic of Virginia, *Doswellia kaltenbachi* Weems, 1980, was placed in its own monotypic suborder, Doswelliina, of the "Thecodontia" by its describer, who considered resemblances between *Doswellia* and the aetosaurs (see below) as convergent. Bonaparte (1982) nevertheless considered *Doswellia* an aberrant aetosaur, while Benton & Clark (1988) were able to find a synapomorphy with the proterochampsids—loss of the postfrontal. I have followed their opinion in provisionally classifying the Doswelliidae as a separate archaeosuchian family. The tarsus of *Doswellia* is not known.

The problematic genus *Lotosaurus* Zhang, 1975 from the Late Triassic of China, which has not yet been completely described, seems to be a derived rauisuchian with edentulous jaws and neural spines elongated into a ridge or sail along the back. I have only seen photographs of a mounted specimen (Olshevsky, 1991) whose general stance and pose suggest either an erythrosuchian or a rauisuchian. I have provisionally lumped it and other problematic Triassic "sailbacked" genera into the family Ctenosauriscidae of the parasuborder Rauisuchia. I know of no cladistic analysis of the thecodontians that attempts to classify these forms. Since *Lotosaurus* lacked dentition, it is not quite clear whether it was carnivorous or herbivorous; in the latter case, it and the other ctenosauriscids might require their own pseudosuchian suborder.

Pseudosuchians were thus a rather diverse and important group of thecodontians. In assembling this order, I have mainly followed the systematic work of Reig (1961), Charig & Reig (1970), Sill (1967, 1974), Krebs (1976), Bonaparte (1982, 1984), Benton & Clark (1988), and Sennikov (1989, 1990) – insofar as they do not conflict with one another.

Order Parasuchia

The parasuchians, or phytosaurs, are a monophyletic group of Late Triassic thecodontians of worldwide provenance (Hunt & Lucas, 1991). They are universally considered to have been large, riparian or lacustrine predators that occupied an ecological niche later taken over by the crocodilians, which convergently acquired many parasuchian anatomical characters (*cf.* Hunt, 1989). By comparison with most other archosaurian orders, the parasuchian fossil record is strikingly robust, including many hundreds of specimens ranging from isolated teeth to complete skulls and skeletons, dozens of species, and about a score of genera, all classifiable in but a single family. Much individual variation due to growth allometry and sexual dimorphism is present, and specimens often exhibit morphologies transitional between established species and genera. Their fossil record is so rich that they are routinely used as stratigraphic markers in the Upper Triassic of the southwestern United States. All this has contributed to the proliferation of synonymies and renamings in systematic studies of the group.

The reason for this is quite clear: Parasuchians were well adapted to life in a freshwater aquatic environment, which coincidentally happens to be an environment in which fossilization is very likely to occur. Virtually all of parasuchian evolution took place just where its record had the best chance of being preserved.

By contrast, ancestral parasuchians are absent from the fossil record (which might lead one to suspect that they were upland forms that did not live near rivers). Parasuchians were highly derived thecodontians whose independent evolutionary history extends back into the Middle or even the Early Triassic.

It is rather unfortunate that parasuchians are usually called "phytosaurs" in the literature. The term Parasuchia was coined by Lydekker in 1885, preceding by 45 years the term Phytosauria, created by Camp (1930). "Parasuchian" means "beside crocodile," a succinct description of the numerous anatomical convergences of parasuchians with crocodilians, but "phytosaur" means "plant lizard," an allusion to a supposed herbivorous diet. Anyone who has beheld parasuchian teeth knows they were not herbivores! For these reasons I prefer the name Parasuchia for this order.

Recent work has gotten the formidable task of disentangling parasuchian taxonomy well underway. The present list organizes the parasuchians according to the systematic studies in Gregory, 1962; Westphal, 1976; Ballew, 1989; Hunt, 1989; and Hunt & Lucas, 1989 and 1991.

Order Aetosauria

The aetosaurs are usually grouped as a pseudosuchian family within the traditional "Thecodontia," but I consider them sufficiently different from the pseudosuchians that they warrant a separate order. They were the only known thecodontians to adapt to a herbivorous diet. (It is not clear which of the three major herbivorous archosaur clades – the aetosaurs, the ornithischians, or the sauropodomorphs – became plant-eaters first. The earliest known aetosaurs are from the Carnian, however, somewhat earlier than the earliest known ornithischian, *Pisanosaurus*, and the earliest prosauropods [Hunt, 1991].) Their relationship with the other thecodontians is difficult to establish, but Benton & Clark (1988) include them in the clade Pseudosuchia on the basis of a number of minor synapomorphies. This means they could be derived archaeosuchians (paralleling *Doswellia*), erythrosuchians, rauisuchians, or an autapomorphic group.

All known aetosaurs were quite similar to one another morphologically and fall into a single family, Stagonolepididae (whose name takes precedence over Aetosauridae by a mere two months). They all had thick-boned skulls with piglike snouts, peglike teeth, and antorbital fenestrae inset into deep fossae. The articulation point of the lower jaw was located somewhat below the tooth row. Their dermal armor, their most prominent characteristic, was developed into latitudinal rows of slender, rectangular plates that encased the animal dorsally and ventrally. Rows of lateral spines ran from the neck and shoulders to the tail in some genera. The pattern of the armor is diagnostic to the generic level (R. A. Long, pers. comm.). All the aetosaurs were plantigrade, semi-erect quadrupeds with CN tarsi.

Order Crocodylia

The Crocodylia is a well-studied archosaur clade extant from the Middle Triassic to the present (Steel, 1973). I can think of no reason save tradition to account for why it has been maintained as an order separate from the thecodontians in most archosaurian classifications. Benton & Clark (1988) restrict the term Crocodylia to the "crown group," that is, the smallest clade containing all the living crocodilians. This clade and related ones are grouped together and nested in a series of larger clades that culminates in the most inclusive clade, the Crocodylomorpha (Walker, 1970). But it is this group, not the "crown group," that many authorities (*e.g.*, Carroll, 1988; Sues, 1989; Buffetaut, 1989) consider to be the Crocodylia, and I follow this usage here. The clades included by Benton & Clark in the Crocodylomorpha may be accommodated as subtaxa and parataxa within the Crocodylia, but I do not deal with the advanced groups here. Only those taxa with morphologies close enough to those of other thecodontians to have been occasionally included with them in other taxonomies are listed.

Some of the earliest crocodilians (sphenosuchians and possibly trialestians) show specializations for quadrupedal running, including a slender body, fully erect long legs, and elongated proximal carpal elements. The elongate carpals in particular persist even in extant forms and are an excellent synapomorphy uniting all the crocodilians. Crocodilians are morphologically conservative, never straying far from their original *Bauplan*, and they are, of course, the archetypal CN-ankled, parasagittally armored thecodontians. All these considerations assure ordinal status for the group within the Thecodontia.

It is interesting that the Crocodylia probably originated as a group of small, swift, quadrupedal predators. It was only after the extinction of the parasuchians opened up an ecological niche for large, riparian predators that one group of crocodilians (protosuchians) occupied it, essentially abandoning its cursorial adaptations in favor of much greater size and weight, relatively shorter legs, and a semi-erect stance. Even so, crocodilians did not lose all their adaptations for speed; extant forms are still capable of galloping when necessary to capture a meal (Ross & Garnett, eds., 1989: 49). The last of the small, swift forms, the hallopodans, apparently became extinct at the end of the Jurassic.

In this table, the less-advanced crocodilians are grouped primarily according to Steel (1973), as modified by the additional taxonomic work of Crush (1984) and Benton & Clark (1988). The orders Trialestia and Sphenosuchia seem not to be ancestral to any later groups, but I have listed the Protosuchia as a parasuborder because it is probably ancestral to all the later (unlisted) crocodilian groups. It and its descendant groups (including the "crown group" Crocodylia) comprise the clade Crocodyliformes of Benton & Clark.

Order Hupehsuchia

Nanchangosaurus and *Hupehsuchus*, two genera of highly derived aquatic reptiles from the Middle Triassic of China, had been described only briefly (Wang, 1959; Young & Dong, 1972) until a thorough redescription was published by Carroll & Dong (1991). Young & Dong erected a new suborder, Hupehsuchia, for *Hupehsuchus* and tentatively classified the Hupehsuchia as highly derived, aquatic archosaurs. *Hupehsuchus* was later synonymized with *Nanchangosaurus* (Dong, 1979).

Carroll & Dong's work clearly established that the two genera were separate both morphologically and temporally, and that the Hupehsuchia was different enough from all other reptiles to warrant raising the group to a full order. Detailed anatomical restudy, however, failed to reveal anything more about the relationships of the Hupehsuchia than that the order belonged somewhere in the parasubclass Diapsida. They did not, however, find any characters that would preclude its placement within the Archosauria. I must add parenthetically that Carroll & Dong's restudy made hash of my comments about *Hupehsuchus* in a recent book review (Olshevsky, 1991).

Parasagittal dermal armor and a small, modified antorbital fenestra present in *Hupehsuchus* and *Nanchangosaurus* suggest to me that the Hupehsuchia may be placed very provisionally within the parasuperorder Thecodontia. *Hupehsuchus* displays a primitive mesotarsal ankle and pentadactyl manus and pes that were highly modified into paddles. This indicates that if the Hupehsuchia does belong in the Thecodontia, it represents a separate lineage whose origin lies in yet another as-yet-unknown group of proterosuchians.

Parasuperorder: Thecodontia Owen, 1859

Census (excluding Crocodylia): 6 orders, 15 families, 115 genera (29 doubtful), 171 species (58 doubtful)

Paraorder: Proterosuchia Broom, 1906

Census: 2 families, 10 genera, 12 species

Family: MESENOSAURIDAE Romer, 1956

Census: 1 genus, 1 species

Genus: *Mesenosaurus* Efremov, 1940
  = *Mesonosaurus* Ivakhnenko & Kurzanov, 1979 [*sic*]
  M. romeri Efremov, 1940 (Type)

Family: PROTEROSUCHIDAE von Huene, 1914

Census: 8 genera, 10 species

= Chasmatosauridae Haughton, 1924
= Chasmatosaurinae Kuhn, 1966
= Pelycosimiidae Abel, 1919
= Proterosuchia Broom, 1906 *vide* von Huene, 1908
= Proterosuchinae Tatarinov, 1961

NOTE: This family was initially proposed by Broom (1906) as a monotypic suborder containing only the genus *Proterosuchus*. Von Huene (1908) treated it as a family, but the name was first given its proper familial spelling in von Huene, 1914.

Genus: *Ankistrodon* Huxley, 1865
  = *Ankistridon* von Huene, 1942 [*sic*]
  = *Epicampodon* Lydekker, 1885
  A. indicus Huxley, 1865 (Type)
    = *Chasmatosaurus indicus* (Huxley, 1865)
    = *Epicampodon indicus* (Huxley, 1865) Lydekker, 1885
    = *Thecodontosaurus indicus* (Huxley, 1865)

Genus: *Archosaurus* Tatarinov, 1960
  A. rossicus Tatarinov, 1960 (Type)

Genus: *Chasmatosaurus* Haughton, 1924
  = *Champsosaurus* Romer, 1971/Cope, 1877 [*sic*]
  C. vanhoepeni Haughton, 1924 (Type)
    = *Proterosuchus vanhoepeni* (Haughton, 1924)
    = *Chasmatosaurus van Hoepeni* von Huene, 1926 [*sic*]
    = *Chasmatosaurus alexanderi* Hoffman, 1965
  C. yuani Young, 1936
  C. ultimus Young, 1964
    = *Chasmatosaurus yuani* Young, 1958 *non* Young, 1936

Genus: *Elaphrosuchus* Broom, 1946 (juvenile *Chasmatosaurus*?)
  E. rubidgei Broom, 1946 (Type)

Genus: *Fugusuchus* Cheng, 1980
  F. hejiapanensis Cheng, 1980 (Type)

Genus: *Kalisuchus* Thulborn, 1979
  K. rewanensis Thulborn, 1979 (Type)

Genus: *Proterosuchus* Broom, 1903 (= *Chasmatosaurus*?)
  P. fergusi Broom, 1903 (Type)

Genus: *Tasmaniosaurus* Camp & Banks 1978
  = *Tasmaniasaurus* Dziewa, 1980 [*sic*]
  = *Tasmaniosaurus* Cosgriff, 1974 [*nomen nudum*]
  = *Tasmaniosaurus* Banks, Cosgriff & Kemp, 1978 [*nomen nudum*]
  T. triassicus Camp & Banks, 1978 (Type)
    = *Tasmaniosaurus triassicus* Cosgriff, 1974 [*nomen nudum*]
    = *Tasmaniosaurus triassicus* Banks, Cosgriff & Kemp 1978 [*nomen nudum*]

Genus: [To be described from the Triassic of the Soviet Union; Sennikov, 1990]

PROTEROSUCHIA *incertae sedis*

Census: 1 genus, 1 species

Genus: *Exilisuchus* Ochev, 1979
  E. tubercularis Ochev, 1979 (Type)

Genus: *Rysosteus* Owen, 1841 [*nomen nudum*]
  = *Ryzosteus* L. B. Halstead & Nicoll, 1971 [*sic*]
  No type species named

Order: Ornithosuchia Bonaparte, 1971

Census: 3 families, 14 genera (3 doubtful), 15 species (3 doubtful)

Parafamily: EUPARKERIIDAE von Huene, 1920

Census: 6 genera, 7 species

= Euparkeriinae Sennikov, 1989
= Dorosuchinae Sennikov, 1989

Genus: *Dorosuchus* Sennikov, 1989
  D. neoetus Sennikov, 1989 (Type)

Genus: *Euparkeria* Broom, 1913
  = *Browniella* Broom, 1913
  = *Euparkia* Thulborn, 1979 [*sic*]
  E. capensis Broom, 1913 (Type)
    = *Browniella africana* Broom, 1913

Genus: *Halazhaisuchus* Wu, 1982
  H. qiaoensis Wu, 1982 (Type)

Genus: *Turfanosuchus* Young, 1973
  T. dabanensis Young, 1973 (Type)
  T. shageduensis Wu, 1982

Genus: *Wangisuchus* Young, 1964
  W. tzeyii Young, 1964

Genus: *Xilousuchus* Wu, 1981
  X. sapingensis Wu, 1981 (Type)

Family: ERPETOSUCHIDAE Watson, 1917

Census: 2 genera, 2 species

Genus: *Erpetosuchus* Newton, 1894
  = *Erpethosuchus* Bonaparte, 1971 [*sic*]
  = *Herpetosuchus* Boulenger, 1903 [*sic*]
  E. granti Newton, 1894 (Type)

Genus: *Parringtonia* von Huene, 1939
  P. gracilis von Huene, 1939 (Type)

Family: ORNITHOSUCHIDAE von Huene, 1908

Census: 6 genera (3 doubtful), 6 species (3 doubtful)

Genus: *Avalonianus* Kuhn, 1961 [*nomen dubium*]
  = *Abalonia* Romer, 1966 [*sic*]
  = *Avalonia* Seeley, 1898/Walcott, 1889 [*nomen dubium*]
  = *Picrodon* Seeley, 1898 [*nomen dubium*]
  A. sanfordi (Seeley, 1898) (Type)
    = *Avalonia sanfordi* Seeley, 1898 [*nomen dubium*]

= *Picrodon herveyi* Seeley, 1898 [*nomen dubium*]

Genus: *Basutodon* von Huene, 1932 [*nomen dubium*]
B. ferox von Huene, 1932 (Type)

Genus: *Ornithosuchus* Newton, 1894
= *Dasygnathoides* Kuhn, 1961
= *Dasygnathus* Huxley, 1877/MacLeay, 1819
= *Desygnathus* Reig, 1961 [*sic*]
O. longidens (Huxley, 1877) (Type)
= *Dasygnathus longidens* Huxley, 1877
= *Dasygnathoides longidens* (Huxley, 1877)
= *Ornithosuchus woodwardi* Newton, 1894
= *Ornithosuchus taylori* Broom, 1913

Genus: *Riojasuchus* Bonaparte, 1969
R. tenuisceps Bonaparte, 1969 (Type)

Genus: *Venaticosuchus* Bonaparte, 1971
V. rusconii Bonaparte, 1971 (Type)
= *Ornithosuchus rusconii* (Bonaparte, 1971)

Genus: *Zatomus* Cope, 1871 [*nomen dubium*]
Z. sarcophagus Cope, 1871 (Type)

Genus: [To be described from the Ghost Ranch Quarry; M. Parrish, pers. comm.]

Order: Pseudosuchia Zittel, 1887–90

Census: 4 suborders, 7 families, 50 genera (7 doubtful), 67 species (18 doubtful)

Suborder: Archaeosuchia Sill, 1967

Census: 3 families, 7 genera, 8 species

Family: PROTEROCHAMPSIDAE Sill, 1967

Census: 4 genera, 5 species

= Cerritosauridae Bonaparte, 1971

Genus: *Cerritosaurus* Price, 1946
C. binsfeldi Price, 1946 (Type)

Genus: *Chanaresuchus* Romer, 1971
= *Chanaeresuchus* Camp & Banks, 1978 [*sic*]
= *Chaparesuchus* Arcucci, 1989 [*sic*]
C. bonapartei Romer, 1971 (Type)

Genus: *Gualosuchus* Romer, 1971
G. reigi Romer, 1971 (Type)

Genus: *Proterochampsa* Reig, 1959
P. barrionuevoi Reig, 1959 (Type)
P. nodosa Barberena, 1982

Genus: *Tropidosuchus* Arcucci, 1989 [*nomen nudum*]
T. romeri Arcucci, 1989 (Type)

NOTE: The above genus and species were described by A. Arcucci in her 1988 Master's degree dissertation but have not yet been formally published. The names appeared in print in articles by Arcucci in 1989.

Genus: [To be described from the Upper Petrified Forest Member of the Chinle Formation; R. A. Long, pers. comm.; Murry & Long, 1989]

Family: RHADINOSUCHIDAE Hoffstetter, 1955

Census: 2 genera, 2 species

Genus: *Procerosuchus* von Huene, 1942
P. celer von Huene, 1942 (Type)

Genus: *Rhadinosuchus* von Huene, 1942
R. gracilis von Huene, 1942 (Type)

Family: DOSWELLIIDAE Weems, 1980
Census: 1 genus, 1 species

= Doswelliinae Weems, 1980

Genus: *Doswellia* Weems, 1980
D. kaltenbachi Weems, 1980 (Type)
NOTE: This family is classified in this suborder provisionally. Bonaparte (1982) considers it aetosaurian.

Parasuborder: Erythrosuchia Bonaparte, 1982

Census: 1 family, 12 genera (4 doubtful), 16 species (6 doubtful)

Parafamily: ERYTHROSUCHIDAE Watson, 1917
Census: 12 genera (4 doubtful), 16 species (6 doubtful)

= Erythrosuchinae Tatarinov, 1961
= Garjainiidae Ochev, 1958
= Shansisuchidae Young, 1964
= Shansisuchinae Kuhn, 1966
= Vjushkoviidae von Huene, 1960

Genus: *Chalishevia* Ochev, 1980
C. cothurnata Ochev, 1980 (Type)

Genus: *Chasmatosuchus* von Huene, 1940
= *Chasmathosuchus* Ochev & Shishkin, 1989 [*sic*]
= *Chasmatosaurus* Ochev, 1979/Haughton, 1924 [*sic*]
C. rossicus von Huene, 1940 (Type)
?C. parvus von Huene, 1940 [*nomen dubium*]

Genus: *Crenelosaurus* Ortlam, 1967 [*nomen dubium*]
C. nigrosilvanus Ortlam, 1967 (Type)

Genus: *Cuyosuchus* Reig, 1961
= *Chigutisaurus* Rusconi, 1947 (postcranial)
C. huenei Reig, 1961 (Type)
= *Chigutisaurus tunuyanensis* Rusconi, 1947 (postcranial)

Genus: *Dongusia* von Huene, 1940 [*nomen dubium*]
D. colorata von Huene, 1940 (Type)
= *Erythrosuchus coloratus* (von Huene, 1940) [*nomen dubium*]

Genus: *Erythrosuchus* Broom, 1905
= *Erytherosuchus* von Huene, 1942 [*sic*]
E. africanus Broom, 1905 (Type)
E. magnus Ochev, 1980

Genus: *Gamosaurus* Ochev, 1979
G. lozovskii Ochev, 1979 (Type)

Genus: *Garjainia* Ochev, 1958
G. prima Ochev, 1958 (Type)
= *Erythrosuchus primus* (Ochev, 1958)
= *Chasmatosuchus vjushkovi* Ochev, 1961

Genus: *Ocoyuntaia* Rusconi, 1947 [*nomen dubium*]
O. arquata Rusconi, 1947 (Type)

Genus: *Seemania* von Huene, 1958 [*nomen dubium*]
S. palaeotriadica von Huene, 1958 (Type)

Genus: *Shansisuchus* Young, 1959
= *Shanisisuchus* Cruickshank, 1979 [*sic*]
S. shansisuchus Young, 1964 (Type)
S. heiyuekouensis Young, 1964 [*nomen dubium*]
S. kuyeheensis Cheng, 1980

Genus: *Vjushkovia* von Huene, 1960
= *Vjushkoia* Reig, 1961 [*sic*]
= *Vjushkovia* von Huene, 1959 [*nomen nudum*]
V. triplicostata von Huene, 1960 (Type)
= *Erythrosuchus triplicostatus* (von Huene, 1960)

Genus: [To be described from Yerrapali, India; Robinson, 1967]

Genus: [To be described from the Late Triassic of the Soviet Union; Sennikov, 1990]

Parasuborder: Rauisuchia Bonaparte, 1982

Census: 1 family, 24 genera (2 doubtful), 34 species (9 doubtful)

Family: RAUISUCHIDAE Price, 1946

Census: 20 genera, 23 species

- **= Prestosuchidae Romer, 1966**
- **= Raisuchidae Reig, 1961 [*sic*]**
- **= Rauisuchinae Von Huene, 1936 [*nomen nudum*]**
- **= Rauisuchinae Von Huene, 1938 [*nomen nudum*]**
- **= Rauisuchinae von Huene, 1942**

Genus: *Bromsgroveia* Galton, 1985
- *B. walkeri* Galton, 1985 (Type)

Genus: *Dongusuchus* Sennikov, 1988
- = *Donguchus* Sennikov, 1990 [*sic*]
- *D. efremovi* Sennikov, 1988 (Type)

Genus: *Energosuchus* Ochev, 1986
- = *Energosuchus* Ochev, 1982 [*nomen nudum*]
- *E. garjainovi* Ochev, 1986 (Type)

Genus: *Fasolasuchus* Bonaparte, 1981
- = *Fasolasuchus* Bonaparte, 1978 [*nomen nudum*]
- = *Fasolosuchus* Galton, 1985 [*sic*]
- *F. tenax* Bonaparte, 1981 (Type)
  - = *Fasolasuchus tenax* Bonaparte, 1978 [*nomen nudum*]

Genus: *Fenhosuchus* Young, 1964
- = *Fenchosuchus* Sennikov, 1988 [*sic*]
- *F. cristatus* Young, 1964 (Type)

Genus: *Heptasuchus* Dawley, Zawiskie & Cosgriff, 1979 (= *Poposaurus*?)
- *H. clarki* Dawley, Zawiskie & Cosgriff, 1979 (Type)

Genus: *Jaikosuchus* Sennikov, 1990
- *J. magnus* (Ochev, 1979) (Type)
  - = *Chasmatosuchus magnus* Ochev, 1979

Genus: *Jushatyria* Sennikov, 1985
- *J. vjushkovi* Sennikov, 1985 (Type)

Genus: *Luperosuchus* Romer, 1971
- *L. fractus* Romer, 1971 (Type)

Genus: *Mandasuchus* Charig *vide* Krebs, 1976
- = *Mandasuchus* Charig, 1956 [*nomen nudum*]
- = *Mandasuchus* Charig, 1967 [*nomen nudum*]
- *M. tanyauchen* Charig *vide* Krebs, 1976 (Type)
  - = *Mandasuchus tanyauchen* Charig, 1967 [*nomen nudum*]

Genus: *Nyasasaurus* Charig, 1967 [*nomen nudum*]
- = *Nyasaurus* White, 1973 [*sic*]
- *N. cromptoni* Charig, 1967 (Type)

Genus: *Prestosuchus* von Huene, 1942
- *P. chiniquensis* von Huene, 1942 (Type)
- *P. loricatus* von Huene, 1942

Genus: *Rauisuchus* von Huene, 1942
- = *Rauisuchus* von Huene, 1936 [*nomen nudum*]
- = *Rauisuchus* von Huene, 1938 [*nomen nudum*]
- *R. tiradentes* von Huene, 1942 (Type)
  - = *Rauisuchus tiradentes* von Huene, 1938 [*nomen nudum*]

Genus: *Saurosuchus* Reig, 1959
- = *Saurosuchos* Reig, 1961 [*sic*]
- = *Saurusochus* Reig, 1961 [*sic*]
- *S. galilei* Reig, 1959 (Type)
  - = *Saurusochus galilei* Reig, 1961 [*sic*]

Genus: *Stagonosuchus* von Huene, 1938
- *S. major* (Haughton, 1932) (Type)
  - = *Stenaulorhynchus major* Haughton, 1932
  - = *Stagonosuchus nyassicus* von Huene, 1938
  - = *Stagonosuchus tanganyikaensis* Boonstra, 1953

Genus: *Ticinosuchus* Krebs, 1965
- *T. ferox* Krebs, 1965 (Type)

Genus: *Tikisuchus* Chatterjee & Majumdar, 1987
  = *Tikisuchus* Chatterjee & Hotton, 1986 [*nomen nudum*]
  T. romeri Chatterjee & Majumdar, 1987 (Type)

Genus: *Tsylmosuchus* Sennikov, 1990
  = *Thecodontosaurus* Yakovlev, 1916 *non* Riley & Stutchbury, 1836
  T. jakovlevi Sennikov, 1990 (Type)
  T. samariensis Sennikov, 1990
  T. donensis Sennikov, 1990

Genus: *Vjushkovisaurus* Ochev, 1982
  V. berdjanensis Ochev, 1982 (Type)

Genus: *Vytshegdosuchus* Sennikov, 1988
  V. zheshartensis Sennikov, 1988 (Type)

Genus: *Youngosuchus* Sennikov, 1985
  Y. sinensis (Young, 1973)
    = *Vjushkovia sinensis* Young, 1973
    = *Vjushkovia sinensia* Young, 1973*

Genus: [To be described from Kupferzell, Germany; Wild, 1980]

Genus: [To be described from Bukobay, Soviet Union; Ochev, 1979; Sennikov, 1990]

RAUISUCHIA *incertae sedis*

Census: 4 genera (2 doubtful), 11 species (9 doubtful)

= Palaeosauridae von Huene, 1932
= Palaeosauriscidae Kuhn, 1959
= Pallisteriidae Charig, 1967 [*nomen nudum*]
= Zanclodontidae Marsh, 1882

Genus: *Gracilisuchus* Romer, 1972
  G. stipanicicorum Romer, 1972 (Type)

Genus: *Palaeosauriscus* Kuhn, 1959 [*nomen dubium*]
  = *Palaeosaurus* Riley & Stutchbury, 1836/Geoffroy Saint-Hilaire, 1833 [*nomen dubium*]
  P. cylindrodon (Riley & Stutchbury, 1836) (Type)
    = *Palaeosaurus cylindrodon* Riley & Stutchbury, 1836 [*nomen dubium*]
    = *Thecodontosaurus cylindrodon* (Riley & Stutchbury, 1836) von Huene, 1908 [*nomen dubium*]
    = *Palaeosaurus cylindricum* Riley & Stutchbury, 1836 [*sic*]
  ?*P. platyodon* (Riley & Stutchbury, 1836) [*nomen dubium*]
    = *Palaeosaurus platyodon* Riley & Stutchbury, 1836 [*nomen dubium*]
    = *Rileya platyodon* (Riley & Stutchbury, 1836) [*nomen dubium*]
    = *Thecodontosaurus platyodon* (Riley & Stutchbury, 1836) von Huene, 1908 [*nomen dubium*]
  NOTE: The above species is probably a parasuchian.
  ?*P. stricklandi* (Davis, 1881) [*nomen dubium*]
    = *Palaeosaurus stricklandi* Davis, 1881 [*nomen dubium*]
  NOTE: The above species is probably a parasuchian.
  ?*P. subcylindrodon* (von Huene, 1908) [*nomen dubium*]
    = *Thecodontosaurus subcylindrodon* von Huene, 1908 [*nomen dubium*]
    = *Palaeosaurus subcylindrodon* (von Huene, 1908) [*nomen dubium*]
  NOTE: The above species may be a herrerasaurian (*cf.* Galton, 1984).

Genus: *Pallisteria* Charig, 1967 [*nomen nudum*]
  P. angustimentum Charig, 1967 (Type)

Genus: *Spinosuchus* von Huene, 1932
  = *Spinosaurus* Chatterjee, 1986/Stromer, 1915 [*sic*]
  S. caseanus von Huene, 1932 (Type)

Genus: *Zanclodon* Plieninger, 1846 [*nomen dubium*]
  = *Smilodon* Plieninger, 1846/Lund, 1842
  Z. laevis (Plieninger, 1846) (Type)
    = *Smilodon laevis* Plieninger, 1846 [*nomen dubium*]
    = *Zanclodon plieningeri* E. Fraas, 1896 [*nomen dubium*]
  ?*Z. crenatus* (Plieninger, 1846) [*nomen dubium*]
    = *Smilodon crenatus* Plieninger, 1846 [*nomen dubium*]

?Z. *bavaricus* E. Fraas *vide* Sandberger, 1894
[*nomen dubium*]
?Z. *schutzii* E. Fraas, 1900 [*nomen dubium*]
= *Teratosaurus schutzii* (E. Fraas, 1900)
[*nomen dubium*]
?Z. *silesiacus* Jaekel, 1910 [*nomen dubium*]
= *Megalosaurus silesiacus* (Jaekel, 1910)
[*nomen dubium*]

NOTE: The above genus is not thecodontian and will be redescribed by Galton & Sues (P. M. Galton, pers. comm.).

Suborder: Poposauria nov.

Census: 1 family, 5 genera (1 doubtful), 6 species (2 doubtful)

Family: TERATOSAURIDAE Cope, 1871

Census: 5 genera (1 doubtful),
6 species (2 doubtful)

= Poposauridae Nopcsa, 1928

Genus: *Arizonasaurus* Welles, 1947
A. babbitti Welles, 1947 (Type)

Genus: "Chatterjeea" Murry & Long, 1989 [to be described]
"C. elegans" Murry & Long, 1989 [to be described]

NOTE: This species is to be based on part of the *Postosuchus kirkpatricki* type specimen, which is now known to be composite. See Note for *Postosuchus* below.

Genus: *Dolichobrachium* Williston, 1904 [*nomen dubium*]
D. gracile Williston, 1904 (Type)

Genus: *Poposaurus* Mehl, 1915
P. gracilis Mehl, 1915 (Type)
= *Poposaurus agilis* Galton, 1977 [*sic*]
[New species to be described from the *Paleorhinus* horizon of the Lower Dockum Formation of the southwestern United States; R. A. Long, pers. comm.]

Genus: *Postosuchus* Chatterjee, 1985
= *Lythodynastes* Lufkin *vide* Dedera, 1983 [*nomen nudum*]
= *Lythrodynaestes* Ash, 1985 [*nomen nudum*; *sic*]
= *Lythrodynastes* Trimble, 1984 [*nomen nudum*]
P. kirkpatricki Chatterjee, 1985 (Type)

NOTE: A Chinle Formation teratosaurid, to have been named *Lythrodynastes* (R. A. Long, pers. comm.), is now considered to be synonymous with this Dockum Formation genus. The name of the Chinle "genus" has appeared in print with various spellings but without formal description. The *Postosuchus* material is actually composite and includes at least one other poposaurid genus and species; see "Chatterjeea" above.

Genus: *Teratosaurus* von Meyer, 1861
= *Cladeiodon* Owen, 1841
= *Claderodon* Agassiz, 1846 [*sic*]
= *Cladyodon* Owen, 1842 [*sic*]
= *Kladeisteriodon* Plieninger, 1846 [*sic*]
= *Kladyodon* Plieninger, 1846 [*sic*]
T. suevicus von Meyer, 1861 (Type)
= *Cladeiodon lloydii* Owen, 1841
= *Claderodon lloydii* (Owen, 1841)
= *Cladyodon lloydii* (Owen, 1841)
= *Kladeisteriodon lloydii* (Owen, 1841)
= *Kladyodon lloydii* (Owen, 1841)
= *Teratosaurus lloydii* (Owen, 1841)
?T. *bengalensis* Das-Gupta, 1929 [*nomen dubium*]

NOTE: Reference of this genus by Galton (1985) to the same family as *Poposaurus* mandates the use of Teratosauridae as the family name instead of Poposauridae.

Pseudosuchia *incertae sedis*

Census: 1 family, 2 genera, 3 species (1 doubtful)

Family: CTENOSAURISCIDAE **Kuhn, 1964**
Census: 2 genera, 2 species

= Ctenosauridae Kuhn, 1961
= Lotosauridae Zhang, 1975

Genus: *Ctenosauriscus* Kuhn, 1964
 = *Ctenosaurus* von Huene, 1902/Fitzinger, 1843
 C. koeneni (von Huene, 1902) (Type)
  = *Ctenosaurus koeneni* von Huene, 1902

Genus: *Hypselorhachis* Charig, 1967 [*nomen nudum*]
 H. mirabilis Charig, 1967 (Type)
 NOTE: This species is supposed to possess vertebrae with tall neural spines.

Genus: *Lotosaurus* Zhang, 1975
 L. adentus Zhang, 1975 (Type)

Family:TELEOCRATERIDAE **Romer, 1966 [*nomen nudum*]**
Census: 0 genera, 1 doubtful species

Genus: *Teleocrater* Charig, 1956 [*nomen nudum*]
 ?*T. alophos* (Haughton, 1932) [*nomen dubium*]
  = *Thecodontosaurus alophos* Haughton, 1932 [*nomen dubium*]
 T. rhadinus Charig, 1967 (Type)
 NOTE: This undescribed genus and family are referred to this order provisionally.

Order: Parasuchia Huxley, 1875

Census: 1 family, 23 genera (16 doubtful), 56 species (32 doubtful)

Family: PARASUCHIDAE **Lydekker, 1885**
Census: 23 genera (16 doubtful), 56 species (32 doubtful)

= Angistorhininae Camp, 1930
= Mystriosuchidae von Huene, 1915
= Mystriosuchinae Chatterjee, 1978
= Parasuchinae Chatterjee, 1978
= Phytosauridae Lydekker, 1888
= Phytosaurinae Camp, 1930

Genus: *Angistorhinopsis* von Huene, 1922 [*nomen dubium*]
 A. ruetimeyeri (von Huene, 1911) (Type)
  = *Angistorhinopsis rütimeyeri* (von Huene, 1911) [*nomen dubium*]*
  = *Mystriosuchus ruetimeyeri* von Huene, 1911 [*nomen dubium*]
  = *Mystriosuchus rütimeyeri* von Huene, 1911 [*nomen dubium*]*
  = *Rutiodon ruetimeyeri* (von Huene, 1911) Gregory, 1962 [*nomen dubium*]
  = *Rutiodon rütimeyeri* (von Huene, 1911) Gregory, 1962 [*nomen dubium*]*

Genus: *Angistorhinus* Mehl, 1913
 = *Angustorhinus* Ochev & Shishkin, 1989 [*sic*]
 = *Brachysuchus* Case, 1929
 A. grandis Mehl, 1913 (Type)
 A. gracilis Mehl, 1915
 A. maximus Mehl, 1928
 ?*A. megalodon* (Case, 1929) Gregory, 1969
  = *Brachysuchus megalodon* Case, 1929
  = *Phytosaurus megalodon* (Case, 1929) Gregory, 1962
 A. alticephalus Stovall & Wharton, 1936
 A. aeolamnis Eaton, 1965
 A. talainti Dutuit, 1977

Genus: *Belodon* von Meyer, 1842
 = *Beldon* Mehl, 1915 [*sic*]
 = *Belondon* Gregory, 1962 [*sic*]
 B. plieningeri von Meyer, 1842 (Type)

  - = *Mystriosuchus plieningeri* (von Meyer, 1842) von Huene, 1911
  - = *Phytosaurus plieningeri* (von Meyer, 1842)
  - = *Mystriosuchus ingens* E. Fraas, 1896
  - = *Belodon ingens* (E. Fraas, 1896)
  - = *Belondon plieningeri* (von Meyer, 1842) Gregory, 1962 [*sic*]
- ?*B. lepturus* Cope, 1870 [*nomen dubium*]
  - = *Phytosaurus lepturus* (Cope, 1870) [*nomen dubium*]
- ?*B. arenaceus* (E. Fraas, 1896) [*nomen dubium*]
  - = *Zanclodon arenaceus* E. Fraas, 1896 [*nomen dubium*]
  - = *Mystriosuchus arenaceus* (E. Fraas, 1896) [*nomen dubium*]
  - = *Phytosaurus arenaceus* (E. Fraas, 1896) [*nomen dubium*]

Genus: *Centemodon* Lea, 1856 [*nomen dubium*]
- *C. sulcatus* Lea, 1856 (Type)
  - = *Paleorhinus sulcatus* (Lea, 1856) [*nomen dubium*]
  - = *Rutiodon sulcatus* (Lea, 1856) [*nomen dubium*]

NOTE: The above genus may not be a parasuchian (Weems, 1980).

Genus: *Clepsysaurus* Lea, 1851 [*nomen dubium*; = *Rutiodon*?]
- = *Clepsisaurus* Emmons, 1856 [*sic*]
- = *Clepysaurus* Kuhn, 1933 [*sic*]
- *C. pennsylvanicus* Lea, 1851 (Type)
  - = *Phytosaurus pennsylvanicus* (Lea, 1851) Gregory, 1962 [*nomen dubium*]
  - = *Rutiodon pennsylvanicus* (Lea, 1851) [*nomen dubium*]
- *C. veatleianus* Cope, 1877 [*nomen dubium*]

Genus: *Coburgosuchus* Heller, 1954 [*nomen dubium*]
- = *Coburgosaurus* Heller, 1954 [*sic*]
- *C. goeckeli* Heller, 1954 (Type)
  - = *Phytosaurus goeckeli* (Heller, 1954) [*nomen dubium*]

Genus: *Compsosaurus* Leidy, 1856 [*nomen dubium*; = *Rutiodon*?]
- *C. priscus* Leidy, 1856 (Type)
  - = *Belodon priscus* (Leidy, 1856) [*nomen dubium*]
  - = *Palaeosaurus priscus* (Leidy, 1856) [*nomen dubium*]
  - = *Phytosaurus priscus* (Leidy, 1856) [*nomen dubium*]

Genus: *Eurydorus* Leidy, 1859 [*nomen dubium*; = *Rutiodon*?]
- *E. serridens* Leidy, 1859 (Type)
  - = *Belodon serridens* (Leidy, 1859) [*nomen dubium*]
  - = *Clepsysaurus serridens* (Leidy, 1859) Case, 1930 [*nomen dubium*]
  - = *Phytosaurus serridens* (Leidy, 1859) [*nomen dubium*]

Genus: *Heterodontosuchus* Lucas, 1898 [*nomen dubium*]
- *H. ganei* Lucas, 1898 (Type)
  - = *Nicrosaurus ganei* (Lucas, 1898) Westphal, 1976 [*nomen dubium*]
  - = *Phytosaurus ganei* (Lucas, 1898) Gregory, 1962 [*nomen dubium*]

Genus: *Mesorhinosuchus* Kuhn, 1961 [*nomen dubium*; = *Paleorhinus*?]
- = *Mesorhinus* Jaekel, 1910/Ameghino, 1885 [*nomen dubium*]
- *M. fraasi* (Jaekel, 1910) (Type)
  - = *Mesorhinus fraasi* Jaekel, 1910 [*nomen dubium*]

Genus: *Mystriosuchus* E. Fraas, 1896
- *M. planirostris* (von Meyer, 1863) (Type)
  - = *Belodon planirostris* von Meyer, 1863
  - = *Phytosaurus planirostris* (von Meyer, 1863)

Genus: *Nicrosaurus* O. Fraas, 1866
- = *Lophoprosopus* Mehl, 1915
- = *Lophorhinus* Mehl, 1915 [*sic*]
- = *Microsaurus* Romer, 1956/DeJean, 1833 [*sic*]
- *N. kapffi* (von Meyer, 1861) (Type)
  - = *Belodon kapffi* von Meyer, 1861
  - = *Lophoprosopus kapffi* (von Meyer, 1861) Mehl, 1915
  - = *Lophorhinus kapffi* (von Meyer, 1861) Mehl, 1915 [*sic*]
  - = *Phytosaurus kapffi* (von Meyer, 1861)
  - = *Phytosaurus kapfi* Gregory, 1962 [*sic*]
  - = *Belodon kapfii* Hunt & Lucas, 1989 [*sic*]
- ?*N. superciliosus* (Cope, 1893) [*nomen dubium*]

= *Belodon superciliosus* Cope, 1893 [*nomen dubium*]
= *Phytosaurus superciliosus* (Cope, 1893) [*nomen dubium*]
?*N. validus* (Marsh, 1893) [*nomen nudum*]
= *Belodon validus* Marsh, 1893 [*nomen nudum*]
= *Machaeroprosopus validus* (Marsh, 1893) [*nomen nudum*]
= *Phytosaurus validus* (Marsh, 1893) [*nomen nudum*]

Genus: *Omosaurus* Leidy, 1856 [*nomen dubium*; = *Rutiodon*?]
O. perplexus Leidy, 1856 (Type)

Genus: *Pachysuchus* Young, 1951 [*nomen dubium*]
P. imperfectus Young, 1951 (Type)
= *Pachysuchus imperfecta* Young, 1951 [*nomen dubium*]*

Genus: *Palaeoctonus* Cope, 1877 [*nomen dubium*; = *Rutiodon*?]
= *Palaeochtinus* Mehl, 1915 [*sic*]
= *Palaeoctomus* von Huene, 1902 [*sic*]
P. appalachianus Cope, 1877 (Type)
P. aulacodus Cope, 1878 [*nomen dubium*]
= *Suchoprion aulacodus* (Cope, 1878) [*nomen dubium*]
P. dumblianus Cope, 1893 [*nomen dubium*]
= *Nicrosaurus dumblianus* (Cope, 1893) Westphal, 1976 [*nomen dubium*]
= *Phytosaurus dumblianus* (Cope, 1893) Gregory, 1962 [*nomen dubium*]
P. orthodon Cope, 1893 [*nomen dubium*]
= *Nicrosaurus orthodon* (Cope, 1893) [*nomen dubium*]
= *Phytosaurus orthodon* (Cope, 1893) Gregory, 1962 [*nomen dubium*]

Genus: *Paleorhinus* Williston, 1904
= *Ebrachosuchus* Kuhn, 1936
= *Francosuchus* Kuhn, 1932 [*nomen dubium*]
= *Palaeorhinus* Jaekel, 1910 [*sic*]
= *Promystriosuchus* Case, 1922 [*nomen dubium*]
P. bransoni Williston, 1904 (Type)
= *Paleorhinus (Paleorhinus) bransoni* (Williston, 1904) Westphal, 1976
= *Parasuchus (Paleorhinus) bransoni* (Williston, 1904) Chatterjee, 1978
= *Promystriosuchus ehlersi* Case, 1922 [*nomen dubium*]
= *Paleorhinus ehlersi* (Case, 1922) Gregory, 1962 [*nomen dubium*]
= *Paleorhinus (Paleorhinus) ehlersi* (Case, 1922) Westphal, 1976 [*nomen dubium*]
= *Parasuchus (Paleorhinus) ehlersi* (Case, 1922) Chatterjee, 1978 [*nomen dubium*]
= *Paleorhinus parvus* Mehl, 1928
= *Paleorhinus (Paleorhinus) parvus* (Mehl, 1928) Westphal, 1976
= *Parasuchus (Paleorhinus) parvus* (Mehl, 1928) Chatterjee, 1978
= *Paleorhinus scurriensis* Langston, 1949
= *Paleorhinus (Paleorhinus) scurriensis* (Langston, 1949) Westphal, 1976
=*Parasuchus (Paleorhinus) scurriensis* (Langston, 1949) Chatterjee, 1978
?*P. broilii* (Kuhn, 1932) Gregory, 1962 [*nomen dubium*]
= *Francosuchus broilii* Kuhn, 1932
= *Paleorhinus (Francosuchus) broilii* (Kuhn, 1962) Westphal, 1976
= *Francosuchus latus* Kuhn, 1932
= *Paleorhinus latus* (Kuhn, 1932)
= *Paleorhinus (Francosuchus) latus* (Kuhn, 1932) Westphal, 1976
= *Ebrachosuchus angustifrons* Kuhn, 1936
= *Francosuchus angustifrons* (Kuhn, 1936)
= *Paleorhinus angustifrons* (Kuhn, 1936)
= *Paleorhinus (Francosuchus) angustifrons* (Kuhn, 1936) Westphal, 1976
= *Mystriosuchus plieningeri* Kuhn, 1936 *non* (von Meyer, 1842)
P. neukami (Kuhn, 1936) Gregory, 1962
= *Ebrachosuchus neukami* Kuhn, 1936
= *Francosuchus neukami* (Kuhn, 1936)
= *Paleorhinus (Francosuchus) neukami* (Kuhn, 1936) Westphal, 1976
?*P. trauthi* (von Huene, 1939) [*nomen dubium*]
= *Francosuchus trauthi* von Huene, 1939 [*nomen dubium*]
= *Paleorhinus (Francosuchus) trauthi* (von Huene, 1939) Westphal, 1976 [*nomen dubium*]
P. magnoculus Dutuit, 1977
= *Parasuchus (Paleorhinus) magnoculus* (Dutuit, 1977) Chatterjee, 1978

P. hislopi Hunt & Lucas, 1991
= *Parasuchus (Paleorhinus) hislopi* Chatterjee, 1978 *non* (Lydekker, 1885)

NOTE: Gregory (1962) partitioned *Paleorhinus* into two subgenera, *Paleorhinus* and *Francosuchus*, the latter containing all the species previously included in the genera *Francosuchus* and *Ebrachosuchus*. Westphal (1976) followed Gregory and wrote the species names explicitly using subgeneric notation, which Gregory did not do. Chatterjee (1978), however, excluded *Francosuchus* from synonymy with *Paleorhinus* and considered *Paleorhinus* to be a junior synonym of *Parasuchus*, with *Parasuchus* and *Paleorhinus* subgenera of *Parasuchus*. Although Chatterjee did not do so explicitly in his paper, this placed all species of *Paleorhinus* into the subgenus *Parasuchus (Paleorhinus)*. Hunt & Lucas (1991) revised the genus *Paleorhinus* and eliminated the subgenera, declaring *Parasuchus* to be a *nomen dubium* but treating it as a probable synonym of *Paleorhinus* on the basis of the material described by Chatterjee (1978). Because this would make the doubtful *Parasuchus* a senior subjective synonym of *Paleorhinus*, however, *Parasuchus* is considered a separate genus to be isolated from synonymy. The skeletons in Chatterjee (1978) do represent a distinctive Maleri Formation species of *Paleorhinus*, which Hunt & Lucas referred to as *Paleorhinus hislopi*.

Von Huene (1940) based the name *Brachysuchus maleriensis* on the parasuchian material originally part of the composite type specimen of *Parasuchus hislopi*, so *Brachysuchus maleriensis* must be regarded as an objective junior synonym of *Parasuchus hislopi*.

Genus: *Parasuchus* Huxley, 1870 [*nomen dubium*]
P. hislopi Lydekker, 1885 (Type)
= *Parasuchus (Parasuchus) hislopi* (Lydekker, 1885) Chatterjee, 1978 [*nomen dubium*]
= *Paleorhinus hislopi* (Lydekker, 1885) Hunt & Lucas, 1991 [*nomen dubium*]
= *Brachysuchus maleriensis* von Huene, 1940 [*nomen dubium*]
= *Nicrosaurus maleriensis* (von Huene, 1940) Westphal, 1976 [*nomen dubium*]
= *Phytosaurus maleriensis* (von Huene, 1940) Colbert, 1958 [*nomen dubium*]
NOTE: See Note for *Paleorhinus*.

Genus: *Phytosaurus* Jaeger, 1828 [*nomen dubium*]
= *Cubicodon* Jaeger, 1828 [*sic*]
= *Cylindricodon* Jaeger, 1828 [*sic*]
P. cylindricodon Jaeger, 1828 (Type)
= *Belodon cylindricodon* (Jaeger, 1828) [*nomen dubium*]
= *Phytosaurus cylindricon* Mehl, 1915 [*sic*]
?*P. cubicodon* Jaeger, 1828 [*nomen dubium*]
= *Belodon cubicodon* (Jaeger, 1828) [*nomen dubium*]
= *Phytosaurus cubicron* Mehl, 1915 [*sic*]

Genus: *Pseudopalatus* Mehl, 1928 (= *Mystriosuchus*?)
= *Lophosaurus* Hay, 1929/Fitzinger, 1843 [*sic*]
P. pristinus Mehl, 1928 (Type)
= *Rutiodon pristinus* (Mehl, 1928)
= *Machaeroprosopus tenuis* Camp, 1930 (in part)
= *Rutiodon tenuis* (Camp, 1930) Gregory, 1962 (in part)
P. buceros (Cope, 1881)
= *Belodon buceros* Cope, 1881
= *Lophoprosopus buceros* (Cope, 1881)
= *Lophosaurus buceros* (Cope, 1881) Hay, 1929 [*sic*]
= *Machaeroprosopus buceros* (Cope, 1881)
= *Metarhinus buceros* (Cope, 1881) Jaekel, 1910
= *Nicrosaurus buceros* (Cope, 1881) Murry & Long, 1989
= *Phytosaurus buceros* (Cope, 1881)
= *Rutiodon buceros* (Cope, 1881)
= *Typothorax buceros* (Cope, 1881)
= *Machaeroprosopus tenuis* Camp, 1930 (in part)
= *Rutiodon tenuis* (Camp, 1930) Gregory, 1962 (in part)
P. mccauleyi Ballew, 1989

Genus: *Rileyasuchus* Kuhn, 1961 [*nomen dubium*]
= *Rileya* von Huene, 1902/Howard, 1888
= *Rileyia* von Huene, 1902 [*sic*]
= *Rylea* Mehl, 1915 [*sic*]

R. bristolensis (von Huene, 1902) (Type)
= *Rileya bristolensis* von Huene, 1902 [*nomen dubium*]
= *Palaeosaurus platyodon* Riley & Stutchbury, 1840 *non* Riley & Stutchbury, 1836 [*nomen dubium*]
= *Rileya platyodon* (Riley & Stutchbury, 1840) von Huene, 1908 [*nomen dubium*]
= *Rileya stutchburyi* von Huene, 1920 [*nomen dubium*]
= *Rileya stutchburi* von Huene, 1920 [*nomen dubium*]*

Genus: *Rutiodon* Emmons, 1856
= *Leptosuchus* Case, 1922
= *Machaeorprosopus* Gregory, 1962 [*sic*]
= *Machaeroprosopus* Mehl, 1916
= *Metarhinus* Jaekel, 1910/Osborn, 1908
= *Palaeonornis* Emmons, 1857
= *Rhytidiodon* Cope, 1866 [*sic*]
= *Rhytidodon* Cope, 1866 [*sic*]
= *Rhytiodin* Mehl, 1915 [*sic*]
= *Rhytiodon* Cope, 1866 [*sic*]
R. carolinensis Emmons, 1856 (Type)
= *Belodon carolinensis* (Emmons, 1856)
= *Mystriosuchus carolinensis* (Emmons, 1856)
= *Palaeosaurus carolinensis* (Emmons, 1856)
= *Phytosaurus carolinensis* (Emmons, 1856)
= *Rhytidodon carolinensis* (Emmons, 1856)
= *Rhytiodin carolinensis* (Emmons, 1856)
= *Palaeonornis struthionoides* Emmons, 1857

NOTE: The above genus and species were originally described as avian, but the type specimen clearly "consists of the mid-section of a rostrum of a phytosaur (*cf. Rutiodon*)" (D. Baird, quoted in Brodkorb, 1978). It was recently figured by Baird (1986; *The Mosasaur 3*: 139).

= *Rhytidodon rostratus* Marsh, 1896
= *Mystriosuchus rostratus* (Marsh, 1896)
= *Phytosaurus rostratus* (Marsh, 1896) McGregor, 1906
= *Rutiodon rostratus* (Marsh, 1896)
= *Rutiodon manhattanensis* von Huene, 1913
= *Clepsysaurus manhattanensis* (von Huene, 1913)
= *Phytosaurus manhattanensis* (von Huene, 1913) Gregory, 1962

NOTE: The above species is probably a large male *Rutiodon carolinensis* (D. Baird, pers. comm.).

= *Phytosaurus rostrastus* Ballew, 1989 [*sic*]
?*R. leaii* (Emmons, 1856) [*nomen dubium*]
= *Clepsisaurus leaii* Emmons, 1856 [*nomen dubium*]
= *Belodon leaii* (Emmons, 1856) [*nomen dubium*]
= *Phytosaurus leaii* (Emmons, 1856) [*nomen dubium*]
?*R. scolopax* (Cope, 1881) Gregory, 1962 [*nomen dubium*]
= *Belodon scolopax* Cope, 1881 [*nomen dubium*]
= *Phytosaurus scolopax* (Cope, 1881) McGregor, 1906 [*nomen dubium*]
= *Belodon scopax* Mehl, 1915 [*sic*]
= *Lophorhinus scopax* Mehl, 1915 [*sic*]
= *Palaeorhinus scopax* Mehl, 1915 [*sic*]
?*R. validus* (Mehl, 1916) [*nomen dubium*]
= *Machaeroprosopus validus* Mehl, 1916 *non* (Marsh, 1893) [*nomen dubium*]
= *Clepsysaurus validus* (Mehl, 1916) [*nomen dubium*]
= *Phytosaurus validus* (Mehl, 1916) Gregory, 1962 [*nomen dubium*]
R. doughtyi (Case, 1920) Gregory, 1962
= *Phytosaurus doughtyi* Case, 1920
= *Machaeroprosopus doughtyi* (Case, 1920) Case, 1930
?*R. gracilis* (Case, 1920) [*nomen nudum*]
= *Machaeroprosopus gracilis* Case, 1920 [*nomen nudum*]
R. andersoni (Mehl, 1922) Gregory, 1962 [*nomen dubium*]
= *Machaeroprosopus andersoni* Mehl, 1922 [*nomen dubium*]
R. crosbiensis (Case, 1922) Gregory, 1962
= *Leptosuchus crosbiensis* Case, 1922
= *Leptosuchus imperfectus* Case, 1922 [*nomen dubium*]
= *Leptosuchus imperfecta* Case, 1922 [*nomen dubium*]*
= *Rutiodon imperfectus* (Case, 1922) Gregory, 1962 [*nomen dubium*]

= *Rutiodon imperfecta* (Case, 1922) Gregory, 1962 [*nomen dubium*]*
= *Leptosuchus studeri* Case & White, 1934
= *Rutiodon studeri* (Case & White, 1934) Gregory, 1962
R. adamanensis (Camp, 1930) Gregory, 1962
= *Machaeroprosopus adamanensis* Camp, 1930
R. gregorii (Camp, 1930) Ballew, 1989
= *Machaeroprosopus gregorii* Camp, 1930
= *Nicrosaurus gregorii* (Camp, 1930) Gregory, 1969
= *Phytosaurus gregorii* (Camp, 1930) Gregory, 1962
R. lithodendrorum (Camp, 1930) Gregory, 1962
= *Machaeroprosopus lithodendrorum* Camp, 1930
R. zunii (Camp, 1930) Gregory, 1962
= *Machaeroprosopus zunii* Camp, 1930

Genus: *Suchoprion* Cope, 1877 [*nomen dubium*]
S. cyphodon Cope, 1877 (Type)
= *Palaeoctonus cyphodon* (Cope, 1877) [*nomen dubium*]
?*S. sulcidens* Cope, 1878 [*nomen dubium*]

Genus: *Termatosaurus* von Meyer & Plieninger, 1844 [*nomen dubium*; = *Belodon*?]
T. albertii von Meyer & Plieninger, 1844 (Type)
= *Mystriosuchus albertii* (von Meyer & Plieninger, 1844) E. Fraas, 1896 [*nomen dubium*]
= *Termatosaurus alberti* Gregory, 1962 [*sic*]
?*T. crocodilinus* Quenstedt, 1858 [*nomen dubium*]

Genus: [To be described; an "advanced" genus; Gregory, 1957; Hunt, 1991]

Order: Aetosauria Nicholson & Lydekker, 1889

Census: 1 family, 16 genera (3 doubtful), 19 species (5 doubtful)

Family: STAGONOLEPIDIDAE
Lydekker, July 1887

Census: 15 genera (2 doubtful), 18 species (4 doubtful)

= Stagonolepidae Agassiz, 1844*
= Aethosauridae Baur, September 1887
= Aetosauridae Cope, 1889
= Desmatosuchinae von Huene, 1942
= Episcoposaurinae von Huene, 1942
= Stagonolepidiidae Bonaparte, 1971 [*sic*]
= Stagonolepinae von Huene, 1942 [*sic*]

Genus: *Acompsosaurus* Mehl, 1915 [*nomen dubium*; = *Stagonolepis*?)
A. wingatensis Mehl, 1915 (Type)
= *Typothorax wingatensis* (Mehl, 1915) [*nomen dubium*]

NOTE: The type specimen is lost (Long & Ballew, 1985). Hunt & Lucas (1989) assert that the figured type material most closely resembles *Stagonolepis* (but not *Typothorax*), of which the genus may be a junior synonym.

Genus: *Aetosauroides* Casamiquela, 1960
= *Aetosaurioides* Reig, 1961 [*sic*]
A. scagliai Casamiquela, 1960 (Type)
= *Aetosaurioides scagliai* Reig, 1961 [*sic*]
A. inhamandensis Zacarias, 1982 *vide* Barberena, Araujo & Lavina, 1985 [*nomen nudum*]
A. subsulcatus Zacarias, 1982 *vide* Barberena, Araujo & Lavina, 1985 [*nomen nudum*]

Genus: *Aetosaurus* O. Fraas, 1877
= *Aëtosaurus* O. Fraas, 1877*
= *Aeotsaurus* Reig, 1961 [*sic*]
A. ferratus O. Fraas, 1877 (Type)
= *Aëtosaurus ferratus* O. Fraas, 1877*
A. crassicauda E. Fraas, 1907
= *Aëtosaurus crassicauda* E. Fraas, 1907*

Genus: *Argentinosuchus* Casamiquela, 1960
A. bonapartei Casamiquela, 1960 (Type)

Genus: *Chilenosuchus* Casamiquela, 1980
C. forttae Casamiquela, 1980 (Type)

Genus: *Desmatosuchus* Case, 1920
  D. haplocerus (Cope, 1892) (Type)
    = *Episcoposaurus haplocerus* Cope, 1892
    = *Desmatosuchus spurensis* Case, 1920

Genus: *Dyoplax* O. Fraas, 1867
  D. arenaceus O. Fraas, 1867 (Type)

Genus: *Ebrachosaurus* Kuhn, 1936 [*nomen dubium*]
  E. singularis Kuhn, 1936 (Type)

Genus: *Fukangolepis* Young, 1978 [*nomen dubium*]
  F. barbaros Young, 1978 (Type)

Genus: *Longosuchus* Hunt & Lucas, 1990
  L. meadei (Sawin, 1947) (Type)
    = *Typothorax meadei* Sawin, 1947

Genus: *Neoaetosauroides* Bonaparte, 1969
  N. engaeus Bonaparte, 1969 (Type)

Genus: *Paratypothorax* Long & Ballew, 1985
  P. andressi Long & Ballew, 1985 (Type)
    = *Paratypothorax ornatus* Murry, 1986 [*sic*]

Genus: *Stagonolepis* Agassiz, 1844
  = *Caliptosuchus* Ash, 1985 [*sic*]
  = *Calyptosuchuas* Long & Ballew, 1985 [*sic*]
  = *Calyptosuchus* Long & Ballew, 1985
  = *Staganolepis* von Huene, 1902 [*sic*]
  = *Steganolepis* Mehl, 1915 [*sic*]
  S. robertsoni Agassiz, 1844 (Type)
  S. wellesi (Long & Ballew, 1985) Murry & Long, 1989
    = *Calyptosuchus wellesi* Long & Ballew, 1985

Genus: *Stegomus* Marsh, 1896
  S. arcuatus Marsh, 1896 (Type)
  S. arcuatus arcuatus (Marsh, 1896) Jepsen, 1948
  S. arcuatus jerseyensis Jepsen, 1948

Genus: *Typothorax* Cope, 1875
  = *Episcoposaurus* Cope, 1887
  = *Thypothorax* Reig, 1961 [*sic*]
  = *Typothoras* Jacobs & Murry, 1980 [*sic*]
  T. coccinarum Cope, 1875 (Type)
    = *Episcoposaurus horridus* Cope, 1887
  ?*T. punctulatus* Rusconi, 1947 [*nomen dubium*]
    = *Typothorax pustulatus* Reig, 1961 [*sic*]

Genus: [To be described from the Middle Triassic of Tunisia; L. B. Halstead & Stewart, 1970]

Genus: [To be described from the *Rutiodon zunii* level of the Petrified Forest Member of the Chinle Formation; R. A. Long, pers. comm.]

AETOSAURIA *incertae sedis*

Census: 1 doubtful genus, 1 doubtful species

Genus: *Adamanasuchus* [Anonymous] 1983 [*nomen nudum*, in *Arizona Highways*, February 1983]
  A. rectori [Anonymous] 1983 (Type)

Genus: *Hoplitosuchus* von Huene, 1938 [*nomen dubium*]
  = *Hoplitosaurus* von Huene, 1938/Lucas, 1902 [*sic*]
  H. raui von Huene, 1938 (Type)

Order: Crocodylia Gmelin, 1788

Census: 4 suborders (listed), 10 families, 27 genera, 30 species (1 doubtful)

NOTE: This section of the archosaur taxa table comprises only the "lower" crocodilians. Many of these taxa have at times been classified as either dinosaurs or thecodontians, so their inclusion in a table otherwise devoted to the *non-crocodilian* archosaurs is partially justifiable. But the crocodilian suborders Mesosuchia and Eusuchia remain excluded.

Suborder: Trialestia Crush, 1984

Census: 1 family, 1 genus, 1 species

Family: TRIALESTIDAE Bonaparte, 1982

Census: 1 genus, 1 species

= Triassolestidae Bonaparte, 1970

Genus: *Trialestes* Bonaparte, 1982
= *Triassolestes* Reig, 1963/Tillyard, 1918
T. romeri (Reig, 1963) (Type)
= *Triassolestes romeri* Reig, 1963

NOTE: S. Chatterjee has examined the material of the above genus and notes that the crocodile-reversed tarsus precludes it from assignment to the Crocodylia (R. Molnar, pers. comm.). The type specimen may be composite, including both theropod and ornithosuchid material as well as crocodilian material.

Suborder: Sphenosuchia Bonaparte, 1971

Census: 4 families, 11 genera, 12 species

Family: PEDETICOSAURIDAE van Hoepen, 1915

Census: 3 genera, 3 species

= Saltoposuchidae Crush, 1984

Genus: *Pedeticosaurus* van Hoepen, 1915
= *Pediticosaurus* Gow & Kitching, 1988 [*sic*]
P. leviseuri van Hoepen, 1915 (Type)

Genus: *Saltoposuchus* von Huene, 1921
S. connectens von Huene, 1921 (Type)
= *Saltoposuchus longipes* von Huene, 1921

Genus: *Terrestrisuchus* Crush, 1984 (= *Saltoposuchus*?)
T. gracilis Crush, 1984 (Type)

Family: HEMIPROTOSUCHIDAE Crush, 1984

Census: 1 genus, 1 species

Genus: *Hemiprotosuchus* Bonaparte, 1969
H. leali Bonaparte, 1969 (Type)

Family: SPHENOSUCHIDAE von Huene, 1922

Census: 6 genera, 7 species

Genus: *Barberenasuchus* Mattar, 1987
= *Barbarenasuchus* Parrish, 1991 [*sic*]
B. brasiliensis Mattar, 1987 (Type)

Genus: *Dibothrosuchus* Simmons, 1965
= *Dibthrosuchus* Dong, 1980 [*sic*]
D. elaphros Simmons, 1965
D. xingsuensis Wu, 1986

Genus: *Hesperosuchus* Colbert, 1952
H. agilis Colbert, 1952 (Type)
[New species to be described from Texas; R. A. Long, pers. comm.]

Genus: *Pseudhesperosuchus* Bonaparte, 1969
= *Pseudohesperosuchus* Crush, 1984 [*sic*]
P. jachaleri Bonaparte, 1969

Genus: *Sphenosuchus* Haughton, 1915
S. acutus Haughton, 1915 (Type)

Genus: *Strigosuchus* Simmons, 1965
S. licinus Simmons, 1965 (Type)

Genus: [To be described from the McCoy Brook Formation of Nova Scotia; Sues & Galton, 1987]

Family: LEWISUCHIDAE [*nomen novum ex* Lewisuchinae]

Census: 1 genus, 1 species

= Lewisuchinae Paul, 1988

Genus: *Lewisuchus* Romer, 1972
L. admixtus Romer, 1972 (Type)

Parasuborder: Protosuchia Mook, 1934

Census: 4 families, 14 genera, 15 species

Family: PROTOSUCHIDAE Brown, 1933

Census: 11 genera, 11 species

= Archaeosuchidae Brown, 1933
= Stegomosuchidae von Huene, 1922

Genus: *Baroqueosuchus* Busbey & Gow, 1984
B. haughtoni Busbey & Gow, 1984 (Type)
NOTE: See note for *Lesothosuchus*.

Genus: *Clarencea* Brink, 1959
= *Clarenceia* Romer, 1966 [*sic*]
= *Clarencia* Brink, 1959 [*sic*]
= *Clarensia* Gow & Kitching, 1988 [*sic*]
C. gracilis Brink, 1959 (Type)
= *Clarensia gracilis* (Brink, 1959)
NOTE: Gow & Kitching (1988) attempt to revise the spelling of the name of this genus, but this is impermissible under ICZN rules.

Genus: *Dianosuchus* Young, 1982
D. changchiawaensis Young, 1982 (Type)

Genus: *Eopneumatosuchus* Crompton & Smith, 1980
= *Eupneumatosuchus* Crush, 1984 [*sic*]
E. colberti Crompton & Smith, 1980 (Type)

Genus: *Erythrochampsa* Haughton, 1924
E. longipes (Broom, 1904) (Type)
= *Notochampsa longipes* Broom, 1904
NOTE: Gow & Kitching (1988) synonymize this genus with *Notochampsa*.

Genus: *Lesothosuchus* Whetstone & Whybrow, 1983 (= *Baroqueosuchus*?)
L. charigi Whetstone & Whybrow, 1983 (Type)
NOTE: Gow & Kitching (1988) assert that the diagnosis of the genus *Lesothosuchus* is inadequate and reject the name in favor of *Baroqueosuchus*, apparently a junior synonym.

Genus: *Microchampsa* Young, 1951
M. scutata Young, 1951 (Type)

Genus: *Notochampsa* Broom, 1904
N. istedana Broom, 1904 (Type)
NOTE: See notes for *Erythrosuchus* and *Orthosuchus*.

Genus: *Orthosuchus* Nash, 1968
O. stormbergi Nash, 1968 (Type)
NOTE: Gow & Kitching (1988) synonymize this genus with *Notochampsa*.

Genus: *Protosuchus* Brown, 1933
= *Archaeosuchus* Brown, 1933/Broom, 1905
P. richardsoni (Brown, 1933) (Type)
= *Archaeosuchus richardsoni* Brown, 1933

Genus: *Stegomosuchus* von Huene, 1922
S. longipes (Emerson & Loomis, 1904) (Type)
= *Stegomus longipes* Emerson & Loomis, 1904

Genus: [To be described from the McCoy Brook Formation of Nova Scotia (Sues & Olsen, 1987]

Family: PLATYOGNATHIDAE Simmons, 1965

Census: 1 genus, 1 species

Genus: *Platyognathus* Young, 1944
P. hsui Young, 1944 (Type)

Family: EDENTOSUCHIDAE Young, 1973

Census: 1 genus, 1 species

Genus: *Edentosuchus* Young, 1973
E. tienshanensis Young, 1973 (Type)
[One or two new species to be described from the Glen Canyon Group; Clark & Fastovsky, 1986]

Genus: [To be described from the Glen Canyon Group; Clark & Fastovsky, 1986]

Family: GOBIOSUCHIDAE Osmólska, 1972

Census: 1 genus, 2 species

Genus: *Gobiosuchus* Osmólska, 1972
G. kielanae Osmólska, 1972 (Type)
G. parvus Efimov, 1983
[New species to be described from Mongolia; Osmólska, 1972]

Suborder: Hallopoda Marsh, 1881

Census: 1 family, 1 genus, 2 species (1 doubtful)

Family: HALLOPODIDAE Marsh, 1881

Census: 1 genus, 2 species (1 doubtful)

= Hallopidae Carroll, 1988 [*sic*]

Genus: *Fruitachampsa* [Anonymous] 1986 [*nomen nudum*, in *Earthwatch* magazine, January-February 1986]
F. callisoni [Anonymous] 1986 (Type)

Genus: *Hallopus* Marsh, 1877
H. victor (Marsh, 1877) (Type)
= *Nanosaurus victor* Marsh, 1877
?H. celerrimus E. Fraas, 1912 [*nomen dubium*]

NOTE: This species is probably a synonym of *Procompsognathus triassicus* (R. E. Molnar, pers. comm.).

Order: Hupehsuchia Young & Dong, 1972

Census: 1 family, 2 genera, 2 species

Family: NANCHANGOSAURIDAE Wang, 1959

Census: 2 genera, 2 species

= Hupehsuchidae Young & Dong, 1972

Genus: *Hupehsuchus* Young *vide* Young & Dong, 1972
H. nanchangensis Young *vide* Young & Dong, 1972 (Type)

Genus: *Nanchangosaurus* Wang, 1959
N. suni Wang, 1959 (Type)

Genus: [To be described from the Middle Triassic Jialingjiang Formation of China; Carroll & Dong, 1991]

Thecodontia incertae sedis

Genus: [To be described from the Chinle Formation; R. A. Long, pers. comm.]

Genus: [To be described from the Chinle Formation; R. A. Long, pers. comm.]

Notes and New Taxa

Pterosaur Phylogeny

IN SOME WAYS, despite their extreme adaptations for powered flight and their hairlike insulative "pelage," the pterosaurs comprise the most primitive of the archosaurian clades characterized by modified or advanced mesotarsal (AM) ankles. Pterosaur tarsi are very small and difficult to study, but it is clear that they featured reduced calcanea (Wellnhofer, 1991: 57), in contrast with the enlarged, tuberal calcanea of the semi-erect and fully erect thecodontians. Pterosaurs retained a plesiomorphically pentadactyl pes (the fifth digit was reduced or vestigial in advanced forms) in which the metatarsals showed little or no tendency to merge into a single unit, as they did in theropod dinosaurs. Corresponding to the reduced calcaneum, the pterosaur fibula was also reduced, becoming progressively smaller in more advanced genera until it was entirely lost in most Cretaceous forms. Reduction of the fibula and calcaneum is a synapomorphy that might unite the pterosaurs with the dinosaur clades among the archosaurs.

All known pterosaur genera lacked a mandibular fenestra; all other known archosaurs more advanced than proterosuchians possessed a mandibular fenestra (it became secondarily closed in advanced sauropods and ornithischians but did exist in the primitive ones). It is possible that the fenestra closed secondarily in pterosaurs, too, but if so, it is absent even in the earliest known forms. In view of the trend toward lightening of the skull in pterosaurs by *enlargement* of the cranial fenestrae, one might expect a mandibular fenestra—had it been present in ancestral pterosaurs—to have *widened* rather than closed.

Finally, most if not all pterosaurs seem to have been quadrupedal with a sprawling or semi-erect stance when grounded (Unwin, 1987, 1988; Wellnhofer, 1988). Evidence that they were bipedal (Padian, 1983a, 1983b; Bennett, 1990) seems to me to indicate only that they could walk bipedally when necessary—for example, to take off from level ground—but not that this was their habitual or obligatory stance. The hind limb in most pterosaur genera (*Pteranodon* is an exception) was approximately as long as the forelimb from the shoulder to the joint between metacarpal IV and the first wing phalanx. This suggests that the hind limbs lengthened in step with the enlarging forelimb, in turn suggesting that they were of comparable importance in terrestrial locomotion. Additionally, the pelvis was wide with an imperforate acetabulum, and the hind limbs were outwardly directed, slender, and gracile (in contrast to the theropods, for example, in which the hind limbs were downwardly directed and extraordinarily powerful, even in the small forms).

These considerations prompt me to imagine that pterosaurs originated independently within one of those all-purpose groups of sprawling proterosuchians, diverging away from the Thecodontia like the dinosaurian clades but perhaps even earlier. The existence of hairlike "pelage" in a few well-preserved specimens (Broili, 1927; Sharov, 1971) makes it reasonable to assume that all pterosaurs shared a similar integument. This, together with their obvious specializations for powered flight, is strong evidence that pterosaurs were endothermic, tachymetabolic animals much like extant birds. Endothermy may be a synapomorphy uniting pterosaurs with the theropodomorph archosaurs. This, in turn, could mean that pterosaur "pelage" was derived from a stage in the evolution of feathers (but see the discussion of *Sharovip-*

teryx that follows). Lack of any specimens identifiable as ancestral pterosaurs prior to the Late Triassic, however, when they appear abruptly and well evolved in the fossil record of Europe, makes further comment on their origins highly speculative. Recent cladistic analyses (*cf.* Benton, 1990a) confirm the Pterosauria as a sister group to the dinosaurian clades, but for reasons stated earlier and elaborated in the Dinosaur Phylogeny section, I do not accept the pterosaur-dinosaur clade as being particularly closely related to the Ornithosuchia. (This, incidentally, may also mean that the mandibular fenestra developed independently in thecodontians and in dinosaurs.)

PTEROSAUR FLIGHT

The vast structural differences between pterosaur and avian wings make it obvious that flight arose independently within the two groups. Nevertheless, there were undoubtedly functional similarities in how this occurred in the groups, the result of aerodynamic constraints on vertebrate anatomy (Peters & Gutmann, 1985).

Most pterosaur specimens that display wing impressions seem never to show traces of a tail membrane, although *Sordes pilosus* evidently retained one (Sharov, 1971; Wellnhofer, 1991). So there may have been a uropatagial stage at some early time in pterosaur evolution. In 1971, Sharov reported a peculiar gliding reptile from the Norian of central Russia in which the principal aerodynamic surface was an extensive uropatagium. It is possible that *Sharovipteryx* (originally called *Podopteryx*) might have been a derived uropatagial pterosaurian. Recently redescribed by Gans, Darevski & Tatarinov (1987), *Sharovipteryx* possessed several characters suggesting a relationship with the pterosaurs, including a reduced fibula, a pentadactyl pes, and a mandible lacking a fenestra. It may also have had a prepubic bone, which is a pterosaur autapomorphy. But Gans, *et al.* report no antorbital fenestra, which would remove *Sharovipteryx* from the Archosauria. The skull of the only available specimen, however, is split apart horizontally, and evidence for an antorbital fenestra could well be lost. It is also possible that the fenestra merged with the narial opening as in later pterosaurs, because Gans, *et al.* report long and slender nares in *Sharovipteryx.* Finally, they report skin impressions that show small keeled scales along the back, not the hairlike "pelage" of pterosaurs. If *Sharovipteryx* were indeed a derived pre-pterosaur, then pterosaur "pelage" and feathers must have originated independently.

The primary lift forces in pre-pterosaurs were almost certainly generated by lateral patagial membranes stretching along the sides of the body between the forelimbs and hind limbs, as illustrated by Peters & Gutmann. Such membranes could have continued backward to envelop the hind limbs or tail in a uropatagium, but if so, it was lost early in the lineage leading to the traditional pterosaur orders. A gliding pre-pterosaur would have resembled a reptilian flying squirrel, and the gradual enlargement of the aftmost manual digits to support larger and more efficient membraneous wings seems the most natural way for the pterosaurs to have evolved.

Encumbered by their wing membranes, which almost certainly involved fore and hind limbs, the earliest pterosaurs would have been unable to evolve a fully erect bipedal stance. In later pterosaurs, the hind limb and pelvis had become highly adapted to a semi-erect stance that probably did not allow more than a facultative bipedality, even though the wing membrane may actually have been free of the hind limb. Lacking a secondary locomotor ability, pterosaurs would seldom have evolved flightless forms, in marked contrast to avian evolutionary history.

Pterosaurs were clearly a very diverse group of archosaurs, of which we have good samples from only a handful of localities. At Solnhofen, for example, pterosaurs outnumber archaeopterygids by scores of species to one. I have no doubt that a naturalist thrust back in time to any epoch of the Jurassic or Cretaceous would find pterosaurs nearly as common and diverse as modern birds. Competition from pterosaurs undoubtedly restricted avian diversification until birds became more efficient fliers than pterosaurs, sometime before the Early Cretaceous (when the fully volant Chinese birds appeared). Thereafter, birds slowly replaced the smaller pterosaurs. When the large pterosaurs became extinct at the end of the Mesozoic, there were no small pterosaurs from which new groups could radiate, and the establishment of birds as the dominant aerial vertebrates was complete.

PTEROSAUR ORDERS

In view of pterosaurs' early divergence from the other archosaurs and the specializations for flight that affected every part of their anatomy, raising the traditional order Pterosauria to a superorder on a taxonomic par with the Thecodontia and the three dinosaurian groups is certainly justified. As such it forms a clade partitionable into two or three ordinal-level taxa. These are discussed individually below.

Regarding the pterosaurs, a marvelous book (Wellnhofer, 1991) was recently published that covers the group from all aspects: phyletic, taxonomic, anatomic, functional, behavioral, and historical. It is most remarkable—and very welcome—that the volume is intended for a general readership, even though it contains much of technical interest. I consider it a *tour de force* among popular paleontological publications and a splendid entry into the pterosaur literature. Except for adding the sharovipterygians and desynonymizing a few genera commonly synonymized with others, my classification follows the one used therein and in Wellnhofer's (1976) earlier monograph.

Order Sharovipterygia

The tail-gliding reptile *Sharovipteryx* was morphologically so different from other archosaurs that it clearly requires a new order, Sharovipterygia. Where to place this order within (or outside) the Archosauria is moot, but inasmuch as *Sharovipteryx* seems anatomically closest to the pterosaurs, I have tentatively classified the order Sharovipterygia within the superorder Pterosauria.

The problematic small archosaur *Scleromochlus* has been suggested as related to pterosaur ancestry (Huene, 1914). In its relative skull and limb proportions—very large skull relative to body, very small forelimbs and enormously long hind limbs—it is remarkably similar to *Sharovipteryx*; all that is needed is the trace of a uropatagium to completely confirm their phyletic closeness. The *Scleromochlus* specimens illustrated by Huene bear a remarkable superficial resemblance to the *Sharovipteryx* type specimen. Huene described a robust calcaneum in *Scleromochlus*, and his sketch of the animal (reproduced in Wellnhofer, 1991) shows a fenestrated mandible, but I think these determinations are questionable (Padian [1984] noted a mesotarsal ankle for *Scleromochlus*). In the table, I have synonymized the family Sharovipterygidae with Huene's Scleromochlidae and classified it in the Sharovipterygia. A redescription of *Scleromochlus* is required to confirm or deny this assignment.

Paraorder Rhamphorhynchoidia

The two traditional suborders of the Pterosauria are here raised to orders within the superorder. As more pterosaur specimens are collected and the true diversity of the superorder becomes evident, the number of pterosaur orders will certainly increase.

A minor point that seems to have escaped attention is the spelling of the names Rhamphorhynchoidia and Pterodactyloidia. These have invariably been spelled with the ending -oidea; but this ending is reserved for superfamilies, according to the ICZN (1985). So I have slightly changed the ending to -oidia, which is appropriate to both subordinal and ordinal levels.

Wellnhofer (1991) tabulates the numerous differences between the Rhamphorhynchoidia and the Pterodactyloidia, and I follow his classification here. Among other things, the rhamphorhynchoids had jaws with numerous large teeth; separate narial and antorbital openings; a short metacarpus; a backwardly directed occipital condyle (so that the skull was more or less in line with the neck); a long pedal digit V; and (usually) a long tail. Because the rhamphorhynchoids are regarded as ancestral to the later pterodactyloids, possibly through the Anurognathidae, a family of short-tailed rhamphorhynchoids, the Rhamphorhynchoidia is listed as a paraorder.

Order Pterodactyloidia

Pterosaurs in this order were characterized by jaws with fine teeth, few teeth, or none at all; nares and antorbital fenestrae merged into a single opening; a long metacarpus; a downwardly directed occipital condyle (so that the skull was held at an angle to the neck); a reduced pedal digit V; and a short tail. Whereas rhamphorhynchoids remained relatively small, some pterodactyloids grew to spectacular sizes – the largest-known flying animals that ever existed. Rhamphorhynchoids were fliers whose aerodynamic stability was abetted to some extent by their tails. Pterodactyloids, lacking tails, must were unstable fliers, in the sense that they had to adjust their flight constantly by muscular effort. They were thus more maneuverable and efficient fliers than rhamphorhynchoids, which may have aided the dramatic increase in size within the group.

Superorder: Pterosauria Kaup, 1834

Census: 3 orders, 17 families, 59 genera (9 doubtful), 122 species (36 doubtful)

Order: Sharovipterygia nov.

Census: 1 family, 2 genera, 2 species

Family: SCLEROMOCHLIDAE von Huene, 1914

Census: 2 genera, 2 species

= Podopterygidae Sharov, 1971
= Sharovipterygidae Tatarinov, 1989

Genus: *Scleromochlus* Woodward, 1907
= *Schlermochlus* Glut, 1972 [*sic*]
= *Sclermochlus* Glut, 1972 [*sic*]
S. taylori Woodward, 1907 (Type)

Genus: *Sharovipteryx* Cowen, 1981
= *Podopterix* Ivakhnenko, 1978 [*sic*]
= *Podopteryx* Sharov, 1971/Selys-Longchamps, 1871
S. mirabilis (Sharov, 1971) (Type)
= *Podopteryx mirabilis* Sharov, 1971
= *Podopterix mirabilis* Ivakhnenko, 1978 [*sic*]

Paraorder: Rhamphorhynchoidia Plieninger, 1901

Census: 4 families, 18 genera (2 doubtful), 29 species (5 doubtful)

Family: EUDIMORPHODONTIDAE Wellnhofer, 1978

Census: 1 genus, 1 species

Genus: *Eudimorphodon* Zambelli, 1973
E. ranzii Zambelli, 1973 (Type)

Family: DIMORPHODONTIDAE Seeley, 1870

Census: 2 genera, 2 species

= Dimorphodontinae Hooley, 1913

Genus: *Dimorphodon* Owen, 1859
D. macronyx (Buckland, 1829) (Type)
= *Pterodactylus macronyx* Buckland, 1829
= *Rhamphorhynchus macronyx* (Buckland, 1829)
= *Pterodactylus marderi* Owen, 1874 [*nomen dubium*]

Genus: *Peteinosaurus* Wild, 1978
P. zambellii Wild, 1978 (Type)

Genus: [To be described from the Dockum Formation of Texas; S. Chatterjee, pers. comm.]

Family: ANUROGNATHIDAE Nopcsa, 1928

Census: 2 genera, 2 species

Genus: *Anurognathus* Döderlein, 1923
= *Anuroganthus* Young, 1964 [*sic*]
A. ammoni Döderlein, 1923 (Type)

Genus: *Batrachognathus* Riabinin, 1948
B. volans Riabinin, 1948 (Type)

Family: RHAMPHORHYNCHIDAE Seeley, 1870

Census: 12 genera (2 doubtful), 23 species (5 doubtful)

= Campylognathoidinae Kuhn, 1967
= Parapsicephalinae Kuhn, 1967
= Rhamphorhynchinae Nopcsa, 1928
= Scaphognathidae Hooley, 1913
= Scaphognathinae Hooley, 1913

Genus: *Angustinaripterus* He, Yan & Su, 1983
= *Angustinarhipterus* Dong, 1987 [*sic*]
A. longicephalus He, Yan & Su, 1983 (Type)
= *Angustinarhipterus congicephalus* Dong, 1987 [*sic*]

Genus: *Campylognathoides* Strand, 1928
= *Camplyognathus* Romer, 1966 [*sic*]
= *Campylognathus* Plieninger, 1894/Reuter, 1890
= *Compylognathus* Coombs, 1972 [*sic*]
C. liasicus (Quenstedt, 1858)
= *Pterodactylus liasicus* Quenstedt, 1858
= *Campylognathus liasicus* (Quenstedt, 1858)
C. zitteli (Plieninger, 1894) (Type)
= *Campylognathus zitteli* Plieninger, 1894
C. indicus Jain, 1974

Genus: *Comodactylus* Galton, 1981
C. ostromi Galton, 1981 (Type)

Genus: *Dorygnathus* Wagner, 1860
D. banthensis (Theodori, 1830) (Type)
= *Ornithocephalus banthensis* Theodori, 1830
= *Dimorphodon banthensis* (Theodori, 1830)
= *Pterodactylus banthensis* (Theodori, 1830)
= *Rhamphorhynchus banthensis* (Theodori, 1830)
= *Pterodactylus macronyx* von Meyer, 1831 *non* Buckland, 1829 [*nomen dubium*]
= *Rhamphorhynchus macronyx* (von Meyer, 1831) [*nomen dubium*]
= *Pterodactylus goldfussi* Theodori, 1848 [*nomen dubium*]
= *Rhamphorhynchus goldfussi* (Theodori, 1848) [*nomen dubium*]
D. mistelgauensis Wild, 1971

Genus: *Nesodactylus* Colbert, 1969
= *Nesodon* Jensen & Ostrom, 1977/Owen, 1840 [*sic*]
N. hesperius Colbert, 1969 (Type)
= *Nesodon hesparius* Jensen & Ostrom, 1977 [*sic*]

Genus: *Odontorhynchus* Stolley, 1936 [*nomen dubium*]
O. aculeatus Stolley, 1936 (Type)

Genus: *Parapsicephalus* Arthaber, 1918
= *Parapsicethalus* Romer, 1966 [*sic*]
P. purdoni (Newton, 1888) (Type)
= *Scaphognathus purdoni* Newton, 1888

Genus: *Preondactylus* Wild, 1983
P. buffarinii Wild, 1983 (Type)

Genus: *Rhamphocephalus* Seeley, 1880 [*nomen dubium*]
= *Dolichorhamphus* Seeley, 1885
= *Dolichorhampus* Romer, 1966 [*sic*]
= *Rhampocephalus* Romer, 1966 [*sic*]
R. bucklandi (von Meyer, 1832) (Type)
= *Pterodactylus bucklandi* von Meyer, 1832 [*nomen dubium*]
= *Rhamphorhynchus bucklandi* (von Meyer, 1832) [*nomen dubium*]
= *Pterodactylus duncani* Owen, 1874 [*nomen dubium*]
= *Pterodactylus kiddii* Owen, 1874 [*nomen dubium*]
?*R. depressirostris* (Huxley, 1859) [*nomen dubium*]

    - = *Rhamphorhynchus depressirostris* Huxley, 1859 [*nomen dubium*]
    - = *Pterodactylus aclandi* Owen, 1874 [*nomen dubium*]
  - ?*R. prestwichi* Seeley, 1880 [*nomen dubium*]
    - = *Dolichorhamphus prestwichi* (Seeley, 1880) [*nomen dubium*]

Genus: *Rhamphorhynchus* von Meyer, 1846

- = *Ornithopterus* von Meyer, 1846 [*nomen dubium*]
- = *Pteromonodactylus* Teriaev, 1967
- = *Ramphorhynchus* von Meyer, 1847 [*sic*]
- = *Rhamphorhynchys* Rao & Shah, 1982? [*sic*]
- *R. muensteri* (Goldfuss, 1831)
  - = *Ornithocephalus muensteri* Goldfuss, 1831
  - = *Ornithocephalus münsteri* Goldfuss, 1831*
  - = *Pterodactylus muensteri* (Goldfuss, 1831)
  - = *Pterodactylus münsteri* (Goldfuss, 1831)*
  - = *Rhamphorhynchus suevicus* O. Fraas, 1855 [*nomen dubium*]
  - = *Pterodactylus hirundinaceus* Wagner, 1857 [*nomen dubium*]
  - = *Rhamphorhynchus hirundinaceus* (Wagner, 1857) [*nomen dubium*]
  - = *Rhamphorhynchus curtimanus* Wagner, 1858
  - = *Rhamphorhynchus longimanus* Wagner, 1858
  - = *Rhamphorhynchus meyeri* Owen, 1870
  - = *Rhamphorhynchus phyllurus* Marsh, 1882
  - = *Pteromonodactylus phyllurus* (Marsh, 1882)
  - = *Rhamphorhynchus megadactylus* von Koenigswald, 1931
  - = *Rhamphorhynchus carnegiei* Koh, 1937
- *R. longicaudus* (Münster, 1839) (Type)
  - = *Pterodactylus longicaudus* Münster, 1839
  - = *Odontorhynchus longicaudus* (Münster, 1839)
  - = *Ornithocephalus longicaudus* (Münster, 1839)
  - = *Rhamphorhynchus longicaudatus* von Ammon, 1884 [*sic*]
- *R. gemmingi* (von Meyer, 1846)
  - = *Pterodactylus gemmingi* von Meyer, 1846
  - = *Ornithocephalus gemmingi* (von Meyer, 1846)
  - = *Pterodactylus lavateri* von Meyer, 1838 [*nomen dubium*]
  - = *Ornithopterus lavateri* (von Meyer, 1838) [*nomen dubium*]
- *R. jessoni* Lydekker, 1890 [*nomen dubium*]
- *R. longiceps* Woodward, 1902
  - = *Ornithocephalus giganteus* Oken, 1819 [*nomen dubium*]
  - = *Pterodactylus giganteus* (Oken, 1819) [*nomen dubium*]
  - = *Pterodactylus grandis* Cuvier, 1824 [*nomen dubium*]
  - = *Ornithocephalus grandis* (Cuvier, 1824) [*nomen dubium*]
  - = *Rhamphorhynchus grandis* (Cuvier, 1824) [*nomen dubium*]
  - = *Pterodactylus secundarius* von Meyer, 1843 [*nomen dubium*; juvenile?]
  - = *Ornithocephalus secundarius* (von Meyer, 1843) [*nomen dubium*; juvenile?]
  - = *Rhamphorhynchus kokeni* Plieninger, 1907
- ?*R. tendagurensis* Reck, 1931
- *R. intermedius* Koh, 1937
- [New large species to be described; Wellnhofer, 1991: 151]

Genus: *Scaphognathus* Wagner, 1861

- = *Brachytrachelus* Giebel, 1850 [*nomen oblitum*]
- = *Pachyramphus* Romer, 1966 [*sic*]
- = *Pachyrhamphus* Fitzinger, 1843 [*nomen oblitum*]
- = *Pycnorhamphus* Zittel, 1882 [*sic*]
- *S. crassirostris* (Goldfuss, 1831) (Type)
  - = *Pterodactylus crassirostris* Goldfuss, 1831
  - = *Brachytrachelus crassirostris* (Goldfuss, 1831)
  - = *Ornithocephalus crassirostris* (Goldfuss, 1831)
  - = *Pachyrhamphus crassirostris* (Goldfuss, 1831)
  - = *Rhamphorhynchus crassirostris* (Goldfuss, 1831)

Genus: *Sordes* Sharov, 1971

- = *Sordus* Bakker, 1975 [*sic*]
- *S. pilosus* Sharov, 1971 (Type)

RHAMPHORHYNCHOIDIA *incertae sedis*

Census: 1 genus, 1 species

Genus: *Rhamphinion* Padian, 1984
  = *Rhamphion* Fraser & Unwin, 1990 [*sic*]
  R. jenkinsi Padian, 1984 (Type)

Genus: [To be described from Cene, near Bergamo, Italy; Fraser & Unwin, 1990]

Genus: [To be described from southern Austria; Fraser & Unwin, 1990]

Genus: [To be described from the Triassic of Kalgary, western Texas; Murry, 1986]

Order: Pterodactyloidia Plieninger, 1901

Census: 12 families, 39 genera (7 doubtful), 91 species (31 doubtful)

Family: PTERODACTYLIDAE Bonaparte, 1838

Census: 6 genera (1 doubtful), 22 species (14 doubtful)

= Gallodactylinae Fabre, 1981
= Ornithocephalidae Hay, 1902
= Ptenodraconinae Hooley, 1913
= Pterodactylae Bonaparte, 1838
= Pterodactyli von Meyer, 1830
= Pterodactylia Blainville, 1835
= Pterodactylina Bonaparte, 1838
= Pterodactylinae Williston, 1892

Genus: *Cycnorhamphus* Seeley, 1870
  = *Cygnorhamphus* Seeley, 1870 [*sic*]
  = *Cynorhamphus* Romer, 1966 [*sic*]
  C. suevicus (Quenstedt, 1855) Seeley, 1870 (Type)
    = *Pterodactylus suevicus* Quenstedt, 1855 *non* Oken, 1825
    = *Gallodactylus suevicus* (Quenstedt, 1855) Fabre, 1974
    = *Pterodactylus wuerttembergicus* Quenstedt, 1854 [*nomen nudum*]
    = *Pterodactylus württembergicus* Quenstedt, 1854 [*nomen nudum*]*
    = *Pterodactylus eurychirus* Wagner, 1957
    = *Pterodactylus (Ornithocephalus) eurychirus* (Wagner, 1857)
    = *Ornithocephalus eurychirus* (Wagner, 1857)
    = *Pterodactylus suevicus eurychirus* Wagner, 1858
    = *Pterodactylus wurtembergicus* Fabre, 1981 [*sic*]

Genus: *Dermodactylus* Marsh, 1881 [*nomen dubium*]
  = *Dermadactylus* Brown, 1943 [*sic*]
  D. montanus (Marsh, 1878) (Type)
    = *Pterodactylus montanus* Marsh, 1878 [*nomen dubium*]

Genus: *Diopecephalus* Seeley, 1871
  D. longicollum (von Meyer, 1854) Seeley, 1871 (Type)
    = *Pterodactylus longicollum* von Meyer, 1854
    = *Gallodactylus longicollum* (von Meyer, 1854) Fabre, 1974
    = *Pterodactylus longipes* Münster, 1836 [*nomen oblitum*]
    = *Ornithocephalus longipes* (Münster, 1836) [*nomen oblitum*]
    = *Pterodactylus (Ornithocephalus) vulturinus* Wagner, 1857
    = *Pterodactylus vulturinus* (Wagner, 1857)
    = *Ornithocephalus vulturinus* (Wagner, 1857)
    = *Pterodactylus longicollis* von Meyer, 1858 [*sic*]
    = *Pterodactylus suevicus* O. Fraas, 1878 *non* Oken, 1825
    = *Cycnorhamphus fraasi* Seeley, 1901
    = *Pterodactylus fraasi* (Seeley, 1901)

Genus: *Gallodactylus* Fabre, 1974
  G. canjuersensis Fabre, 1974 (Type)

Genus: *Herbstosaurus* Casamiquela, 1974
  H. pigmaeus Casamiquela, 1974 (Type)

Genus: *Pterodactylus* Rafinesque, 1815
- = *Macrotrachelus* Giebel, 1850
- = *Ornithocephalus* Sömmering, 1812 [*nomen oblitum*]
- = *Perodactylus* Plieninger, 1929 [*sic*]
- = *Ptenodracon* Lydekker, 1888
- = *Pterodactyle* Cuvier, 1809 [*nomen oblitum*]
- = *Pterodracon* Lydekker, 1888 [*sic*]
- = *Pterotherium* Fischer, 1813 [*nomen oblitum*]
- *P. antiquus* (Sömmering, 1812) (Type)
  - = *Ornithocephalus antiquus* Sömmering, 1812
  - = *Ornithocephalus brevirostris* Sömmering, 1817 (juvenile)
  - = *Ptenodracon brevirostris* (Sömmering, 1817) (juvenile)
  - = *Pterodactylus brevirostris* (Sömmering, 1817) (juvenile)
  - = *Pterodactylus longirostris* Cuvier, 1819
  - = *Macrotrachelus longirostris* (Cuvier, 1819)
  - = *Ornithocephalus longirostris* (Cuvier, 1819)
  - = *Pterodactylus suevicus* Oken, 1825 [*nomen dubium*]
  - = *Pterodactylus crocodilocephaloides* Ritgen, 1829 [*nomen dubium*]
  - = *Pterodactylus spectabilis* von Meyer, 1861
- *P. kochi* (Wagner, 1837)
  - = *Ornithocephalus kochii* Wagner, 1837
  - = *Diopecephalus kochi* (Wagner, 1837)
  - = *Pterodactylus meyeri* Münster, 1842 (juvenile)
  - = *Ornithocephalus meyeri* (Münster, 1842) (juvenile)
  - = *Pterodactylus scolopaciceps* von Meyer, 1850
  - = *Rhamphorhynchus scolopaciceps* (von Meyer, 1858)
  - = *Pterodactylus elegans* Broili, 1925 *non* Wagner, 1861
  - = *Pterodactylus westmani* Wiman, 1927
  - = *Pterodactylus cormoranus* Döderlein, 1929
  - = *Pterodactylus elegans* Edinger, 1941 *non* Wagner, 1861
- *P. ornis* Giebel, 1847 [*nomen dubium*]
- *P. gracilis* Theodori, 1852 [*nomen dubium*]
- *P. micronyx* von Meyer, 1856
  - = *Pterodactylus nettecephaloides* Ritgen, 1826 [*nomen oblitium*]
  - = *Ornithocephalus redenbacheri* Wagner, 1851 [*nomen oblitium*]
  - = *Pterodactylus redenbacheri* (Wagner, 1851) [*nomen oblitium*]
  - = *Pterodactylus pulchellus* von Meyer, 1861
  - = *Pterodactylus elegans* Rikovsky, 1925 *non* Wagner, 1861
- ?*P. propinquus* Wagner, 1857 [*nomen dubium*]
  - = *Ornithocephalus propinquus* (Wagner, 1857) [*nomen dubium*]
- ?*P. primus* Deffner & O. Fraas, 1859 [*nomen dubium*]
- ?*P. cirinensis* von Meyer, 1860 [*nomen dubium*]
  - = *Pterodactylus cerinensis* Lortet, 1892 [*sic*]
- ?*P. grandipelvis* von Meyer, 1860 [*nomen dubium*]
- *P. elegans* Wagner, 1861
- ?*P. hopkinsi* Seeley, 1864 [*nomen nudum*]
- ?*P. macrurus* Seeley, 1869 [*nomen dubium*]
- ?*P. nobilis* Owen, 1869 [*nomen dubium*]
  - = *Ornithocheirus nobilis* (Owen, 1869) [*nomen dubium*]
  - = *Ornithochirus nobilis* (Owen, 1869) [*nomen dubium*]
- ?*P. suprajurensis* Sauvage, 1873 [*nomen dubium*]
  - = *Rhamphorhynchus suprajurensis* (Sauvage, 1873) [*nomen dubium*]
- ?*P. manseli* Owen, 1874 [*nomen dubium*]
  - = *Rhamphorhynchus manseli* (Owen, 1874) [*nomen dubium*]
- ?*P. playdelli* Owen, 1874 [*nomen dubium*]
- ?*P. arningi* Reck, 1931 [*nomen dubium*]
- ?*P. maximus* Reck, 1931 [*nomen dubium*]

Family: GERMANODACTYLIDAE Young, 1964

Census: 1 genus, 2 species

Genus: *Germanodactylus* Young, 1964
- = *Germodactylus* Wellnhofer, 1980 [*sic*]
- *G. rhamphastinus* (Wagner, 1851)
  - = *Ornithocephalus rhamphastinus* Wagner, 1851

= *Diopecephalus rhamphastinus* (Wagner, 1851)
= *Pterodactylus rhamphastinus* (Wagner, 1851)
= *Pterodactylus medius* Münster, 1831
= *Pterodactylus intermedius* Goldfuss, 1831 [*sic*]
= *Pterodactylus dubius* Münster, 1832
= *Ornithocephalus dubius* (Münster, 1832)
= *Pterodactylus ramphatilus* Weigelt, 1927 [*sic*]
= *Germanodactylus ramphatilus* Weigelt *vide* Schaefer, 1989 [*sic*]
G. cristatus (Wiman, 1925) (Type)
= *Pterodactylus cristatus* Wiman, 1925
= *Pterodactylus kochi* Plieninger, 1901 (err. "Wagler, 1837") *non* Wagner, 1837
= *Germanodactylus kochi* (Plieninger, 1901)
= *Germodactylus cristatus* Wellnhofer, 1980 [*sic*]

Family: CTENOCHASMATIDAE
Nopcsa, 1928

Census: 3 genera, 5 species

Genus: *Ctenochasma* von Meyer, 1852
C. roemeri von Meyer, 1852 (Type)
C. gracile Oppel, 1862
C. porocristatum de Buisonje, 1981
= *Ctenochasma porocristata* de Buisonje, 1981*

NOTE: Genera ending in *-chasma* are neuter, not feminine, and so take neuter adjectival specific names. Hence the spelling change to *C. porocristatum*.

Genus: *Gnathosaurus* von Meyer, 1834
G. subulatus von Meyer, 1834 (Type)
= *Crocodilus multidens* Münster, 1832
= *Gnathosaurus multidens* (Münster, 1832)
= *Gavialis priscus* Quenstedt, 1855 [*nomen dubium*]

Genus: *Huanhepterus* Dong, 1982
= *Huanhopterus* Dong, 1987 [*sic*]
H. quingyangensis Dong, 1982 (Type)
= *Huanhopterus qinyangensis* Dong, 1987 [*sic*]

Family: PTERODAUSTRIDAE
Bonaparte, 1971

Census: 1 genus, 1 species

= Pterodaustriidae Bonaparte, 1971*

Genus: *Pterodaustro* Bonaparte, 1969
P. guinazui Bonaparte, 1969 (Type)
= *Pterodaustro guiñazui* Bonaparte, 1969*

Family: DSUNGARIPTERIDAE
Young, 1964

Census: 4 genera, 5 species (1 doubtful)

Genus: *Dsungaripterus* Young, 1964
D. weii Young, 1964 (Type)
?*D. brancai* (Reck, 1931) [*nomen dubium*]
= *Pterodactylus brancai* Reck, 1931 [*nomen dubium*]

Genus: *Noripterus* Young, 1973
N. complicidens Young, 1973 (Type)

Genus: *Phobetor* Bakhurina, 1986
= *Fabeter* Ivakhnenko & Korabelnikov, 1987 [*sic*]
P. parvus (Bakhurina, 1982) (Type)
= *Dsungaripterus parvus* Bakhurina, 1982
= *Fabeter parvus* Ivakhnenko & Korabelnikov, 1987 [*sic*]

NOTE: The above genus was named without formal description in a review article (*Priroda 1986*(7): 27–36), but it is treated as valid by Wellnhofer (1991). A recently published anonymous museum pamphlet on Mongolian fossils (in Russian) illustrates a *Phobetor* skull and refers it to the Ornithocheiridae.

Genus: *Puntanipterus* Bonaparte & Sanchez, 1974
= *Puntaniptero* [Anonymous] 1976 [*sic*]
= *Putanipterus* Carroll, 1987 [*sic*]
P. globosus Bonaparte & Sanchez, 1974 (Type)

Family: ORNITHOCHEIRIDAE (Seeley, 1870)

Census: 5 genera, 25 species (8 doubtful)

= Ornithocheirae Seeley, 1870
= Ornithocheirinae Plieninger, 1907

Genus: *Araripesaurus* Price, 1971
A. castilhoi Price, 1971 (Type)

Genus: *Brasileodactylus* Kellner, 1984
B. araripensis Kellner, 1984 (Type)
= *Brasileodactylus araripendis* Kellner, 1989 [*sic*]

Genus: *Cearadactylus* Leonardi & Borgomanero, 1983
C. atrox Leonardi & Borgomanero, 1983 (Type)
NOTE: This genus may require placement in its own family (P. Wellnhofer, pers. comm. at 1989 SVP annual meeting).

Genus: *Ornithocheirus* Seeley, 1869
= *Cimoliornis* Owen, 1846
= *Cretornis* Fritsch, 1880 [*nomen dubium*]
= *Lithosteornis* Gervais, 1844 [*nomen nudum*]
= *Lonchodectes* Hooley, 1914
= *Ornithochirus* Lydekker, 1888/Cope, 1872 [*sic*]
= *Osteornis* Gervais, 1844 [*nomen nudum*]
= *Palaeornis* Mantell, 1835/Vigors, 1825
= *Ptenodactylus* Seeley, 1869
?*O. clifti* (Mantell, 1835)
= *Palaeornis clifti* Mantell, 1835
= *Ornithochirus clifti* (Mantell, 1835)
= *Pterodactylus clifti* (Mantell, 1835)
= *Osteornis ardeaceus* Gervais, 1844 [*nomen nudum*]
= *Lithosteornis ardeaceus* (Gervais, 1844) [*nomen nudum*]
= *Pterodactylus silvestris* Owen, 1845
= *Pterodactylus sylvestris* Plieninger, 1929 [*sic*]
?*O. diomedeus* (Owen, 1844)
= *Osteornis diomedeus* Owen, 1844
= *Cimoliornis diomedius* Owen, 1846
= *Ornithocheirus diomedius* (Owen, 1846)
= *Ornithochirus diomedius* (Owen, 1846)
= *Pterodactylus diomedius* (Owen, 1846)
= *Pterodactylus conirostris* Owen, 1850 [*nomen dubium*]
O. giganteus (Bowerbank, 1846) [*nomen dubium*]
= *Pterodactylus giganteus* Bowerbank, 1846 *non* Oken, 1819 [*nomen dubium*]
= *Lonchodectes giganteus* (Bowerbank, 1846) [*nomen dubium*]
= *Ornithochirus giganteus* (Bowerbank, 1846) [*nomen dubium*]
= *Ornithodesmus giganteus* (Bowerbank, 1846) [*nomen dubium*]
O. compressirostris (Owen, 1851) (Type)
= *Pterodactylus compressirostris* Owen, 1851
= *Lonchodectes compressirostris* (Owen, 1851)
= *Ornithocheirus compressiformis* Gaal, 1926 [*sic*]
O. cuvieri (Bowerbank, 1851)
= *Pterodactylus cuvieri* Bowerbank, 1851
= *Coloborhynchus cuvieri* (Bowerbank, 1851)
= *Ornithochirus cuvieri* (Bowerbank, 1851)
= *Ptenodactylus cuvieri* (Bowerbank, 1851)
?*O. fittoni* (Owen, 1859)
= *Pterodactylus fittoni* Owen, 1859
= *Ornithochirus fittoni* (Owen, 1859)
= *Ptenodactylus fittoni* (Owen, 1859)
?*O. sedgwicki* (Owen, 1859)
= *Pterodactylus sedgwicki* Owen, 1859
= *Coloborhynchus sedgwicki* (Owen, 1859)
= *Ornithochirus sedgwicki* (Owen, 1859)
= *Ptenodactylus sedgwicki* (Owen, 1859)
O. machaerorhynchus (Seeley, 1864) [*nomen dubium*]
= *Pterodactylus machaerorhynchus* Seeley, 1864 [*nomen dubium*]
= *Lonchodectes machaerorhynchus* (Seeley, 1864) [*nomen dubium*]
= *Ptenodactylus machaerorhynchus* (Seeley, 1864) [*nomen dubium*]
= *Ornithocheirus machaeorhynchus* Wellnhofer, 1978 [*sic*]
O. oweni (Seeley, 1864) [*nomen nudum*]
= *Pterodactylus oweni* Seeley, 1864 [*nomen nudum*]
= *Lonchodectes oweni* (Seeley, 1864) [*nomen nudum*]

= *Ptenodactylus oweni* (Seeley, 1864) [*nomen nudum*]
O. brachyrhinus (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus brachyrhinus* Seeley, 1869 [*nomen nudum*]
O. colorhinus (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus colorhinus* Seeley, 1869 [*nomen nudum*]
O. dentatus (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus dentatus* Seeley, 1869 [*nomen nudum*]
O. enchorhynchus (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus enchorhynchus* Seeley, 1869 [*nomen nudum*]
O. macrorhinus (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus macrorhinus* Seeley, 1869 [*nomen nudum*]
O. microdon (Seeley, 1869) [*nomen dubium*]
= *Ptenodactylus microdon* Seeley, 1869 [*nomen dubium*]
= *Lonchodectes microdon* (Seeley, 1869) [*nomen dubium*]
O. nasutus (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus nasutus* Seeley, 1869 [*nomen nudum*]
O. oxyrhinus (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus oxyrhinus* Seeley, 1869 [*nomen nudum*]
= *Pterodactylus oxyrhinus* (Seeley, 1869) [*nomen nudum*]
O. polyodon (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus polyodon* Seeley, 1869 [*nomen nudum*]
O. scaphorhynchus (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus scaphorhynchus* Seeley, 1869 [*nomen nudum*]
= *Lonchodectes scaphorhynchus* (Seeley, 1869) [*nomen nudum*]
O. tenuirostris (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus tenuirostris* Seeley, 1869 [*nomen nudum*]
= *Lonchodectes tenuirostris* (Seeley, 1869) [*nomen nudum*]
?*O. curtus* (Seeley, 1870) [*nomen dubium*]
= *Pterodactylus curtus* Seeley, 1870 [*nomen dubium*]
= *Ornithochirus curtus* (Seeley, 1870) [*nomen dubium*]
O. huxleyi Seeley, 1870 [*nomen dubium*]
O. xyphorhynchus Seeley, 1870 [*nomen dubium*]
= *Ornithochirus xyphorhynchus* (Seeley, 1870) [*nomen dubium*]
O. daviesii (Owen, 1874)
= *Pterodactylus daviesii* Owen, 1874
= *Lonchodectes daviesii* (Owen, 1874)
= *Ornithochirus daviesii* (Owen, 1874)
= *Ornithocheirus denticulatus* Seeley, 1870 [*nomen dubium*]
= *Ornithochirus denticulatus* (Seeley, 1870) [*nomen dubium*]
O. sagittirostris (Owen, 1874) [*nomen dubium*]
= *Pterodactylus sagittirostris* Owen, 1874 [*nomen dubium*]
= *Lonchodectes sagittirostris* (Owen, 1874) [*nomen dubium*]
= *Ornithodesmus sagittirostris* (Owen, 1874) [*nomen dubium*]
O. hlavatschi (Fritsch, 1880) [*nomen dubium*]
= *Cretornis hlavatschi* Fritsch, 1880 [*nomen dubium*]
= *Ornithochirus hlavatschi* (Fritsch, 1880) [*nomen dubium*]
= *Ornithocheirus hlavaci* Fritsch, 1905 [*sic*]
O. bunzeli Seeley, 1881
?*O. hilsensis* Koken, 1883 [*nomen dubium*]
O. wiedenrothi Wild, 1990

Genus: *Santanadactylus* de Buisonje, 1980
= *Sandactylus* Bowler, 1989 [*sic*]
S. brasilensis de Buisonje, 1980 (Type)
S. araripensis Wellnhofer, 1985
S. pricei Wellhofer, 1985
?*S. spixi* Wellhofer, 1985

NOTE: Bennett, 1989 considers *Santanadactylus araripensis* and *S. pricei* to be pteranodontids and *S. spixi* to be a dzungaripterid. Bennett also notes that the type species may be based on a composite specimen: part pteranodontid, part something else.

Family: CRIORHYNCHIDAE Hooley, 1914

Census: 3 genera, 5 species (1 doubtful)

Genus: *Araripedactylus* Wellnhofer, 1977
A. dehmi Wellnhofer, 1977 (Type)

Genus: *Criorhynchus* Owen, 1874
= *Amblydectes* Hooley, 1914 [*nomen nudum*]
= *Coloborhynchus* Owen, 1874
C. simus (Owen, 1861) (Type)
= *Pterodactylus simus* Owen, 1861
= *Ornithocheirus simus* (Owen, 1861)
= *Pterodactylus woodwardi* Owen, 1861
= *Criorhynchus woodwardi* (Owen, 1861)
= *Ornithocheirus woodwardi* (Owen, 1861)
= *Ptenodactylus woodwardi* (Owen, 1861)
= *Ornithocheirus carteri* Seeley, 1869 [*nomen nudum*]
= *Criorhynchus carteri* (Seeley, 1869) [*nomen nudum*]
= *Ornithocheirus platyrhinus* Seeley, 1869 [*nomen nudum*]
= *Criorhynchus platyrhinus* (Seeley, 1869) [*nomen nudum*]
= *Coloborhynchus clavirostris* Owen, 1874
= *Criorhynchus clavirostris* (Owen, 1874)
= *Ornithocheirus clavirostris* (Owen, 1874)
C. capito (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus capito* Seeley, 1869 [*nomen nudum*]
= *Ornithocheirus capito* (Seeley, 1869) [*nomen nudum*]
C. crassidens (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus crassidens* Seeley, 1869 [*nomen nudum*]
= *Amblydectes crassidens* (Seeley, 1869) [*nomen nudum*]
= *Ornithocheirus crassidens* (Seeley, 1869) [*nomen nudum*]
C. eurygnathus (Seeley, 1869) [*nomen nudum*]
= *Pterodactylus eurygnathus* Seeley, 1869 [*nomen nudum*]
= *Amblydectes eurygnathus* (Seeley, 1869) [*nomen nudum*]
= *Ornithocheirus eurygnathus* (Seeley, 1869) [*nomen nudum*]
C. platystomus (Seeley, 1869) [*nomen nudum*]
= *Ptenodactylus platystomus* Seeley, 1869 [*nomen nudum*]
= *Amblydectes platystomus* (Seeley, 1869) [*nomen nudum*]
= *Ornithocheirus platystomus* (Seeley, 1869) [*nomen nudum*]
= *Ornithochirus platystomus* (Seeley, 1869) [*nomen nudum*]
C. reedi (Seeley, 1870) [*nomen dubium*]
= *Ornithocheirus reedi* Seeley, 1870 [*nomen dubium*]

Genus: *Tropeognathus* Wellnhofer, 1987
T. mesembrinus Wellnhofer, 1987 (Type)
= *Anhanguera mesembrinus* (Wellnhofer, 1987)
T. robustus Wellnhofer, 1987
= *Anhanguera robustus* (Wellnhofer, 1987)

NOTE: P. Wellnhofer (pers. comm. at 1989 SVP annual meeting) regards this genus as a junior synonym of *Araripedactylus*. Kellner & Campos, 1989 regard it as a junior synonym of *Anhanguera*. It is best to keep this genus separate until more Santana pterosaur material is described.

Family: ANHANGUERIDAE Campos & Kellner, 1985

Census: 1 genus, 2 species

Genus: *Anhanguera* Campos & Kellner, 1985
= *Anghanguera* Wellnhofer, 1988 [*sic*]
= *Anhanguera* Campos *vide* Leonardi, 1984 [*nomen nudum*]
A. blittersdorffi Campos & Kellner, 1985 (Type)
A. santanae (Wellnhofer, 1985)
= *Araripesaurus santanae* Wellnhofer, 1985

Family: TAPEJARIDAE Kellner, 1989

Census: 2 genera, 2 species

Genus: *Tapejara* Kellner, 1989
T. wellnhoferi Kellner, 1989 (Type)

Genus: *Tupuxuara* Kellner & Campos, 1988
T. longicristatus Kellner & Campos, 1988 (Type)

NOTE: A. Kellner (pers. comm. at 1989 SVP annual meeting) now believes this genus may be an azhdarchid, based on comparison with undescribed *Quetzalcoatlus* skull material at the Balcones Research Laboratory in Austin, Texas.

Family: NYCTOSAURIDAE Bennett, 1989

Census: 1 genus, 3 species

= Nyctosaurinae Plieninger, 1907

Genus: *Nyctosaurus* Marsh, 1876
= *Nyctodactylus* Marsh, 1881
= *Nytosaurus* Molnar, 1980 [*sic*]
N. gracilis Marsh, 1876 (Type)
= *Nyctodactylus gracilis* (Marsh, 1876)
= *Pteranodon gracilis* (Marsh, 1876)
= *Pteranodon (Nyctosaurus) gracilis* (Marsh, 1876)
= *Nyctosaurus leptodactylus* Williston, 1903
N. lamegoi Price, 1953
= *Pteranodon (Nyctosaurus) lamegoi* (Price, 1953)
N. bonneri (Miller, 1972)
= *Pteranodon (Nyctosaurus) bonneri* Miller, 1972

NOTE: See note for *Pteranodon* below.

Family: PTERANODONTIDAE Marsh, 1876

Census: 5 genera (2 doubtful), 11 species (3 doubtful)

= Ornithostomatidae Williston, 1893
= Pteranodontes Gadow, 1901
= Pteranodontia Marsh, 1876
= Pteranodontinae Kuhn, 1967

Genus: *Apatomerus* Williston, 1903 [*nomen dubium*]
A. mirus Williston, 1903 (Type)

NOTE: *Apatomerus* is probably not pterosaurian and may be a turtle (C. Bennett, pers. comm.; R. E. Molnar, pers. comm.).

Genus: *Bogoliubovia* Nessov & Borkin, 1989
B. orientalis (Bogoliubov, 1914) (Type)
= *Ornithostoma orientale* Bogoliubov, 1914
= *Ornithostoma orientalis* Bogoliubov, 1914*
= *Pteranodon orientalis* (Bogoliubov, 1914)

NOTE: Genera ending in *-stoma* are neuter, not feminine, and so take neuter adjectival specific names. Hence the spelling change to *Ornithostoma orientale*.

Genus: *Geosternbergia* Miller, 1978 [*nomen novum ex subgenero*]
= *Sternbergia* Miller, 1972/Jordan, 1925 (as a subgenus of *Pteranodon*)
G. sternbergi (Harksen, 1966) n. comb. (Type)
= *Pteranodon sternbergi* Harksen, 1966
= *Pteranodon (Sternbergia) sternbergi* (Harksen, 1966)
= *Pteranodon (Geosternbergia) sternbergi* (Harksen, 1966)
G. walkeri (Miller, 1972) n. comb.
= *Pteranodon (Sternbergia) walkeri* Miller, 1972
= *Pteranodon walkeri* (Miller, 1972)
= *Pteranodon (Geosternbergia) walkeri* (Miller, 1972)

NOTE: *Geosternbergia walkeri* may be a growth stage of *G. sternbergi*. See also note for *Pteranodon* below.

Genus: *Ornithostoma* Seeley, 1870 [*nomen dubium*]
O. seeleyi Lydekker, 1904 (Type)

Paragenus: *Pteranodon* Marsh, 1876
= *Ornithochirus* Cope, 1872
= *Ornithostoma* Williston, 1893 *non* Seeley, 1870
P. ingens (Marsh, 1872)
= *Pterodactylus ingens* Marsh, 1872
= *Ornithostoma ingens* (Marsh, 1872)
= *Pteranodon (Longicepia) ingens* (Marsh, 1872)
= *Pteranodon (Pteranodon) ingens* (Marsh, 1872)
= *Ornithochirus umbrosus* Cope, 1872

= *Pteranodon umbrosus* (Cope, 1872)
= *Pterodactylus umbrosus* (Cope, 1872)
= *Pteranodon (Longicepia) marshi* Miller, 1972
= *Pteranodon (Pteranodon) marshi* (Miller, 1972)
= *Pteranodon marshi* (Miller, 1972)
P. occidentalis (Marsh, 1872)
= *Pterodactylus occidentalis* Marsh, 1872
= *Pteranodon (Occidentalia) occidentalis* (Marsh, 1872)
= *Pterodactylus oweni* Marsh, 1871 *non* Seeley, 1864
= *Ornithochirus harpyia* Cope, 1872
= *Ornithocheirus harpyia* (Cope, 1872)
= *Pteranodon (Occidentalia) eatoni* Miller, 1972
= *Pteranodon eatoni* (Miller, 1972)
= *Pteranodon oxydactylus* McGinnis, 1982 [*sic*]
P. velox (Marsh, 1872)
= *Pterodactylus velox* Marsh, 1872
= *Pteranodon comptus* Marsh, 1876
P. longiceps Marsh, 1876 (Type)
= *Pteranodon (Longicepia) longiceps* (Marsh, 1876)
= *Pteranodon (Pteranodon) longiceps* (Marsh, 1876)

NOTE: The above species may be a junior synonym of *Pteranodon ingens*, which would make *P. ingens* the type species of the genus.

P. nanus Marsh, 1881
= *Nyctosaurus nanus* (Marsh, 1881)
?*P. oregonensis* Gilmore, 1928

NOTE: This paragenus is organized according to Wellnhofer (1978) and Schoch (1984). Miller (1972) subdivided the genus into four subgenera: *Longicepia* Miller, 1972 (type species *Pteranodon longiceps* Marsh, 1876), *Occidentalia* Miller, 1972 (type species *Pteranodon (Occidentalia) eatoni* Miller, 1972, based on a specimen originally referred to *Pteranodon occidentalis* Marsh, 1872 in Marsh, 1876), *Sternbergia* Miller, 1972 (type species *Pteranodon sternbergi* Harksen, 1966), and *Nyctosaurus* Marsh, 1876 (type species *Nyctosaurus gracilis* Marsh, 1876). However, *Longicepia* is a junior synonym of *Pteranodon* itself, used as a subgenus, because it contains the type species; *Nyctosaurus* is a genus distinct from *Pteranodon* (Schoch, 1984) that belongs in its own family (Bennett, 1989); *Occidentalia* is simply another junior synonym of *Pteranodon* (Wellnhofer, 1978); and *Sternbergia* is preoccupied, necessitating a name change to *Geosternbergia* (Miller, 1978). Furthermore, the subgenus *Geosternbergia* is here separated from *Pteranodon*, because the shape of the cranial crest of the type skull differs dramatically from those of other specimens referred to *Pteranodon*, the beak of the type skull is relatively longer than those of referred *Pteranodon* specimens, and the beak is curved upward instead of being straight. *Geosternbergia* is, however, almost certainly descended from a species of *Pteranodon*, which makes the latter a paragenus.

Padian (1984) and Bennett (1989) do not consider *Pteranodon oregonensis* to be a pteranodontid; Murry, Winkler & Jacobs (1991) refer the species to the Azdarchidae.

Genus: [To be described from Colorado; may be either a new genus or a new species of *Pteranodon*; C. Bennett, R. Bakker, D. Weishampel, pers. comms.]

Family: AZHDARCHIDAE Padian, 1986

Census: 4 genera (1 doubtful),
4 species (1 doubtful)

= Azhdarchinae Nessov, January 1984
= Titanopterygiidae Padian, December 1984

Genus: *Arambourgiania* Nessov & Borkin, 1989
= *Titanopteryx* Arambourg, 1959/Preoccupied
A. philadelphiae (Arambourg, 1959) (Type)
= *Titanopteryx philadelphiae* Arambourg, 1959
[New species to be described; Baird, 1986]

Genus: *Azhdarcho* Nessov, 1984
= *Azhdarcho* Nessov, 1982 [*nomen nudum*]
A. lancicollis Nessov, 1984 (Type)
= *Azhdarcho imparidens* Nessov, 1982 [*nomen nudum*]

Genus: *Doratorhynchus* Seeley, 1875 [*nomen dubium*]
  D. validus (Owen, 1870) (Type)
    = *Pterodactylus validus* Owen, 1870 [*nomen dubium*]
    = *Cycnorhamphus validus* (Owen, 1870) [*nomen dubium*]
    = *Ornithocheirus validus* (Owen, 1870) [*nomen dubium*]
    = *Ornithochirus validus* (Owen, 1870) [*nomen dubium*]
    = *Doratorhynchus validum* Owen, 1891 [*sic*]

Genus: *Quetzalcoatlus* Lawson, 1975 [*nomen nudum*]
  Q. northropi Lawson, 1975 (Type)

NOTE: Despite numerous popular accounts of this "largest known flying animal," this genus remains formally undescribed and is technically a *nomen nudum*. In view of their exceptional nature and popular exposure, this genus and its type species are included in this family's census. More than one species may be represented in the referred material from Texas.

PTERODACTYLOIDIA *incertae sedis*

Census: 3 doubtful genera, 4 species (3 doubtful)

Genus: *Laopteryx* Marsh, 1881 [*nomen dubium*]
  L. prisca Marsh, 1881 (Type)
    = *Laopteryx priscus* Marsh, 1881 [*nomen dubium*]*

NOTE: The above genus was originally described as avian, but it is "almost certainly a pterosaur" (Brodkorb, 1978). This assignment has been confirmed by Ostrom, 1986.

Genus: *Mesadactylus* Jensen & Padian, 1989 [*nomen dubium*]
  M. ornithosphyos Jensen & Padian, 1989 (Type)

Genus: *Pricesaurus* Martins Neto, 1986 [*nomen dubium*]
  P. megalodon Martins Neto, 1986 (Type)

Genus: [To be described by S. Howse & Andrew Milner]
  [Type species to be redescribed]
    = *Ornithodesmus latidens* Seeley, 1901

NOTE: The genus *Ornithodesmus*, formerly classified as a pterosaur, is to be redescribed as a theropod dinosaur (*SVP Bulletin* #145: 43; Wellnhofer, 1991), but the referred species *O. latidens* represents a new family of "duck-billed" pterosaurs. Because this species has a warped deltopectoral crest on the humerus, however, Bennett (1989) considers it to be related to the Pteranodontidae.

Dinosaur Phylogeny

ON AUGUST 2, 1841, Sir Richard Owen, in an address to the British Association for the Advancement of Science (11th Meeting, Plymouth), created the name Dinosauria to denote "a distinct tribe or sub-order of Saurian Reptiles." In the lengthy published version of this report (Owen, 1842), the Dinosauria comprised just three genera of large fossil reptiles, all British: *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*.

Forty-six years later, the number of genera referable to the Dinosauria had increased by more than an order of magnitude. Dinosaurian morphology had become much better known as a result of discoveries in Europe and North America, and it was becoming clear that a single reptilian order could not accommodate the entire range of dinosaurian diversity. Thus Harry Govier Seeley, in an address to the same Association (57th Meeting, Manchester, 1887), split the Dinosauria into two orders: Saurischia and Ornithischia (Seeley, 1888). Within a few decades, Seeley's dinosaur taxonomy superseded classifications proposed by Cope (1870), Marsh (1895), Nopcsa (1915), and others, and it has survived essentially unchanged to the present. The dinosaurs became widely recognized as a diphyletic group, because the orders Saurischia and Ornithischia were thought to have descended independently from the order Thecodontia.

Now, more than a century after Seeley's work was published, the number of dinosaur genera has again grown by roughly an order of magnitude. Seeley's classification is still used in most works, but as I noted earlier, it has become clear to me that dinosaurs were too morphologically diverse to be adequately classified in only two orders. A revised classification of the dinosaurs that reflects something of the accumulated knowledge of the past hundred years is long overdue.

Thus, as part of my reorganization of the archosaurs, I have made a number of changes to the traditional classification of the dinosaurs. Many of these are cosmetic, in the sense that the organization of the groups is not changed, only their hierarchic levels within the Linnaean taxonomy are. Other changes are more fundamental, however, and in some cases proposed changes may at first sight seem to conflict with the results of modern systematic studies. It is the purpose of this section to justify my changes and to convince readers that the classification presented here is at least broadly correct—and perhaps more useful than others previously proposed.

DEFINING DINOSAURS

Dinosaurs are the best-known and most diverse of the archosaurs. Animals commonly called dinosaurs first appear in the fossil record early in the Late Triassic (Carnian). Even at this stage of dinosaur diversification, the three major superorders – Theropodomorpha, Sauropodomorpha, and Ornithischia – are readily distinguishable (Sues, 1990; Galton, 1990; Weishampel & Witmer, 1990). Recent cladistic analyses of the dinosaurs, summarized by Benton (1990a), have indicated that the dinosaurs plus the birds comprise a genuine clade within the clade Archosauria. This means not only that all three dinosaur lineages were descended from a common ancestor, but also that *everyone would agree that this common ancestor was itself a dinosaur.* This requirement of dinosaur monophyly is not often emphasized in dinosaur taxonomic analyses.

Dinosaur monophyly is a matter of definition. There is no doubt that within the clade Archosauria a smallest clade exists that comprises all the animals commonly called dinosaurs. By coincidence, this clade is congruent to the smallest clade containing Owen's original three genera and the genus *Cetiosaurus*. Owen described *Cetiosaurus*—though not as a dinosaur—the same year he proposed the term Dinosauria. So there are good historical as well as phyletic reasons for naming this particular clade Dinosauria. Since, as noted earlier, this clade also includes the birds, I would define Dinosauria as a parataxon: the clade Dinosauria minus the clade Aves.

For reasons that follow, however, I believe that the parataxon Dinosauria includes animals that most dinosaurologists would hesitate to call dinosaurs: small, bipedal runners such as *Lagosuchus*; arboreal climbers and gliders such as *Megalancosaurus* and *Longisquama*; birdlike animals such as *Protoavis* and *Archaeopteryx*; and a wide range of other small, as-yet-undiscovered forms with features transitional among the dinosaurian and avian lineages. There is also some chance that the clade Dinosauria includes the clade Pterosauria; if so, I would not hesitate to remove it, too, from the parataxon Dinosauria. It seems to me that we are left with two choices: either we call those unusual archosaurs dinosaurs, or we agree that the dinosaurs were polyphyletic (Charig, 1982).

In this work, I use the term "dinosaur" informally for any animal in the parataxon Dinosauria as just described. I do not intend to formalize the parataxon, however, because so many basal dinosaurs remain undiscovered that the detailed relationships among the three major dinosaurian subclades cannot be elucidated. In a cladogram, the dinosaur node would appear as an unresolved trichotomy (at least).

ORIGIN OF THE ERECT STANCE

Most workers (*e.g.*, Charig, 1972, 1982; Bakker, 1986; Paul, 1988b; Benton, 1990a; and others) regard the trend toward an erect stance as a key feature of dinosaurian evolution. Originating as sprawling proterosuchian archosaurs with primitive mesotarsal ankles, the dinosaurs evolved into fully erect animals with advanced mesotarsal (AM) ankles. This adaptation made dinosaurs efficient foragers and runners capable of outrunning predators with less-advanced locomotor ability (such as therapsids) and overtaking less-advanced prey. More than anything else, this is considered the reason for the success dinosaurs enjoyed throughout the Jurassic and Cretaceous periods.

Charig (1972) gave a very clear exposition of the evolution of erect stance in thecodontians. The first stage is represented by the sprawling proterosuchians, with a primitive mesotarsal ankle. The second stage is represented by the semi-erect erythrosuchids and other thecodontians with CN and CR ankles. Dinosaurs and pterosaurs were the end products of this series, equipped with a fully erect stance and AM ankles. The major problem with this scenario, as Charig himself noted (1972: 152), is the difficulty of deriving the AM ankle from a CN/CR ankle. He considered this obstacle not insurmountable, but he also suggested that the dinosaurian ankle may have derived directly from the primitive mesotarsal ankle via a small, light "pseudosuchian, as yet unknown."

In the scenario proposed here, Charig's unknown pseudosuchian is, naturally, a basitheropod theropodomorph. A small, lightly built form would not require the evolution of a complicated, weight-bearing CN/CR tarsus but could evolve an erect gait and an AM ankle directly from the primitively mesotarsal hind limb possessed by the earliest archosaurs.

Exactly how erect stance and the associated AM ankle evolved among the dinosaurs remains a matter of debate. Chatterjee (1985), for example, has argued for a diphyletic origin of the AM ankle. Gauthier (1986a) and Benton (1990a), on the other hand, supported the idea that the AM ankle developed from the CR ankle of the ornithosuchians by including *Ornithosuchus* close to the dinosaurian branch of their cladograms. Bakker (1986: 450–451, 456), in his own archosaur phylogeny, suggested that the ornithosuchians are best grouped with the CN-ankled thecodontians, away from the pterosaurian and dinosaurian lineages. Although Bakker did not disclose all of his reasons for thinking so, he did cite several ornithosuchid apomorphies that appear in no other archosaur lineage. The AM-ankled dinosaurs are depicted by Bakker as a lineage independent of the CN/CR-ankled thecodontians.

The first question that needs to be addressed is, Why did the semi-erect and fully erect stances evolve at all? Most extant reptiles, even large ones—those that have legs and use them, that is—walk in a sprawling stance and never evolved an erect stance. Crocodilians are a special case: As noted earlier, they did evolve fully erect forms but later adopted a riparian lifestyle and reverted to a semi-erect stance. They retain only vestiges of their former locomotor ability.

I believe the answer to this question lies in the development of the elevated aerobic capacity afforded by a four-chambered heart (Regal & Gans, 1980). The non-mammalian four-chambered heart is thought to be a synapomorphy uniting extant crocodilians and birds, and if so, it must have arisen in a common ancestor of both groups. Only one group is available in which to classify this ancestor, assuming it was an archosaur of some kind and not an earlier predecessor, and that is the Proterosuchia.

Extant non-archosaurian reptiles possess three-chambered hearts, which are less efficient at blood oxygenation. It is likely that this is the principal reason that most extant reptiles engage in sit-and-wait behavioral patterns. With the evolution of the four-chambered heart, archosaurs would have possessed the metabolic equipment for sustained foraging activity and escape from pursuit by therapsid predators. (As mammalian ancestors, therapsids were undoubtedly equipped with their own version of a four-chambered heart by then.) The development of the four-chambered heart probably slightly preceded the improvements in stance among the archosaurs, but it is equally possible that the circulatory and locomotor improvements evolved in parallel.

In this work, I take the position that the CN and CR ankles evolved as a result of the increased size and weight that characterized the more advanced thecodontians. This kind of modification of the ankle, in which the calcaneum acquired a large tuber for greater leverage, would have been unnecessary in a semi-erect animal that remained small and light. The pes would have remained plantigrade as the animal walked, and muscular power alone would have been sufficient to maintain its semi-erect posture; the structure of the ankle was simply not particularly important. (At this point, I must ask the reader to take this on faith, because not a single fully terrestrial proterosuchian has yet been identified in the fossil record.)

Reptiles with three-chambered hearts have grown quite large (*e.g.*, *Varanus komodoensis*, tortoises) without having evolved the kinds of weight-related structural modifications to their ankles seen in the semi-erect and fully erect archosaurs. Without the improved aerobic metabolism afforded by a four-chambered heart, however, reptiles with three-chambered hearts could only retain the sprawling posture and sit-and-wait predation strategy of their smaller relatives. The kinds of structural modifications to their limbs required by an improved stance were unnecessary. I suggest that the semi- and fully erect stance in amniotes is well correlated with the presence of a four-chambered heart and an elevated aerobic capacity, rather than the more complicated physiologies associated with endothermy suggested by Ostrom (1980) and Bakker (1980).

The absence of proterosuchians and early theropodomorphs, sauropodomrphs, and ornithischians from the fossil record makes it difficult to track the evolution of the AM ankle. It must be remembered that this occurred in small, lightweight, fully terrestrial, plantigrade proterosuchians in which the tarsal structure was subordinate to the orientation of the femur, epipodials, and pes. Only among such animals would the ankle have retained so much of its original mesotarsal condition. Such animals, unfortunately, would also have been among the least likely to be preserved in the fossil record.

The two epipodial bones in the limbs of the sprawling proterosuchians were surely well adapted to transmitting the horizontal motion of the propodial bones to the plantigrade manus and pes. In particular, the long axes of proximal and distal ends of the tibia were roughly parallel, since in a relaxed position the plantigrade pes extended roughly parallel to the horizontal femur, outward from the body. As the femur straightened and became more vertical, the pes was required to rotate less and less. The long axis of the proximal end of the tibia would have remained aligned in the direction tangential to the limb's motion, but the long axis of its distal end would have become progressively more perpendicular to the direction of the animal's motion. This gave the tibia the torsion characteristic of dinosaurs and birds. The "tibia-twist" was not nearly as evident in pterosaurs as in dinosaurs, because the pterosaur lineage diverged from the dinosaur lineage before the fully erect stance evolved.

Paralleling the tibial change, the femoral head, which inserted into the acetabulum horizontally and loosely in sprawling forms, developed a neck that allowed the femur to be held more firmly at an angle from the horizontal. This eventually became a right angle in fully erect forms; as might be expected, the angle remained intermediate in pterosaurs. As the tibia assumed the primary weight-bearing function of the lower hind limb, the fibula gradually became reduced. The astragalus eventually developed an ascending process and became firmly affixed to the tibia, while the calcaneum shrank along with the fibula. The mesotarsal hinge between the proximal and distal tarsals was thereby converted from a joint that allowed the pes to flex laterally to one that allowed it to flex parallel to the direction of motion.

It should be noted that the changes required for a sprawling, primitive-mesotarsal hind limb to become a fully erect AM hind limb are primarily geometric, and could certainly have occurred independently in more than one lineage. Possession of a fully erect AM hind limb is thus not necessarily a synapomorphy uniting the three dinosaurian lineages into a clade above the proterosuchian level.

Because of the missing fossil record, it is difficult to synchronize the changes in the hind limb with corresponding changes that may have been occurring in the forelimb. In proterosuchians, the hind limb was larger than the forelimb and the more important locomotor organ, so any changes to the forelimb need not have been as pronounced as they were in the hind limb. Once the hind limb had attained a certain degree of semi-erectitude, the forelimb would have been freer to assume non-locomotor functions, such as grasping and climbing, as in extant rats and squirrels. Even many lizards are excellent climbers, so it is not at all difficult to imagine the trees of the Late Permian and Early Triassic replete with many species of sprawling and semi-erect arboreal archosaurs, in addition to the ground-dwelling forms. Those archosaurs that attained a suitable degree of semi-erectitude should no longer be considered proterosuchians; they would have been the earliest members of the dinosaur and pterosaur clades.

EARLY DINOSAURS

It is not known when or in what order the three dinosaurian lineages diverged. Traditionally, the theropods and the sauropodomorphs have been grouped in a single order, Saurischia, which some cladistic studies (*cf.* Benton, 1990a) seem to indicate is monophyletic at a level above the Ornithischia. Benton lists 10 saurischian autapomorphies, but they are not contrasted with corresponding ornithischian autapomorphies. Considering the enormous differences between theropods and sauropodomorphs in their gross morphology and lifestyle, I agree with Charig, Attridge & Crompton (1965) and Charig (1982) that their lineages diverged well before the first prosauropods and theropods appear in the fossil record. Furthermore, if the scenario for theropod origins provided here is reasonably correct, then theropods and sauropodomorphs were even more distantly related than Charig, *et al.* previously imagined.

Sauropodomorphs were large, quadrupedal herbivores with small heads, elongate necks, and functionally pentadactyl manus and pedes (in prosauropods, pedal digit V is reduced or vestigial). Theropods were small to large bipedal carnivores with relatively large heads, short to moderately long necks, functionally tri- or even didactyl manus, and functionally tridactyl pedes. The anatomical feature that compelled earlier paleontologists to unite sauropodomorphs and theropods in the order Saurischia, namely, the "saurischian" pelvis, is actually a plesiomorphic character retained by both groups from nonarchosaurian diapsids. Derived structural differences between sauropodomorph and theropod pelves abound: Sauropodomorphs possessed broad, brachyiliac pelves with relatively short, massive, apronlike pubes and ischia. Theropods had narrow, dolichoiliac pelves with long pubes and slender ischia. Other significant anatomical differences can be found in the skulls, the limbs, the carpi and tarsi, and the vertebral columns. Placing such disparate animals in the same order strikes me as egregious as placing carnivores and elephants in the same order of mammals because they share a similar hip structure.

As mentioned in an earlier section, a generation of paleontologists at one time believed that some prosauropods possessed theropodlike teeth, because such teeth were found in association with prosauropod postcranial material. These are now recognized as the shed teeth of large archosaurian carnivores, such as rauisuchians, ornithosuchians, and herrerasaurians; but the belief that theropods and prosauropods were closely related has not entirely disappeared.

In this work, the order Saurischia is discarded, and its two subdivisions, the Sauropodomorpha and the Theropoda, are essentially raised in rank to superorders; the Theropoda is actually replaced by the parasuperorder Theropodomorpha, a new group that includes the Theropoda as an order and also includes the various ancestral arboreal and volant forms from which I assert the familiar theropods were descended. Among these are the earliest and most primitive known nonthecodontian archosaurs, namely, *Cosesaurus*, *Megalancosaurus*, and *Longisquama*, which clearly require at least one new archosaurian order and perhaps one new order each. I call their new paraorder Basitheropoda to emphasize its ancestral position at the base of the Theropodomorpha.

The second traditional dinosaurian order, the Ornithischia, is a well diagnosed monophyletic assemblage (*cf.* Benton, 1990a). Following the work of Cooper (1985), Sereno (1984, 1986), and others, cladistic analysis of the Ornithischia has become something of a classroom exercise. No less than five slightly different ornithischian cladograms are exhibited by Benton, (1990a: 27). There is little doubt that the ornithischian suborders belong together, but their interrelationships remain controversial.

Be this as it may, the relationship of the ornithischians to the other archosaurs is ambiguous, largely because of the irritatingly bad fossil record. Some workers (Bakker & Galton, 1974; Bonaparte, 1976; Paul, 1984; Cooper, 1985; Bakker, 1986) have considered the Ornithischia closely related to the Sauropodomorpha, via the Prosauropoda; others (*e.g.*, Gauthier, 1986a) consider the group less closely related to the theropods and sauropodomorphs than those two groups are related to each other (this is the traditional viewpoint, of course). The third possibility, that the Ornithischia and the Theropoda are more closely related to each other than either is to the Sauropodomorpha, has received surprisingly little currency. This is odd, because one of the most primitive ornithischians (though not the earliest), *Lesothosaurus*, is not terribly difficult to derive from a suitably primitive theropodomorph. A major obstacle to overcome is the transition from carnivory to herbivory, which is also one of the obstacles to a close relationship between the theropods and the sauropodomorphs. In keeping with the ambiguity of ornithischian relationships within the Archosauria, I have raised Seeley's order to a superorder, and raised its five recognized suborders to orders. These five ornithischian orders represent five quite distinctive *Baupläne* that definitely require ordinal status among the dinosaurs. As a superorder, the Ornithischia acquires the same taxonomic level as the other two dinosaurian groups.

The remainder of this section deals primarily with the phylogeny of the theropodomorphs; the phylogenies of the sauropodomorphs and the ornithischians are covered in subsequent sections. Theropodomorph phylogeny is intimately connected with the origin of bipedality, endothermy, and flight in birds, so the discussion will focus on those aspects first.

THE ORIGINS OF AVIAN FLIGHT

The proximate cause of the evolution of flight is predation. This is just as true for insects (the "ultimate" prey animals) as it is for bats, birds, and pterosaurs: No other plausible cause, such as the quests for food and living space, has the immediacy of a fast and successful escape from something that wants to eat you. On the other hand, because the metabolic cost of flight is high, a population of flying animals thrust into a regime from which predation pressure is absent, such as island isolation, will quickly evolve flightless forms, unless they are so highly adapted to flight that they cannot. The re-evolution of flightless forms in the absence of predation strongly supports the thesis that predation is the proximate cause of the evolution of flight.

Since most animals are subject to predation, there is considerable selection pressure to evolve the ability to fly. I cannot comment on the evolution of flight in insects, but among the extant vertebrates each of the major classes, from bony fish to mammals, exhibits gliding or flying forms. As might be expected, such volant creatures are small and lightweight; the evolution of flight by large, heavy vertebrates is almost certainly impossible. This is not to say that flying forms cannot attain large size, but only that they surely did not originate that way.

Two excellent books on the origin and evolution of flight have recently been published: *The Beginnings of Birds* (Hecht, Ostrom, Viohl & Wellnhofer, eds., 1985) and *The Origin of Birds and the Evolution of Flight* (Padian, ed., 1986). It is primarily from these two sources that I have arrived at my own opinions on the origins of flight in birds and pterosaurs. In addition, I was heavily influenced by Paul's (1984, 1988b) most curious and unconventional notion that some theropods were secondarily flightless (1988b: 200). Not only do I agree with him, but I think that he did not take the idea far enough. *All* the theropods (specifically, the order Theropoda as described herein) can be understood as having evolved from volant forms, although some underwent considerable evolution as flightless forms after diverging from the main avian lineage.

The discovery of *Archaeopteryx* in the 19th century brought the reptilian ancestry of birds into very sharp focus, and arguments that birds were closely related to dinosaurs were soon brought forth (Huxley, 1868, 1870). In his exhaustive work, *The Origin of Birds*, Heilmann (1927) examined all the known archosaur groups as potential avian ancestors and concluded that birds must have originated within the Pseudosuchia, that is, among bipedal thecodontians (as they were then understood). The discovery of the very birdlike theropod *Deinonychus* (Ostrom, 1970), as well as new specimens of *Archaeopteryx* (*cf.* Ostrom, 1985), returned the theropods to center stage as avian ancestors, where they have remained ever since. Given the strikingly close anatomical resemblance between *Archaeopteryx* and the deinonychosaur theropods (Ostrom, 1976), it is indeed difficult to imagine how any group other than the theropods could henceforth be considered for avian ancestry.

Any scenario of bird origins must address several questions. Among these are the origin and evolution of the fully erect bipedal stance, of feathers, of avian endothermy, and of avian aerodynamics (Charig, 1985). Two scenarios have addressed these questions with some success: the terrestrial, or "ground-up" scenario (Ostrom, 1976), and the arboreal, or "trees-down" scenario. Of these, the latter has been in existence in one form or another since the 19th century (*cf.* Bock, 1985). I have not found the terrestrial scenario at all convincing, simply because it seems physically unfeasible. All of the manifold adaptations for flight – pneumatic skeleton, bipedality, flight feathers, endothermy, wing-stroke articulation of the forelimb, and so forth – would have had to evolve for other reasons and converge miraculously in the single taxon that was the first flying bird. In addition, the creature itself would have had to fight gravity to become airborne. Modern birds can do this, because they have 150 million years of evolution behind them, but I just cannot see the *first* bird doing this. It would be as unlikely as seeing a diver burst up out of the swimming pool to land on the diving board.

So I do not question the theory that flight evolved "trees down." But the versions of this scenario that I have examined have left a few nagging questions that I hope my own version—or *Just So Story*—with its attendant phylogeny of the theropods and birds, will clarify. My procedure is to show how the major anatomical and biological features of birds could plausibly have arisen as preadaptations that, with the passage of time, impelled at least one lineage of small, sprawling archosaurs to evolve feathered flying forms.

Gauthier & Padian (1985: 192) summarized some of my questions about the arboreal theory as follows: "[P]roponents of the idea that avian flight began in trees face a difficult challenge: they must explain why so many features of modern birds, usually deemed to have evolved in the context of flight and arboreality, are present in non-flying coelurosaurian sister groups of birds; and they must grapple with the absence of any obvious arboreal adaptations in *Archaeopteryx*." I answer the first part of the challenge by asserting that the "coelurosaurian sister groups" were the *flightless descendants* of volant forms at various stages in the evolution of powered flight; this is why they possessed avian features. I answer the second part with the question, "How arboreal is 'arboreal'?" Do we mean that the proto-birds were permanent residents in an arboreal regime, feeding, mating, and nesting in the trees? Or do we mean only that the proto-birds habitually sought refuge from predators in the trees but otherwise carried out most of their activities on the ground? Arboreality is notoriously difficult to deduce from skeletal anatomy alone. Given only the skeletons of a chipmunk and a squirrel, could we identify which is the arboreal form? The best we can do with regard to *Archaeopteryx* is to note it has no known feature that would preclude an arboreal lifestyle.

Endothermy and Feathers

Despite an entire AAAS symposium held in 1978 (Thomas & Olson, eds., 1980), we still understand very little about the origins of endothermy and whether, for example, dinosaurs and other non-avian archosaurs were endothermic animals. This is because fossil evidence for endothermy is extremely equivocal. We do know, however, that extant birds are consummate endotherms, and we are fairly certain that the earliest archosaurs were ectotherms, because extant crocodilians—the closest living archosaurian relatives of birds—are.

It is also manifestly clear that a complicated physiological regime such as avian endothermy could not have arisen all at once. It is probably true, I think, that avian flight and avian endothermy evolved in parallel, and by no means particularly rapidly or straightforwardly. Intermediate stages in the evolution of birds must have exhibited intermediate kinds of endothermy, but their exact nature is at present utterly unavailable from the fossil record.

Most workers recognize that *powered* flight is impossible without a metabolism capable of sustained activity. It is difficult to imagine an ectothermic or poikilothermic flying animal grounded until the morning sun raises its body temperature to the point where it can take off. It is equally hard to envision how an unstable flier could keep itself aloft if it required long pauses between bursts of activity. All modern flying birds use their wings and tail feathers to adjust and change course instantaneously in response to the vagaries of air currents, the attacks of predators, and the escape tactics of prey. Anatomical features that indicate powered flight in a fossil vertebrate may therefore be taken as strong evidence for an aerobic metabolism and a fairly high level of endothermy.

Stable, *gliding* flight is another story, however. Since there are extant flying fish, gliding frogs, gliding lizards, and gliding snakes, and gliding reptiles are well known in the fossil record, it is clear that neither an aerobic metabolism nor endothermy are prerequisites for the evolution of gliding. A gliding ectotherm, even one with a two- or three-chambered heart, could while in flight recover from the burst of aerobic activity that launched it and prepare itself for its next burst of activity. If birds (and pterosaurs) originated as stable gliders, they need not have originated as full endotherms.

On the other hand, the Permian period, which immediately preceded the initial radiation of the archosaurs, was a time of climatic cooling and glaciation (Stanley, 1987: 90–107).

During the earlier Carboniferous period, the earth had experienced a more or less uniformly tropical climate favorable to the worldwide spread of ectotherms. The Permian cooling, during which the earth became partitioned into latitudinal climatic zones from equatorial/tropical to polar/arctic, severely challenged the ectotherms caught in the temperate and arctic regions. Most of those ectotherms responded by becoming extinct, but some groups survived by transfering their habitats equatorward, by evolving the ability to hibernate during the winter season, or by acquiring a rudimentary kind of endothermy. For example, the widespread radiation of therapsids during the Permian is partly accounted for by their assumed facultative endothermy (Stanley, 1987: 95–96).

I contend that some of the earliest archosaurs—proterosuchians, as described in this work—also acquired a rudimentary endothermy in response to the Late Permian cooling, independently of but perhaps later than the therapsids. Those first-stage endotherms must have possessed four-chambered hearts, and their lineage had already diverged from that leading to the more advanced thecodontians. And they would have been small forms with the potential for rapid, radiative evolution under the appropriate conditions. Therapsids evidently evolved hair for insulation; early primitively endothermic proterosuchians may have acquired a pelage of thin, elongate scales for the same purpose. Competition with the therapsids, particularly predation by the larger therapsids, would have forced some of those early archosaurs into an arboreal lifestyle, initiating the sequence of evolutionary steps that ultimately led to birds.

The Permian ended with a tremendous mass extinction (Stanley, 1987: 90–107), the terrestrial episode of which left the earth virtually devoid of large therapsid predators (Stanley, 1987: 99). Sloan (as cited by Stanley) has ascribed an episodic pattern to the Late Permian therapsid extinctions. This may have resulted from the evolution of therapsid endothermy in discrete stages as the climate slowly but continuously cooled. A similar pattern may have prevailed among the primitively endothermic proterosuchians. The Early Triassic opened with a fresh therapsid radiation, which eventually led to the appearance of the first mammals. Likewise, there was an archosaur radiation, which eventually led to the appearance of the advanced thecodontians, dinosaurs, and birds. As with the radiation of the first mammals, the details of the Early Triassic archosaur radiation are largely missing from the fossil record, because the animals were small and did not inhabit areas where they were likely to be preserved.

There is no way to determine at what stage in the evolution of endothermy an insulatory pelage was acquired. I assume such a pelage would have evolved at an early stage, because the need to conserve body heat would be very important to an evolving endotherm in which the physiological mechanisms for generating body heat were not as efficient as in extant endotherms. On the other hand, an insulating pelage would probably not have evolved in ectotherms, because it would prevent external heat from entering the body, which is undesirable only when the animal is in danger of overheating. In extant ectotherms, overheating is usually prevented by behavioral mechanisms (such as seeking shade, burrowing, and so forth).

In the final analysis, it is impossible to decide whether feathers appeared before or after first-stage endothermy at the proterosuchian-theropodomorph transition. The earliest featherlike scales may have evolved in conjunction with gliding in ectothermic proterosuchians, later developing into an overall insulating pelage in primitive theropodomorphs; or featherlike scales may have evolved initially for insulation and became elaborated later into appendages for gliding.

The most primitive "feathered" creature known is the small *Longisquama insignis* from the Late Triassic of Russia (originally described as from the Early Triassic but later redated) by paleoentomologist A. G. Sharov (1970). The type specimen is not accessible to me, but photographs of both part and counterpart slabs were published in a popular book on prehistoric reptiles (Benton, 1990b: 86, 87). As described by Sharov, the skull of *Longisquama* possessed temporal, postorbital, antorbital, and mandibular fenestrae, placing it well within the

Archosauria. Only the forequarters of the animal were preserved; the caudal dorsal vertebrae, pelvis, hind limbs, and tail are absent. Sharov figured *Longisquama* with a prominent furcula and relatively large, pentadactyl forelimbs. The most dramatic feature of the specimen, however, is the unmistakeable impression of long, featherlike scales projecting from the dorsal region. Sharov interpreted these as having been attached to the back in life, where they functioned as a parachute to break the animal's fall as it leaped among the trees. This mode of life was recently elaborated by Haubold & Buffetaut (1987), who declared that *Longisquama* possessed a double row of dorsal scales that could be spread into horizontal gliding "wings" by dermal musculature.

At first I was not convinced that either Sharov's or Haubold & Buffetaut's interpretation was correct. The orientation of the featherlike scales relative to the forelimbs raised the possibility that they were attached to the forelimbs instead of the back and lay across the body accidentally. But photographs of fossil impressions of other *Longisquama* "wings" published by Haubold & Buffetaut show that the tips of the feathers curved backward in life. The orientation of the forelimbs of the type specimen makes it virtually certain that had the feathers projected back from the forelimbs, they would have been preserved with their tips oriented *forward*. So the most likely location for *Longisquama*'s wings is indeed the dorsal region.

On the other hand, it does seem as if the specimen's skull was displaced upward when flattened during fossilization. The life restorations commonly seen in popular books (*e.g.*, Benton, 1990b: 86), all based on Sharov's original life restoration (1970: fig. 4) showing the head with a prominent parietal-squamosal projection backward over the neck, may be incorrect. The skull could instead resemble that of a more "orthodox" small theropod or bird, once the distortions are corrected. And I would not be at all surprised if it turns out that *Longisquama* possessed long, fully erect hind limbs and a long, feathered tail. More specimens are needed to decide these issues.

The thin, elongate scales of *Longisquama* undoubtedly derive from a stage in the evolution of feathers. Their position in a double row on the back suggests that they were homologous to the parasagittal dermal scutes characteristic of many thecodontians, and they may have been worked by dermal musculature homologous to that of extant crocodilians. Their existence also suggests that the evolution of featherlike scales may have resulted in a radiation of gliding proterosuchians or basitheropods that used their "feathers" in a variety of ways.

In a study of avian aerodynamics, Balda, Caple & Willis (1985) have cast doubt on the ability of feathered gliders to make the evolutionary transition to powered flight. The existence of dorsal feathers in *Longisquama* suggests how this transition may have occurred. I return to this subject below.

Tail-Gliding

Published studies of the origin of flight in birds have concentrated on their cursorial ability and on their wings (*cf.* Peters & Gutmann, 1985); I know of no study that assesses the value of a feathered tail of a kind similar to that possessed by *Archaȩopteryx* as an airfoil. Yet the development of a lateral fringe of long featherlike scales on the tail was surely the first aerial adaptation to evolve in a primitive, arboreal archosaur. Like the fletching of an arrow, and without providing much lift, such a tail would have given balance, direction, and stability to an animal leaping among fronds and tree branches. When properly oriented, it would also have served as a rudimentary parachute to break long falls; and pulling it up into the slipstream like an aileron would have pitched the glider's body upward for a landing on a vertical treetrunk.

Furthermore, such a tail would have speedily acquired a secondary role as a display organ for sexual selection. By the beginning of the Triassic, tail-gliding, feathered archosaurs could have radiated into hundreds of species with a cosmopolitan distribution. Each species was the potential progenitor of a distinct clade of archosaurs. Some actually were; the others eventually became extinct, replaced by the more efficient fliers that soon evolved.

Archosaurs plesiomorphically had long, moderately flexible tails and a marked size disparity between the smaller fore and the larger hind limbs. Stiffening the tail distally would improve its utility as an airfoil, but improved control of the stiffened airfoil would require intervertebral flexibility at the caudal base. Proximally flexible but distally stiffened tails are found in all theropods, particularly tetanurans (Rowe & Gauthier, 1990). The need to control the tail airfoil would result in more efficient and dynamic caudifemoral musculature, a preadaptation for erect, bipedal, cursorial locomotion.

One possible tail-gliding archosaur was described from the Middle Triassic (Ladinian) of Spain by Ellenberger & de Villalta (1974) and in two further papers by Ellenberger (1977, 1978, neither of which I have yet been able to obtain). *Cosesaurus aviceps* was initially hailed as a probable avian ancestor, an assessment rebutted by Olsen (1979), who classified it as a small eosuchian. Sanz & López-Martínez (1984) essentially agreed with Olsen (without citing his work) when they classifed *Cosesaurus* as a juvenile prolacertiform. Molnar (1985), meanwhile, noted the lack of eosuchian characters and rejected Olsen's identification. He further noted the presence of a small antorbital fenestra, visible in Ellenberger & de Villalta's original photographs. The presence of an antorbital fenestra makes *Cosesaurus* an archosaur; the presence of prolacertiform characters (such as vertebral counts and limb ratios) can easily be attributed to plesiomorphy. As Molnar noted, the skull of the specimen does show a certain similarity to that of *Megalancosaurus preonensis* (Calzavara, Muscio & Wild, 1980), a problematic Late Triassic archosaur from Italy.

If I were called on to display a specimen of a tail-gliding proterosuchian or theropodomorph, *Cosesaurus* probably comes the closest to my idea of what one might look like. In size and general appearance, the specimen strongly resembles *Mesenosaurus*, *Sharovipteryx*, and *Scleromochlus*. Most interestingly, Ellenberger (1977, 1978) figured *Cosesaurus* with feather impressions, particularly along the tail, to support his contention that it was related to the birdlike trackmakers from the Lower Stormberg he had previously described (Ellenberger, 1970, 1972, 1974). The feather impressions were dismissed as artifactual by Sanz & López-Martínez, but I am not so sure. My inclination is to give *Cosesaurus* the benefit of the doubt and include it provisionally as the most primitive member of the Basitheropoda.

Grasping Forelimbs and Canard Wings

Profound difficulties confront all attempts to derive the avian wing from the grasping theropod forelimb. The transition from forelimbs as feathered insect-traps to organs of flight in *Archaeopteryx* (Bakker, 1975; recanted, 1986), for example, is far too unlikely for serious consideration. All known "orthodox" theropods possessed forelimbs much too small to have been preadapted for any kind of flight, particularly since those theropods were mostly large to very large animals that would have required impossibly huge wings and musculature to fly. *Compsognathus*, the smallest "orthodox" theropod, is the only one known whose size fell comfortably into the range of extant birds (Callison & Quimby, 1984), but its forelimbs were much too small to serve as wings (Ostrom, 1978). Indeed, the primary (though not exclusive) evolutionary trend was for theropod forelimbs to become smaller rather than larger, particularly among the carnosaurs (Tucker, 1938). In the scenario presented here, the transition from quadrupedal tail-gliding basitheropod to a form in which the forelimbs possessed both a grasping and an airfoil function occurs quite naturally.

A leaping arboreal quadrupedal tail-glider is aimed head first at its eventual landing point. Regardless of whether it lands forefeet-first or uses its tail to orient its body for a four-point landing, its forelimbs must play a dominant role at the termination of its trajectory; they are perfectly positioned to grasp and hold on to a frond, branch, or treetrunk. As ideal appendages for climbing in an arboreal habitat, large, strong grasping forelimbs would have evolved as natural improvements on the plesiomorphic small forelimbs of the earliest tail-gliders. Such forelimbs are in fact observed in the type specimen of the primitive archosaur *Megalancosaurus* (Calzavara, Muscio & Wild, 1980).

Furthermore, feathers or featherlike scales on the outstretched forelimbs would have been perfectly placed to serve as canard airfoils to adjust the direction of the tail-glider's trajectory. Elongation of the feathers would have accompanied the increase in forelimb size, and a gliding form resembling *Protoavis texensis* (Chatterjee, 1991) could have evolved quite rapidly, well before the end of the Triassic. Like tail-gliders, canard-wing gliders were small forms that must have radiated into hundreds of species, eventually displacing the tail-gliders much as extant passerine birds have partially displaced the less-derived avian groups. Canard-wing gliders equipped with tail airfoils would have been aerodynamically stable fliers for the same reasons that paper and balsa-wood gliders are. With small adjustments of their wings, they could have soared great distances once launched. And as the canard wings adapted to gliding flight, they would have evolved naturally into the larger wings observed in *Archaeopteryx*: powerful appendages with which the animal exercised considerable control over the direction and length of its flight path.

Balda, Caple & Willis (1985) assert that forelimbs adapted for gliding would not be preadapted to evolve into true wings, which provide both lift and thrust for flight. In gliding flight, the wings provide only lift; gravity and air currents supply the energy of motion that the wings convert into lift. Should Balda, *et al.* prove correct, then *Longisquama* shows how protoavian forelimbs might have evolved into true wings. Forelimb feathers are not the only ones that can elongate into gliding wings; as noted above, featherlike scales in the dorsal region of *Longisquama* were elongated into erectile wings. Such dorsal "wings" would have kept the protoavian aloft as easily as elongate forelimb feathers. The forelimbs could then have evolved a true canard function, as mobile anterior auxiliary wings helping to steer the animal in flight. Not needed as primary flight organs, the forelimbs would have been freer to evolve into flapping appendages. As the forelimbs assumed a larger role in flying, the dorsal "wings" would have diminshed, eventually vanishing entirely.

I must confess that I believe *Longisquama* simply to have been one of a multitude of gliding forms into which the archosaurs radiated during the Triassic. I do not find Balda, *et al.*'s argument very convincing; it is more straightforward for true wings to have developed from gliding wings, as indicated by Rayner (1985a, 1985b). Rayner's accounts of the aerodynamics of the gliding-to-flapping transition are eminently clear, readable, and compelling. I hope they are right, so that the dorsal-wing model set forth above proves unnecessary.

One detail confronts any phylogeny in which theropods evolve from small, feathered forms: Why haven't feather impressions been found with theropods other than *Archaeopteryx*? Such feathers were searched for by Ostrom (1978) in *Compsognathus*, but no trace was discovered. Paul (1988b: 121–123) suggests that the larger theropods did not need an insulative pelage, just as large extant mammals that live in tropical climates do not need hair. Skin impressions of large theropods show a scaly integument but absolutely no feathers. Paul's life restorations of the smaller theropods and lagosuchians, however, are imaginatively supplied with feathers, against which, he asserts, the fossil record is simply badly biased. I am convinced that small theropods will eventually be discovered with feather impressions, but I can offer no reason to think this other than my phylogeny.

The Furcula

Clavicles were plesiomorphic in archosaurs (Carroll, 1988), and their function of bracing the pectoral girdle against the sternal elements preadapted them as shock absorbers for arboreal leaping (Haubold & Buffetaut, 1987). The shock-absorbing function of the clavicles improved when they fused into a furcula, and it continued to improve incrementally as the furcula became the unique springlike bone of modern birds. In extant birds, the furcula stores energy for the return stroke of the wings (K. Campbell, pers. comm.), and its shock-absorbing function is now all but lost.

Thulborn (1984) was able to identify furculae in several theropod genera, including even tyrannosaurids, but their absence in most theropod taxa does not preclude a close relationship between theropods and birds, as Heilmann (1927: 183) maintained. Reduction or loss of the clavicles or furcula can be expected in flightless descendants of arboreal gliders and fliers.

Bipedal Stance

Birds and *Homo sapiens* are the only extant vertebrates that are obligatory bipeds; jumping mice and rats are nearly obligatory bipeds. In current bird phylogenies, obligatory bipedality is considered a plesiomorphic character acquired by birds from theropod ancestors. How this unusual and hazardous form of locomotion might have arisen in theropods, however, is usually dealt with *ad hoc*: The theropods were bipedal because they acquired the character plesiomorphically from their "thecodontian" ancestors – and bipedality arose in thecodontians because it *just did*: perhaps as an adaptation for increased speed, or teleologically – *to allow* thecodontians to grasp prey with their forelimbs – and so forth.

Most terrestrial vertebrates are quadrupedal, including the fastest (*Acinonyx*, *Gazella*, *Antilocapra*), and quadrupedal predators have no trouble grasping prey with their jaws. Most quadrupeds can occasionally assume a bipedal stance, and many can even walk or run bipedally for short distances, especially lightweight lizards (Heilmann, 1927: 178), but there seems to be little need for facultative bipedality to become habitual or obligatory. A quadrupedal stance confers locomotor stability, and injury to a limb will not usually immobilize a quadrupedal animal. Bipedal locomotion requires exceptional balancing ability and coordination to avoid falling. These are all compelling reasons why quadrupedality has remained the dominant mode of locomotion among nonavian tetrapods. Bipedal locomotion is not a natural outcome of the progression from sprawling quadruped to semi-erect quadruped to fully erect quadruped. Its prevalence among dinosaurs, particularly theropods, requires explanation.

I assert that the familiar theropods were bipedal because they descended from animals in which *the forelimb was already doing something other than walking*, namely, serving as an appendage for grasping, climbing, gliding, and flying in small, arboreal theropodomorphs. Archosaurs possessed relatively large hind limbs plesiomorphically, and the smaller, lightweight forms were surely capable of rapid bipedal progression when the need arose. A potential for this kind of locomotion has been ascribed to Late Permian eosuchians such as *Heleosaurus* (Carroll, 1976). The scenario presented above for the origin of canard and gliding wings makes it relatively easy to see how a small arboreal form would come to rely less and less on its forelimbs for walking and running. Grounded basitheropods, with their forelimbs encumbered by feathers and specialized for grasping, climbing, and gliding, would come to depend exclusively on their hind limbs for cursorial locomotion.

It is difficult to determine when the basitheropod foot made the transition from plantigrade to digitigrade posture. Digitigrady is commonly held to be an adaptation for increased speed in fully erect animals (Coombs, 1978; Paul, 1988b), and it is difficult to imagine a semi-erect basitheropod in a digitigrade stance. So I presume that the fully erect stance preceded the digitigrade posture: By the time lagosuchians, herrerasaurians, ceratosaurs, and protoaviforms had evolved, fully erect, digitigrade bipedality was the commonest locomotor mode among theropodomorphs.

A subtle anatomical effect may also have contributed to the acquisition of bipedality among the archosaurs. In advanced therapsids, such as *Thrinaxodon*, the vertebral column immediately anterior to the sacrum has a rib-free lumbar region, and the vertebrae are adapted to restricting lateral flexion while permitting increased dorsoventral flexion (Carroll, 1988). This situation undoubtedly coevolved with increased locomotor efficiency and speed and allowed the axial musculature, as well as the appendicular musculature, to participate in running and bounding. In archosaurs, a rib-free lumbar region never evolved. This limited the body's flexibility, so the axial musculature could not readily participate in running. Archosaurs, even small ones, had to rely almost exclusively on limb musculature to run. In bipedal forms, the hind limbs did all the work, and the net evolutionary effect was to greatly increase the size of the already large hind limbs and their associated musculature.

A human runner carrying a long, heavy log is roughly equivalent anatomically to a large walking or running theropod. Theropods adapted to this condition by evolving shortened bodies, retaining the long tail as a counterbalance, and reducing unnecessary spinal flexibility with extra intervertebral articulations. Unneeded for locomotion, the forelimbs became as small as possible without totally losing their prey-handling function.

Bipedality in ornithischians was not accompanied by skeletal pneumatization, so I do not believe the ornithischians evolved from volant forms. Ornithischians may have evolved as herbivores from semi-erect proterosuchians that used their forelimbs and hands to select, pluck, and manipulate the edible parts of plants. Tenuously supporting this hypothesis is the observation that evolutionary loss of manual digits in ornithischians was not nearly as thorough as in theropodomorphs. Many large forms, such as *Iguanodon*, retained a pentadactyl manus. Some of the heavier ornithischians became secondarily quadrupedal, an evolutionary option open to them because they never evolved the highly specialized forelimbs required for gliding or powered flight. Other ornithischian lineages, such as the ankylosaurs and stegosaurs, may not have evolved from bipedal forms at all.

Poposaurians are also thought to have evolved a bipedal stance, but their limb elements are not yet well known. The degree of bipedality prevalent among poposaurians and how this bipedality may have evolved cannot yet be determined with confidence.

Manual and Pedal Digits

Dinosaurs in general and theropodomorphs in particular progressively reduced and then lost some of the digits on both their fore and hind limbs. In the hind limbs, digital reduction is commonly held to be an adaptation for speed: Removal of unnecessary weight from the extremities decreases their moment of inertia around the point of articulation with the body, thereby increasing the efficiency of the appendicular musculature (Coombs, 1978). In most theropods, the pes remained quite symmetric, with the middle digit (III) remaining longest and strongest and the digits on either side (II and IV) being almost as large. Digit I typically was reduced to where it would not contact the ground, while digit V became vestigial and even absent. This disposition of pedal digits defines the paraorder Theropoda in the classification used here; digitigrade theropodomorphs in which digit I retains some weight-bearing function and digit V is not significantly reduced are classified as lagosuchians or herrerasaurians.

Theropodomorph digital loss also occurs in the manus, and it roughly parallels digital loss in the pes. That is, theropods with functionally tridactyl pedes usually (though by no means always) possessed a functionally tridactyl manus. This suggests an ontogenetic parallelism between fore and hind limbs, but if so it is not perfect. Whereas the dominant pedal digits were II, III, and IV, the dominant manual digits are considered to be I, II, and III.

In extant birds, ontogenetic studies show that the digits in the wings, which are fused in all birds except juvenile hoatzins (*Opisthocomus*), are actually digits II–IV (Hinchliffe, 1977, 1985). Tarsitano & Hecht (1980) extrapolated this pattern back to *Archaeopteryx*, asserting that its digits should therefore also be numbered II–IV, and Thulborn & Hamley (1982) suggested that the manual digits in all manually tridactyl theropods should likewise be numbered II–IV. The phyletic significance of this seemingly trivial debate is that if the digits were I–III in theropods and *Archaeopteryx*, then the common ancestry of birds and theropods was considerably more remote than if the digits were II–IV (Hinchliffe, 1985). Unfortunately, not enough primitive tetradactyl theropod manus are known to settle this question. Those that are known, among the ceratosaurs for example, seem to possess the I–III pattern with a reduced digit IV rather than a II–IV pattern with a reduced digit I (Rowe & Gauthier, 1990).

In all known "orthodox" theropods with tridactyl mani, the manus matches that of *Archaeopteryx* in phalangeal counts and morphological conformation of the individual phalanges. The manus of *Archaeopteryx* is so similar to those of deinonychosaurs, in fact, that I enthusiastically support Paul's (1984, 1988b) contention that *Archaeopteryx* is best thought of as a primitive deinonychosaur. In the classification presented here, I consider Archaeopterygidae to be a parafamily within the Deinonychosauria, ancestral to the Dromaeosauridae and Troodontidae. Details of skull structure (*e.g.*, jugal with reduced or absent ascending process: *cf.* Bühler, 1985; Paul, 1988b: 354 actually supplies one!) exclude *Archaeopteryx* itself from ancestry of any other known deinonychosaur, but there were probably dozens or even hundreds of archaeopterygid species worldwide during the Late Jurassic, one of which could well have been "the" ancestral dromaeosaurid and another "the" ancestral troodontid. The digits of *Archaeopteryx* convincingly ally it much more closely to "orthodox" theropods than to modern birds. If Martin's (1985) contention that *Archaeopteryx* is an enantiornithid bird is correct, then perhaps all "orthodox" theropods were not just flightless protoavians but flightless enantiornithids.

All specimens of *Archaeopteryx* in which the feet are preserved show a retroverted digit I (Ostrom, 1985; Wellnhofer, 1991: 179, 180). I cannot believe this is coincidental; it must be because the first digit really did oppose digits II–IV in the foot. This strikes me as an adaptation for perching, and it is evidence that *Archaeopteryx* was more arboreal than cursorial in its lifestyle. Digit I in *Archaeopteryx*, however, is considerably smaller than digits II–IV, so the grip of the foot may not have been particularly strong. In most "orthodox" theropods, pedal digit I is peculiar in that the metatarsal bone is split into an upper and a lower section (Rowe & Gauthier, 1990; Molnar, Kurzanov & Dong, 1990; Barsbold, Maryanska & Osmólska, 1990; Ostrom, 1990) or missing entirely (Barsbold & Osmólska, 1990). This suggests that pedal digit I, unneeded for perching in cursorial theropods, secondarily returned to a more forward orientation. The split metatarsal I is yet another remnant of the basitheropod arboreal volant lifestyle that survived vestigially in theropods.

Wings

The similarity of the forelimb anatomy of certain advanced theropods, such as *Deinonychus*, to that of *Archaeopteryx* was well documented by Gauthier & Padian (1985). Its origination in theropods, however, is unclear until it is realized that it developed first in volant theropods to make flapping, powered flight more efficient. *Archaeopteryx* was surely a capable flier (*cf.* various articles in Hecht, Ostrom, Viohl & Wellnhofer, eds., 1985) whose forelimb retained an excellent grasping function for arboreal climbing, and there is no reason to expect flightless archaeopterygid descendants to foresake this function as predators.

Other Adaptations

Orthodox scenarios for the origin of theropods have difficulty accounting for their pneumatic skeletons. Volant basitheropods, however, surely evolved a pneumatic skeleton as an adaptation for more efficient flight; bone-mass reduction would lower a tail-glider's momentum and kinetic energy, reducing stress on the pectoral girdle when the forelimbs terminated its glide. Bipedal archosaurs that were not theropods, such as ornithopods and (probably) poposaurians, do not exhibit the extensive skeletal pneumatization of theropods, because this character is not a prerequisite for bipedality, and in fact thin, relatively fragile bones represent a structural disadvantage for large predators. Paul (1988b) notes that theropod bone was denser and stronger than the bone of nonpredatory dinosaurs. If this is true, it can be accounted for as a means of overcoming the structural problem of skeletal pneumaticity that the large theropods inherited from their basitheropod forebears.

Small, arboreal climbers and leapers require excellent vision and coordination. These characteristics must have coevolved with the semierect and fully erect stance in basitheropods, when the forelimbs were used for grasping and climbing even before they acquired any volant function. Basitheropods thus became preadapted for the demands of tail-gliding, gliding, and powered flight. Cranial characters that seem to indicate these kinds of sensory-neural improvements have been documented in the protoaviform theropod *Protoavis texensis* by Chatterjee (1991) and used as evidence of a basal position for *Protoavis* with respect to the class Aves. Postcranially, *Protoavis* is solidly a core-group theropod.

COMMENTS ON DINOSAUR DIVERSITY AND EXTINCTION

How many dinosaurs were there? This question was recently addressed by Dodson (1990), who applied statistical methods and a few seemingly reasonable assumptions about collection and preservation biases to the dinosaur fossil record. The total number of dinosaur genera that ever lived, according to his calculations, was somewhere between 645 and 3285, with a most probable value between 900 and 1200.

I was asked the same question in an interview for a popular dinosaur television show, and I estimated the answer in the following way: Dinosaurs dominated the world's terrestrial biota for approximately 150 million years. Extant vertebrates that likewise dominate their domains are bony fish, birds, and mammals, and there are several thousand species of each: over 20,000 species of fish, 9672 species of birds, over 3000 species of mammals. The present epoch is, in my opinion, one of average vertebrate diversity, neither particularly depauperate nor particularly abundant, and "several thousand species" seems to be a number that characterizes the diversity of any large vertebrate group of worldwide distribution. Exactitude is not necessary in this kind of order-of-magnitude calculation, so I chose a figure of 6000 as a likely number of dinosaur species extant at any one epoch.

Dinosaur species seem to have originated, flourished, and become extinct over a period of no more than about 4.5 million years. There are four distinct dinosaur faunas known in the Campanian to Maastrichtian of North America, a period of time spanning about 18 million years; this amounts to an average of 4.5 million years per fauna. At this time scale, even *generic* turnover between the faunas was virtually complete.

One hundred fifty million years thus yields 33 or 34 complete species turnovers among the dinosaurs, which when multiplied by 6000 species per epoch yields a grand total of about 200,000 dinosaur species that ever lived. Assuming an average of 10 species per genus—some extant vertebrate genera have more than 30 species per genus, others have only one or two—this yields 20,000 genera: nearly an order of magnitude more than the maximum figure calculated by Dodson.

What is the source of this huge discrepancy? I see nothing unreasonable about the back-of-the-envelope calculations outlined above. Dodson's assumptions about preservation biases may, however, be too low. There is not enough space here to question all his assumptions in detail; that is the stuff of a separate paper. Instead, I will offer my own thoughts about such biases, and see whether the discrepancy can thereby be explained.

One factor not considered in calculating preservational biases is that all known dinosaur fossils necessarily occur in depositional environments: fluviatile, lacustrine, or aeolian. Such environments presently comprise about 10% of the earth's total land area (a crude estimate based on visual examination of world maps); at any given time, 90% of the world is being eroded away. Epicontinental seas, such as the one that covered North America during the Cretaceous Period, foster the development of fluviatile and lacustrine depositional regions, and the fraction of earth's land area that was depositional then may have attained 25% (Haubold, 1990). Even so, this means that as many as 75–90% of the dinosaur species extant in any one epoch may *never* be found as fossils, simply because they did not live in depositional environments. Another factor is that depositional environments may not be particularly species-rich. Today's tropical rain forests contain the most diverse faunas by far, but such forests are taphonomically inimical to the preservation of fossils.

If dinosaurs diversified into an average of 6000 species per epoch, we might expect that about 600–1500 species lived in or near depositional environments where fossilization could occur. This places a theoretical upper bound on the number of species we could in principle discover. Quite a few such deposits have already been eroded away, taking their loads of species with them, and as a rule, the farther back we go in the Mesozoic, the fewer such deposits remain to be excavated. Note, for example, that the Upper Cretaceous provides the largest number of dinosaur-bearing formations, which I ascribe to this fossilization bias. After taking such biases into account, we are left with the handful of species per epoch that are actually present in our museum collections. The point to ponder is that enough slack exists in the statistics to allow the fossil record to support either Dodson's "lowball" diversity estimates or my "highball" estimates. Consequently, we may have to look elsewhere than the fossil record to calculate dinosaur diversity.

Finally, it should be noted that the bulk of species diversity in extant vertebrate groups lies among the small forms. If there were only large dinosaurs, then Dodson's estimates would certainly be apt, for as he notes, they agree in order of magnitude with the numbers of extant large mammals. But I contend that there were many more small dinosaurs—pigeon- and chicken-size arboreal climbing, gliding, and flying forms—than anyone has previously guessed. Their existence follows from the pattern of archosaurian evolution as outlined in this work. Their physical traces include the unidentifiable small theropod and ornithischian teeth and other skeletal fragments found in many museum collections, and occasional footprint faunas that document a much higher level of dinosaur diversity than do fossilized remains (Lull, 1953; Ellenberger, 1970, 1972, 1974; Olsen & Galton, 1984).

Archosaur Evolutionary Patterns

The observed pattern of archosaur evolution in the Mesozoic is one of rapid radiation, followed by apparent evolutionary stasis, followed by mass extinction, followed by rapid reradiation of surviving groups (if any). There were six major extinctions that affected the archosaurs, beginning with the one that opened the Mesozoic Era and ending with the one that closed it; the archosaurs were affected by some of those extinctions more than by others. I do not intend to address the questions of what caused the extinctions or of how long the extinctions may have lasted. While those are interesting questions, I am more concerned here with the effect of the extinctions on Mesozoic archosaur phylogeny and diversification.

The broad similarities in archosaur evolutionary patterns following extinction events suggest that a single model might account for them all. Central to this model is the existence of one or more "core groups" of small, rapidly evolving (tachytelic), highly diverse archosaurs that comprise an "evolutionary engine" from which the larger, more slowly evolving (bradytelic) forms arise. Being small, core forms are seldom found as fossils, and when they are, they tend to be perplexing animals that seem not to fit into any of the better-known groups. Also, because they were small, core forms were subject to considerable predation pressure, often from their own larger descendants, which tended to keep their evolutionary fecundity in check. But when an extinction event removed this predation pressure, the core groups rapidly radiated to fill the void. As the new forms became large and cosmopolitan, the likelihood of their preservation as fossils rose, and the fossil record displays their "abrupt" appearance. In short, the fossil archosaurs that we have so far discovered seem to be the tip of an evolutionary iceberg.

The Permian-Triassic (P-T) Extinction

When the P-T extinction took place, there were only two extant archosaur orders: the Proterosuchia and (probably) the Basitheropoda. These comprised a core group from which the Early Triassic archosaurs radiated, and they were themselves ultimately descended from a Permian nonarchosaurian diapsid core group. The main tetrapod victims of the P-T extinction were large therapsids, including most if not all of the world's top predators as well as many groups of herbivores. The removal of those forms fostered the first archosaur radiation, not to mention a radiation of new therapsids, which possessed a powerful "evolutionary engine" of their own.

It must be remembered that although the therapsid and archosaurian core groups remained deep in the background insofar as their fossil records are concerned, they were by no means immune from the evolutionary process. They were, however, reasonably immune from the mass-extinction process. Large terrestrial vertebrates possess a slow evolutionary tempo and are unable to find shelter from the usual agents of mass extinction, such as abrupt climatic change, asteroid impact, and so forth. Their usual response to such agents is to become extinct, and since such animals are by virtue of their size prominent in the fossil record, it is their simultaneous disappearance that signals the mass extinction. New *Baupläne* seldom if ever evolve from large terrestrial vertebrates. Rather, the evolution of such animals consists principally of "variations on a theme."

Evolution in a core group occurs at a faster tempo because core-group animals are smaller, have shorter gestation periods, take less time to attain sexual maturity, and have larger litters than large animals. In the absence of predation, this is the source of radiative evolution. But it is also a wellspring of rapid evolution under most other circumstances. When niches for large forms become occupied, core-group evolution produces other core groups instead. New *Baupläne* would thus be a frequent byproduct of core-group evolution. The primary agent of core-group extinction—if this process really occurs, and is not simply an artifact of complete evolutionary turnover—seems to be the constant competition with other core groups, rather than the global extinction events that occur every few score million years. Core-group extinction appears to be steadier and less episodic than the extinctions of larger forms.

The fossil record seems to show gradual archosaur diversification throughout the Early and Middle Triassic at the expense of the remaining large therapsids and other nonarchosaurian diapsid reptiles (Benton, 1986b; Hunt, 1991). In particular, the proterosuchian part of the core group generated a number of ground-dwelling predators, including early ornithosuchians and pseudosuchians. These groups, particularly the pseudosuchians, gradually diversified at the expense of the therapsid and other reptilian groups as the Triassic unfolded. By the beginning of the Late Triassic, several more archosaur orders had appeared in the fossil record, including the Parasuchia, Aetosauria, Hupehsuchia, Crocodylia, and Lagosuchia. Other possible descendants of the proterosuchian core group were ancestral pterosaurs, including the Sharovipterygia and Rhamphorhynchoidia, which undoubtedly constituted a third archosaurian core group.

The proterosuchian "engine" itself gradually faded away, being replaced by the basitheropods as the principal archosaurian core group. The basitheropods had filled many niches as arboreal and small cursorial animals during the Early and Middle Triassic, and they would prove important to the subsequent archosaurian fossil record.

I call the Triassic archosaur core group "basitheropods" out of ignorance of their true diversity. They undoubtedly included a number of lineages, only one of which can properly be called Basitheropoda: the lineage that led to the Theropoda and ultimately the Aves. Other lineages, among which might be "Basisauropoda" and "Basiornithischia," led to the sauropodomorphs and ornithischians, but representatives of those lineages are entirely absent from the fossil record. There is no point in formally naming such groups until at least one member of each can be identified.

The Carnian-Norian (C-N) Extinction

A major extinction occurred at the boundary between the Carnian and Norian epochs of the Late Triassic. The result of the C-N extinction was the removal of most of the remaining large therapsids and some nonarchosaurian diapsids. Among the archosaurs, many large thecodontians vanished, but faunas with crocodilians, large pseudosuchians, parasuchians, and aetosaurs persisted. (The crocodilians actually proved to be quite a durable group, being the only thecodontian order to have survived to the present.) Most interestingly, however, the basitheropod "engine" generated the herrerasaurians, ceratosaurians, and protoaviforms, and early sauropodomorphs and ornithischians entered the fossil record for the first time.

By this time, the basitheropods and protoaviforms were probably widespread and diverse, and they filled the trees with various feathered climbing and gliding forms. Cursorial basitheropods and protoaviforms, lagosuchians, and herrerasaurians were most likely not as diverse, but the *Bauplan* of a small, bipedal predator, with grasping forelimbs where it once had canard wings with claws, had become well established. This body plan persisted in the paraorder Theropoda through the end of the Mesozoic. Among the prey animals seized by the smaller theropods were core-group therapsids, including the earliest true mammals.

Competition from and predation by pterosaurs may have helped to limit the evolution of climbing and gliding core-group archosaurs during the Norian, but the protoaviform core-group undoubtedly flourished. Besides that order and the Theropoda, other Norian core-group orders included the Lesothosauria and the earliest members of the Pachycephalosauria (Pisanosauridae and Heterodontosauridae).

Most emphatically not core-group archosaurs, the early sauropodomorphs took over the large-herbivore niche from large therapsid herbivores, and they enjoyed considerable success throughout the Mesozoic.

The Triassic-Jurassic (T-J) Extinction

A major result of this extinction was the disappearance of all the thecodontian orders except the Crocodylia and possibly the Parasuchia. Theropods, prosauropods and sauropods, lesothosaurians, and ankylosaurians reradiated thereafter, establishing the dinosaurs as the dominant terrestrial megafauna. The Age of Dinosaurs began with this extinction event.

The Pliensbachian-Toarcian (P-T) Extinction

This was primarily a marine extinction, but one possibly related consequence was the disappearance of the prosauropods from the fossil record. Otherwise, the dinosaurs survived this extinction event intact.

The Jurassic-Cretaceous (J-K) Extinction

The J-K extinction is not yet well documented, but one of its consequences was the disappearance of the large diplodocids and brachiosaurids from the northern hemisphere. Most of the other dinosaur groups persisted across the Jurassic-Cretaceous boundary, although the stegosaurians did so as a relict fauna. New kinds of theropods (baryonychids, abelisaurids) and ornithischians (iguanodontids, psittacosaurids) appeared. Nodosaurids, previously rare, radiated into several genera. This event may have been related to the breakup of the supercontinent Pangaea into Laurasian and Gondwanian land masses, because subsequent to the extinction, the fossil records of the northern and southern hemispheres diverge significantly.

The Cretaceous-Tertiary (K-T) Extinction

In terms of popular interest, this extinction event was by far the most significant for the archosaurs. But the most interesting question about this extinction event is not, "What caused it?" but, "Why didn't the archosaurs return, as they had done six times before?" In terms of the model outlined here, the answer is that the archosaur core group no longer included the dinosaurian *Bauplan*. The small arboreal and cursorial dinosaurs had been decimated throughout the Late Cretaceous by competition with placental mammals—the ultimate "therapsid" core group—leaving as survivors only the aerial forms: the class Aves. Large, flightless avian predators and herbivores (*Diatryma*, *Phorusrhacos*, *Onactornis*, *Dinornis*, and so forth) continued to evolve at various times during the Tertiary, bearing the same relationship to volant birds that large dinosaurs bore to core-group dinosaurs. But without grasping forelimbs, such flightless avians were not true dinosaurs. Thus, after serving as dinosaur food for two-thirds of the Mesozoic Era, the mammals had gained some measure of revenge.

Dinosaur Orders

THE THEROPODOMORPHA comprises by far the most problematic archosaurian assemblage. If the scenario for theropodomorph and bird origins described in the previous section proves at all accurate, then the taxonomy of the theropod dinosaurs may require a revision more radical than anything I propose here. The discovery of more specimens of theropodlike avians and birdlike theropods could well make the distinction I have drawn between the Theropoda and Aves too arbitrary to be supported even by a traditionalist like me. In the long run, the entire parasuperorder Theropodomorpha may, perhaps, have to be subsumed into the class Aves. The terms "theropod" and "dinosaur" would lose their phyletic validity, for I cannot imagine that birds will ever come to be thought of as small, flying dinosaurs. The name Aves, after all, has historical priority over Dinosauria.

If the methods of grouping species into higher taxa that are followed in ornithological taxonomy were applied to theropodomorph taxonomy, then many of the suborders listed here in the order Theropoda, and even some of the families, would require orders of their own. Hawks (order Falconiformes) and sparrows (order Passeriformes), for example, seem to me considerably more alike morphologically than do *Tyrannosaurus* and *Oviraptor*. It is a peculiarity of paleornithological taxonomic practice that when a fossil form is identified as a bird, particularly from an epoch prior to the Late Cretaceous, its identifier often creates a monotypic order just for it. So if paleornithologists can consider as orders such groups as Archaeopterygiformes, Enantiornithiformes, Gobipterygiformes, and Protoaviformes, then to these must eventually be added the theropod "orders" Ceratosauria, Carnosauria, Ornithomimosauria, Oviraptorosauria, and Avimimiformes. In the present work, however, I employ a more traditional framework, because conclusive evidence for this kind of theropod polyphyly has only begun to emerge. Detailed evidence that would allow us to disentangle the phyletic relationships among the theropod suborders has presently not advanced much further than the "gut feeling" that we are only scratching the surface. Bearing this caveat in mind, I have identified four orders and paraorders among the theropodomorphs.

Among the characteristics of theropodomorphs are carnivorous dentition (when present); semi-erect to fully erect stance; and tarsus with reduced calcaneum. Impressions of feathers or featherlike scales may be present. The parasuperorder Theropodomorpha is defined as the smallest clade including *Megalancosaurus*, *Longisquama*, and (possibly) *Cosesaurus*, together with all the well-known theropod dinosaurs, *minus* the clade Aves (or Carinatae), as defined in the Archosaur Phylogeny section).

Paraorder Basitheropoda

This paraorder is created for the most primitive theropodomorphs. With only a few referred species so far, some of which will doubtless eventually acquire orders of their own, there is considerable danger that the Basitheropoda will (or already has) become a wastebasket group for peculiar small archosaurs that defy classification into the better established groups. Not helping this situation is the fact that the type specimens of the three listed species are small and difficult to study because they exist only as slab impressions and cannot be examined in three-dimensional detail.

Among the characters to look for in a potential basitheropod are: an antorbital fenestra (plesiomorphic, but its absence would exclude the specimen at once); generally avian appearance of the skull; relatively large, grasping forelimbs; clavicles, fused clavicles, or primitive furcula; sacrum with three or even more vertebrae; incipient or fully evolved AM tarsus, depending on hypothesized semi-erect or fully erect hind-limb stance; reduced calcaneum; pentadactyl manus and pes (plesiomorphic, but a manus or pes with fewer digits would be a derived condition above the Basitheropoda); impressions of featherlike scales or feathers. Future work is necessary to better characterize this order.

Order Lagosuchia

This group was created by Paul (1988b) to accommodate the families Lagosuchidae and Lagerpetonidae. Paul also included the problematic genus *Lewisuchus* in the Lagosuchia, but most authorities now agree it represents a distinct sphenosuchian family (Crocodylia).

The lagosuchians seem to have been a Middle Triassic offshoot of the lineage leading from the basitheropods to the theropods proper; I know of no archosaur that could be considered as descended from any lagosuchian tabulated here. Gauthier & Padian (1985) place *Lagosuchus*, which is the only lagosuchian known from reasonably complete material, between the Ornithosuchidae and Pterosauria plus Dinosauria on the "ornithosuchian" branch of their archosaur cladogram. For reasons previously stated, I believe the Ornithosuchidae and Pterosauria do not belong here, and that Gauthier & Padian's "Dinosauria" is really just the Theropoda. Otherwise, I have followed Gauthier & Padian and Arcucci (1986, 1987) in organizing the Lagosuchia. So far, lagosuchian fossils are restricted to South America, but since they were small archosaurs, they probably had a much wider but still unknown distribution.

Order Herrerasauria

This order, originally created by Galton (1985a) as a theropod infraorder, includes several bipedal carnivorous dinosaurs of apparently basal but otherwise uncertain position close to the Theropoda (Sues, 1990). *Staurikosaurus* and *Herrerasaurus* are the only two herrerasaurian genera at all well understood, and they are different enough from each other to warrant separate families (*cf.* Galton, 1985a).

Excluding the herrerasaurians from the Theropoda are their functionally tetradactyl pedes, in which metacarpal I was reduced but not split as in the theropods. The pelvis was brachyiliac with rather broad, apronlike, slightly retroverted pubes that terminated in a footlike enlargement. News photographs of a recently discovered nearly complete *Herrerasaurus* skull from Argentina show its very theropodlike appearance, so a taxonomic position for the Herrerasauria in a theropod sister group is indeed likely. Like the lagosuchians, herrerasaurians represent a theropodomorph lineage that diverged from the Basitheropoda before pedal digit I was reversed. They are known with certainty only from the Late Triassic (Carnian) of South America, but fossil teeth that may be refereable to herrerasaurians have a nearly worldwide distribution. The usual lack of complete material frustrates knowledge of these dinosaurs.

I have organized the order Herrerasauria according to Galton (1985a) and Sues (1990).

Paraorder Theropoda

This is the most diverse archosaurian order, even with the birds excluded. The fossil record of the theropods begins in the Late Triassic and extends to the very end of the Late Cretaceous. All members of this order were fully erect obligatory bipeds with functionally tridactyl pedes: pedal digit I was usually split or missing and digit V was reduced to a vestigial metatarsal, even in the most primitive forms. The common ancestor of the theropods was almost certainly a highly arboreal canard-wing glider in which manual digit V was absent and digit IV was strongly reduced, perhaps to accommodate elongated wing feathers extending backward from digit II (the longest manual digit).

Most large theropods were predators armed with obviously carnivorous dentition, but other forms were toothless or had dentition specialized for a noncarnivorous diet. Theropods diversified into well over a score of known families, and there were probably many more of which we as yet have no fossil record. Much of the preceding Dinosaur Phylogeny section pertains to the Theropoda, and there is thus no need to repeat that discussion here.

Many of the theropod families, such as the Tyrannosauridae, Dromaeosauridae, Ornithomimidae, and Oviraptoridae, are well-diagnosed taxonomic units, but other families seem to have few distinguishing characters other than large or small size and a plesiomorphic anatomical similarity among their genera that is difficult to characterize. This could well stem from the existence of a large, cryptic theropod tachytelic core group of small, seldom preserved forms from which the larger, better-preserved forms evolved from time to time. Lacking strong synapomorphies with other theropods, the larger species would each constitute a small, monotypic family of its own. In this circumstance, unless the theropod fossil record were to improve considerably, a satisfactory theropod classification would be impossible.

I recognize nine suborders and parasuborders among the theropods, but as I have already noted more than once, their taxonomy will surely undergo considerable revision before it stabilizes.

Parasuborder Ceratosauria

The ceratosaurians are the earliest known and most primitive of the "orthodox" theropods, entering the fossil record in the Late Triassic (Late Carnian), continuing through the Late Jurassic worldwide, and persisting as abelisaurids through the Late Cretaceous in the Gondwanian continents.

This group was diagnosed as a sister group to all other theropods (the clade Tetanurae) by Rowe & Gauthier (1990), whose classification of the early ceratosaurians I have in part followed here. The genera listed by them seem to fall into three families, the Podokesauridae, Halticosauridae, and Ceratosauridae, although Rowe & Gauthier regard the families as wastebasket taxa and do not follow Linnaean systematics beyond naming the entire group Ceratosauria. Ceratosaurians were characterized by, among other things, a large antorbital fenestra with no additional preantorbital fenestrae; a fanglike dentary tooth that fit into a diastema between maxilla and premaxilla that gave the snout a "kink" below the narial opening; crested snout; two pleurocoels in the cervical vertebrae; winglike transverse processes on the dorsal vertebrae; robust scapula; presence of as many as four manual digits, but with digit IV sometimes expressed solely as a metacarpal; considerable fusion of the pelvic elements, and an extra pubic fenestra situated below the obturator foramen; long, rodlike pubes with only a slight distal "foot"; metatarsal elements exhibiting sporadic fusion; and distal third of the tail stiffened. Most of the ceratosaurian taxa reviewed by Rowe & Gauthier did not possess all of those features at the same time, but they possessed enough of them that some kind of close relationship among the taxa is evident.

According to Rowe & Gauthier, ceratosaurian forelimb bones, even the phalanges, were hollow amd thin-walled. I cannot imagine why a predatory dinosaur would evolve such a character, but I can easily understand how this development would improve the efficiency of a volant forelimb, and was passed on to flightless descendants as a structural shortcoming to be made the best of. The pneumatization of ceratosaurian skeletons is, to me, strong evidence of a volant stage in their evolution.

I list six families in the Ceratosauria, including the Abelisauridae and Noasauridae, which Paul (1988b) noted as having ceratosaurian affinities, such as a large antorbital fenestra with no preantorbital fenestrae and tetradactyl forelimbs. The Podokesauridae and Halticosauridae are largely groups of convenience for the smaller and larger early ceratosaurs, and future work will either provide better diagnoses for them or will cause them to be discarded. The Ceratosauridae comprises mainly the genus *Ceratosaurus*, which in some ways is a highly derived ceratosaurian that is clearly different from the podokesaurids and halticosaurids. Finally, the Megalosauridae is included here following a study of the group by Britt (1991).

The abelisaurids of South America are still too poorly known for any firm conclusions to be reached concerning their taxonomy, but some forms (such as *Carnotaurus*) are so highly derived postcranially that a new suborder may be warranted for them.

I consider the Ceratosauria a parasuborder because (as noted by Paul, 1988) it was probably ancestral to the Spinosauria. It is also possible that the carnosaurs and other tetanuran theropods were descended from an as-yet-unknown form resembling *Rioarribasaurus* or *Syntarsus* closely enough to be classified with them.

Suborder Spinosauria

This new suborder comprises two families of probable ceratosaurian descendants, the Baryonychidae and the Spinosauridae. Paul (1988b) noted the resemblance of the kinked-snout premaxilla of podokesaurid and halticosaurid ceratosaurians to the knoblike premaxilla of *Baryonyx*, and further suggested that the low nasal crest of *Baryonyx* might be homologous to the nasal crests of *Dilophosaurus*.

Charig & Milner (1986, 1990) emphatically deny any relationship between the genus *Baryonyx* and the Spinosauria, but at least one apomorphy—the expansion of the dentary symphysis—may place *Baryonyx* into this suborder. The obvious cranial differences between *Baryonyx* and other theropods, as well as the characters documented by Charig & Milner (1990), strongly suggest separating the family Baryonychidae into a new theropod suborder.

Study of the Spinosauridae is hampered by the destruction of the type material during World War II, but when I examined the figures of *Spinosaurus aegyptiacus* (Stromer, 1915), I noticed that the anterior dorsal vertebrae were highly opisthocoelous, indicating that the long neural spines of the genus were mobile. It would not take much dorsoventral flexion of the anterior vertebral column to separate the tips of the long spines, and "arching" the back could have served a thermoregulatory and signaling function in the species.

Suborder Carnosauria

The carnosaurs were most recently described by Molnar, Kurzanov & Dong (1990), whose diagnosis includes mainly minor anatomical features seldom visible in the incomplete material that comprises the usual type specimens. One family, the Tyrannosauridae, constitutes a well-diagnosed clade with genera that can be submitted to cladistic analysis (Bakker, Williams & Currie, 1988), but the other families are more like horizontal grades whose phyletic relationships remain obscure. Most large theropods are known only from scanty material strictly classifiable as Theropoda or Carnosauria *incertae sedis*, but I have managed to sort some of the genera into six families. Some may eventually turn out to be wastebasket categories, but there seems to be little else available. The classification given here follows Paul (1988b) and Molnar, Kurzanov & Dong (1990), insofar as they do not contradict one another. I have provisionally pigeonholed some of the problematic forms dealt with by Molnar (1990) and Norman (1990) into the carnosaur families with appropriate explanatory notes when necessary.

The most primitive carnosaur family is the Eustreptospondylidae. The type genus, *Eustreptospondylus*, is listed by Molnar *et al.* (1990) as a probable carnosaur, and Paul (1988b) grouped that genus and several others into this family. The eustreptospondylids are not very well defined, but some of their characters include a moderately prominent pubic "foot," tall, bladelike neural spines on the dorsal vertebrae, and a straplike scapula. I classified the Wealden genus *Becklespinax* in this family by virtue of its very tall dorsal neural spines and the conformation of its vertebral laminae, which is similar to that in the South American Middle Jurassic genus *Piatnitzkysaurus*.

Problems likewise beset the definition of the Allosauridae, which has only two genera that are at all well known: *Allosaurus* and *Acrocanthosaurus*. Among the characters uniting these two taxa into a family are the very prominent pubic "foot," a broad squamosal-quadrate junction, and an L-shaped proximal end of metatarsal III (as listed by Paul). The proximal end of metatarsal III in the *Valdoraptor* type specimen is worn away, so I cannot tell whether it was L-shaped from the material available to me; classifying *Valdoraptor* in the Allosauridae is thus provisional.

I sympathize entirely with Paul (1988b) in his effort to include some small theropods in the Carnosauria, because the carnosaurs were undoubtedly descended from smaller forms. But the scarcity of complete small-theropod material makes it almost impossible to find such forms.

Numerous apomorphies unite the tyrannosaurid carnosaurs into a single family, including a didactyl manus; narrow, fused nasals; serrated premaxillary teeth with a D-shaped cross-section; jugal foramen; ischium deep proximally but narrow distally; and so forth. Oddly enough, some of these features can also be observed in the small Jurassic theropod *Compsognathus*. It would be marvelous if future work discloses that the smallest-known theropod was close to the ancestry of the largest. I follow Russell (1970), Bakker, Williams & Currie (1988), and Molnar, Kurzanov & Dong (1990) in organizing this family, insofar as they do not contradict one another.

I use the parafamily Aublysodontidae (as described by Molnar & Carpenter, 1989) for tyrannosaurid-like theropods with D-shaped unserrated premaxillary teeth. The aublysodontids were probably ancestral to the tyrannosaurids, but better material is sorely needed to confirm this relationship. Likewise, the Dryptosauridae also shows a relationship with the tyrannosaurids (D. Baird, pers. comm.), but the type genus *Dryptosaurus* needs to be fully redescribed. At the 1990 SVP meeting, R. Denton (pers. comm.) displayed dryptosaurid teeth that lacked serrations on their mesial carinae, so I tentatively refer the tooth genus *Altispinax* to this family. Even if this feature were the result of tooth-to-substrate wear in the living animal, it might have taxonomic validity if it could be shown to be present in the genera consistently.

Parasuborder Protoaviformes

This group was created by Chatterjee (1991) as an avian order to accommodate his birdlike taxon *Protoavis texenis*. Like any monotypic order, it is difficult to characterize, and the range of morphological variation within the group is completely unknown. Chatterjee described in great detail the specialized, highly avian cranial structure of his new species, but the known postcranial material suggests that *Protoavis* was a small, arboreal canard-wing glider of the type described here in the section on Dinosaur Phylogeny.

As a general rule, I have found that cranial features are very variable among the archosaurs, which makes them useful for diagnosing taxa at or below the family level but perhaps misleading for distinguishing taxa above the family level. Archosaur *Baupläne* tend to be body-conservative, so although *Protoavis* exhibits strong avian features in the skull, as might be expected in an arboreal canard-wing glider closely related to true birds, I believe it is best classified as a theropod.

Suborder Coelurosauria

Theropods referred to the suborder Coelurosauria in the past have had a disconcerting history of becoming something else (*e.g.*, ornithomimids, dromaeosaurids, or troodontids) when better material was described. Gauthier (1986a, 1986b) attempted to remedy the situation by redescribing the group as the clade containing the Ornithomimidae plus the Maniraptora, with the Maniraptora in turn being the clade of theropods with an avian forelimb articulation (*cf.* Gauthier & Padian, 1985) – namely, the deinonychosaurs, oviraptorosaurs, *Archaeopteryx*, and birds.

Since I exclude the birds from the Archosauria, I do not use the clade Maniraptora as a taxon. But I regard the known maniraptoran theropods as flightless descendants of volant theropods in which the wing had developed a power stroke and was able to fold up against the body in an avian fashion, as described by Gauthier & Padian (1985).

In the final analysis, I am afraid that most of the genera in the Coelurosauria are simply undiagnosable small theropods (Norman, 1990), and that the suborder must serve as a wastebasket group for such forms. Only two genera, *Compsognathus* and *Ornitholestes*, are known from good material. They have not yet been assigned to any better-diagnosed theropod group, so I have essentially retained the Coelurosauria to accommodate them.

Suborder Ornithomimosauria

This suborder was originally created as a theropod infraorder by Barsbold (1976) to comprise the "ostrich-mimic" dinosaurs of the Early and Late Cretaceous. Largely restricted to North America and Asia, the ornithomimosaurians were eventually subdivided into three families: Harpymimidae, Garudimimidae, Ornithomimidae, and Deinocheiridae. There is a general consensus among theropod specialists (*e.g.*, Paul, 1988b) that the monotypic families Harpymimidae and Garudimimidae are a case of oversplitting, and that the single family Ornithomimidae can accommodate the genera in the latter two families. Other than this, I have for the most part followed Russell (1972) and Barsbold & Osmólska (1990) in organizing the Ornithomimidae.

The Deinocheiridae, however, is a monotypic family based essentially on a pair of enormous theropod forelimbs almost 3 meters long. Described as *Deinocheirus mirificus*, the forelimbs have confounded taxonomists ever since their discovery. I follow Norman (1990) in tentatively including this family in the Ornithomimosauria. In the absence of any other deinocheirid remains, it is difficult to exclude the possibility that the resemblances between *Deinocheirus* and other ornithomimosaurs are the result of convergence.

Ornithomimid forelimbs were relatively long, entirely tridactyl with three subequal digits, and characterized by weakly developed crests for muscular attachment. The hind limbs, on the other hand, were long, slender, and well adapted for running. These features lead me to imagine that ancestral ornithomimids may have originated as cursorial descendants of a small arboreal theropod that was adapted for gliding and soaring but not powered flight. Nicholls & Russell (1981) found that many ornithomimid genera can be differentiated by the structure of their manus.

Suborder Deinonychosauria

This group includes most of the theropod genera that developed a specialized "killer claw" on their pedal digit II. Large pedal unguals are, however, known in some small theropods outside this suborder (such as *Noasaurus*), so it is possible that the presence of this character in the Dromaeosauridae and the Troodontidae is homoplasious. More significant, perhaps, is the extraordinarily birdlike articulation of the forelimb and manus in dromaeosaurids (Gauthier & Padian, 1985), and the birdlike anatomy of the skull in both dromaeosaurids and troodontids. These suggest to me that both families descended from volant theropods that had developed a version of the wingstroke of extant birds. Paul (1984, 1988b) noted a very close relationship between *Archaeopteryx* and the dromaeosaurids, and I have followed this suggestion in placing the Archaeopterygidae in this suborder as a parafamily ancestral to the Dromaeosauridae. Interestingly, all of the well-known dromaeosaurids occur considerably later than *Archaeopteryx* in the fossil record; Paul's hypothesis perhaps accounts for this.

I have organized this suborder primarily according to Ostrom (1990) and Osmólska & Barsbold (1990).

Suborder Oviraptorosauria

The oviraptorosaurs were a small group of highly derived, birdlike maniraptoran theropods known exclusively from the Late Cretaceous of Mongolia. They seem to fall into four families, Caenagnathidae, Elmisauridae, Oviraptoridae, and Ingeniidae, but better material may disclose that some of these families should be subsumed into the others. In the best-known genera, *Oviraptor* and *Conchoraptor*, the skull was almost completely toothless with a strongly reduced maxilla very reminiscent of the condition in modern birds. Postcranially, however, oviraptorosaurs had a typically theropod anatomy. It is plain to me that these cursorial theropods were descended from a group of volant theropods more derived than the archaeopterygids.

I have organized this suborder primarily according to Barsbold, Maryanska & Osmólska (1990) and Currie (1990).

Suborder Avimimiformes

Chatterjee (1991) created this group as an order of primitive avians to accommodate the birdlike form *Avimimus portentosus* from the Late Cretaceous of Mongolia. This was a nearly toothless cursorial form with large, maniraptoran forelimbs that I consider to be yet another flightless descendant of a volant theropod. It does not show a close relationship with other theropods (Norman, 1990) and probably does merit a suborder within the Theropoda.

SAUROPODOMORPH ORDERS

The sauropodomorphs include the enormous quadrupedal, graviportal herbivores with elongate necks and tails. As noted earlier, I do not consider them particularly closely related to the theropodomorphs, because the sauropodomorphs possessed a large suite of autapomorphies setting them apart from the other dinosaurian groups. Although they were highly derived animals, they also displayed a number of primitive features, such as a fully pentadactyl manus and pes, that show early evolutionary divergence. In particular, sauropodomorph skeletons show no evidence of an arboreal stage in their evolution, and no clear evidence that sauropodomorphs endured a bipedal stage, either (Charig, Attridge & Crompton, 1965; Charig, 1982). Most evidence, in fact, suggests that sauropodomorphs evolved directly from as-yet-unknown fully erect quadrupedal archosaurs. There is also no evidence of a tachytelic sauropodomorph core group; their diversity from the Late Triassic to the Late Cretaceous can be entirely accounted for by the bradytelic evolutionary pattern common to large terrestrial vertebrates.

I have very tentatively included the order Segnosauria in the Sauropodomorpha, because the segnosaurians seem like highly derived prosauropods to me. Recent work by D. A. Russell (pers. comm.), however, suggests instead that they were *very* highly derived theropods—as originally classified—and that their resemblance to sauropodomorphs was homoplasious. J. S. McIntosh (pers, comm.) notes that he can see no relationship between segnosaurians and sauropods, and only a slight connection if any with the prosauropods. Barsbold & Maryanska (1990) are noncommittal about the placement of the group, regarding it as Saurischia *sedis mutabilis*, that is, "of changeable position." When Russell's work is published, I will probably have to move the Segnosauria back into the Theropodomorpha as a tenth order, but until then I provisionally retain the group within the Sauropodomorpha.

In elevating the Sauropodomorpha to supraordinal status, it was necessary to decide whether the Prosauropoda and Sauropoda themselves should each become orders. I agree that the sauropods and prosauropods *together* form a distinctive dinosaurian order, but the prosauropod *Bauplan* is merely a variation of the sauropod *Bauplan*, and the Prosauropoda itself was neither diverse enough nor distinct enough from the Sauropoda to require more than subordinal status. The most natural solution was to create a single order within which the prosauropods and the sauropods were suborders. This monophyletic unit I have named the Brontosauria.

Order Brontosauria

Brontosaurs were sauropodomorphs with brachyiliac pelves, as opposed to the segnosaurs, which possessed very broad, "altiliac" pelves. There were also major differences between the two orders in the structure of the skull, forelimb, and pedes. Brontosaurs possessed five columnar metacarpals arranged in a U-shaped arcade, and manual digit I was armed with a large claw. The only known segnosaurian forelimb is that of *Therizinosaurus*, which is about as different from a brontosaur forelimb as a dinosaurian forelimb could be. It was tridactyl, and each digit possessed a huge claw as much as a meter long; the digits were not of equal length, and the humerus had a very prominent deltopectoral crest. If this forelimb is correctly referred to the Segnosauria, then it weakens the argument for including the Segnosauria within the Sauropodomorpha.

Parasuborder Prosauropoda

The most primitive brontosaurs were the prosauropods, which appeared in the fossil record in the Late Triassic and vanished by the end of the Lower Jurassic. As noted earlier, prosauropods were once classified as theropods, but this is no longer thought to be correct. Most of the well-known prosauropod genera seem to fall into an evolutionary series of larger and more graviportal forms that converge on the Sauropoda (Benton, 1990a), but Galton (1990) has determined that the known prosauropods constitute a clade of their own, which diverged from the sauropod clade sometime before the earliest known prosauropod entered the fossil record.

All known prosauropods possessed a strongly reduced metatarsal V with at most one phalanx, even the larger forms (Melanorosauridae and Blikanasauridae). Since sauropods possessed all five pedal digits, none of the known prosauropods could have been an ancestral sauropod. The common ancestor of both suborders, a prosauropodlike sauropodomorph with five robust pedal digits, has yet to be discovered.

Galton (1990) classified the prosauropods into no less than seven families, some monotypic, and I have largely followed his sytem here. The familial differences, which encompass teeth, cranial anatomy, and the structure of the manus and pes, seem real to me; I do not think Galton has oversplit the group, although perhaps the Massospondylidae and Anchisauridae will ultimately prove synonymous. I regard the Prosauropoda as a parasuborder, although none of the known families would contain the ancestral sauropod.

Suborder Sauropoda

As one might imagine, these dinosaurs are the most difficult of all to work with, because of the large size of the specimens and because many key specimens are permanently mounted for museum display. From a systematic standpoint, the lack of associated skull material for most of the known genera presents an acute problem that is only now being overcome. Sauropod taxonomies in which genera are diagnosed on postcranial features, such as the configurations of vertebral laminae, are in various stages of development (Bonaparte, 1986b).

Sauropods differed from prosauropods in being generally much larger and more massively built. Prosauropod skulls were long and narrow, with narial openings situated near the tip of the snout; sauropod skulls tended to be shorter and blunter, and all known skulls show some movement of the narial openings toward the top of the skull. Diplodocid skulls were long and narrow, but the narial openings were located above the orbits. Prosauropod teeth were small, numerous, and of a simple herbivorous design; sauropod teeth were larger, less numerous, and of two derived designs: leaf-shaped and peg-shaped. Prosauropods possessed elongate necks with 10 cervical vertebrae, but sauropod necks had at least 12 and as many as 19 vertebrae. Sauropods had five or six sacral vertebrae, prosauropods three or four. Sauropod dorsal vertebrae usually had substantially taller neural spines than did prosauropod vertebrae, and they were lightened by pleurocoels, which were generally absent from prosauropod vertebrae. In many sauropod genera, the neural spines of the posterior cervicals and anterior dorsals were bifurcated, a character that probably arose more than once as an adaptation for bearing great weight and, perhaps, for control of the neck. The shapes of the chevron bones and caudal vertebrae are also important in sauropod classification.

I classify the sauropods into nine families, primarily following McIntosh (1990). One of the most primitive families, the Cetiosauridae, seems to have been ancestral to many of the later families, so I list it here as a parafamily.

Order Segnosauria

Segnosaurs were characterized by many autapomorphies, especially including their very distinctive "altiliac" pelvis, which was opisthopubic and very broad in dorsal view. The pubis was fused with the ischium in some genera, but was reduced in others. The ungual phalanges were particularly long and laterally compressed, reaching almost a meter in length in *Therizinosaurus*. Although only a few genera have been described, they are so different from other dinosaurs that their ordinal status is practically beyond question, no matter which group they may have originated from.

I recognize two families, Segnosauridae and Therizinosauridae, but the latter family is known essentially from a very large forelimb and isolated unguals. A segnosaurlike pes has also been referred to the Therizinosauridae.

ORNITHISCHIAN ORDERS

There are numerous synapomorphies uniting the various groups within Seeley's order Ornithischia, which for the reasons noted under Dinosaur Phylogeny I retain as a dinosaurian superorder. All dinosaurologists agree that the Ornithischia is monophyletic, and as I mentioned previously, the only disagreements about the ornithischians concern details of the interrelationships of its six major subclades. These groups present six distinctly different *Baupläne* worthy of straightforward classification into six separate orders, namely, Lesothosauria, Ankylosauria, Stegosauria, Pachycephalosauria, Ceratopsia, and Ornithopoda. Three of the orders are parataxa: Lesothosauria, which I consider basal to the orders Ankylosauria, Pachycephalosauria, and Ornithopoda; Ankylosauria, which is most likely ancestral to the Stegosauria; and Pachycephalosauria, which is almost certainly ancestral to the Ceratopsia.

The key autapomorphy of the Ornithischia is the opisthopubic pelvis, which was noted by Seeley (1888) when he created the order. Other splendid autapomorphies are the presence of a predentary bone, extra supraorbital ossifications (such as a palpebral bone), and a pendant fourth trochanter (this may have arisen convergently in some prosauropods: Cooper, 1985). Sereno (1986) listed many more ornithischian characters in his comprehensive cladistic review of the group. All known ornithischians possessed herbivorous dentition, and the shapes of the teeth are generically diagnostic.

Sereno (1986) convincingly grouped the Ankylosauria and Stegosauria into a clade previously called Thyreophora, and the Pachycephalosauria and Ceratopsia into one he named Marginocephalia. On the form of the ischium (lacking an obturator process: Santa Luca, 1980) I would further group these two clades into a larger clade, reflecting their strong distinction from the ornithopods (in which there is always a prominent obturator process), but there is presently less need to name such clades than simply to bear in mind how the ornithischian orders might be related to each other. In Sereno's classification, the Marginocephalia and the Ornithopoda (his Euornithopoda) were grouped into the clade Cerapoda. However, inasmuch as an incipient obturator process does seem to be present in *Lesothosaurus* (Weishampel & Witmer, 1990a: 421; *contra* Sereno, 1991, who nevertheless figured it as a kink in the ventral margin of the ischium in his Figures 9, 10), I believe that the Ornithopoda arose separately from the other ornithischians within the Lesothosauria.

I do not employ the terms Thyreophora and Marginocephalia, despite their usage in *The Dinosauria* (Weishampel, 1990; Coombs, Weishampel & Witmer, 1990a; Dodson, 1990b), because they are redundant with the paraorders Ankylosauria and Pachycephalosauria. Otherwise, the ornithischians are classified here much as they were in *The Dinosauria*. A plausible classification of the Ornithischia into four orders (Lesothosauria, Thyreophora, Marginocephalia, and Ornithopoda) rather than six, with Thyreophora divided into suborders Ankylosauria and Stegosauria, and Marginocephalia into Pachycephalosauria and Ceratopsia, was rejected as too cumbersome.

Paraorder Lesothosauria

This order is erected here for the solitary ornithischian taxon *Lesothosaurus*, whose key character was the lack of lateral maxillary and mandibular emargination for cheeks. This was plesiomorphic for the Ornithischia, but the presence of cheeks in all other well-known ornithischians serves to distinguish this basal order. Other autapomorphies were listed by Weishampel & Witmer (1990a) and Sereno (1991).

Lesothosaurus itself occurs too late (Lower Jurassic) to be ancestral to any known ornithischian taxa, but earlier lesothosaurians were probably ancestral to basal ankylosaurians (such as *Scutellosaurus*) and pachycephalosaurians (such as *Pisanosaurus*). Cheeks may have evolved twice in the Ornithischia, first in the Ankylosauria plus Pachycephalosauria, and again in the Ornithopoda. The incipient obturator process of *Lesothosaurus* places it closer to the Ornithopoda than to the ankylosaurian-pachycephalosaurian clade.

Several other small ornithischians known from fragmentary and incomplete specimens, primarily jaws and teeth, some of which were previously classified in the family Fabrosauridae, are included in the order Lesothosauria *incertae sedis*.

Paraorder Ankylosauria

Ankylosaurians were a major group of ornithischians characterized by broad, low bodies with overall dermal armor consisting of various kinds of keeled scutes, spines, and plates. They originated as small scelidosaurids sometime before the Early Jurassic, remained in the background of the fossil record throughout much of the Middle and Late Jurassic, and finally emerged as important faunal elements during the Early Cretaceous, just as the stegosaurians were diminishing. For many decades, the ankylosaurian fossil record included no forms earlier than Early Cretaceous (the scelidosaurids were then considered stegosaurians), but during the 1980s Galton (*cf.* citations in Coombs & Maryanska, 1990) extended their fossil record back to the Middle Jurassic, and it is now known that the ankylosaurians did not originate at the start of the Cretaceous.

Nopsca (1915) suggested uniting all the armored dinosaurs (stegosaurs, ankylosaurs, and ceratopsians) into the single group Thyreophora. In view of the anatomical differences among the included forms, dinosaurologists did not adopt Nopsca's term. Recently, however, the Thyreophora was revived as the smallest clade uniting all armored ornithischians, from the most primitive known armored form, *Scutellosaurus*, to the stegosaurs and ankylosaurs. The ceratopsians, which lacked dermal armor and belong to a different ornithischian clade, are, however, excluded (Sereno, 1984, 1986; Cooper, 1985; Gauthier, 1986a, 1986b).

I conjecture that dermal armor in the Ankylosauria was homologous to the parasagittal dermal armor observed in most thecodontians and was plesiomorphic to the order Ornithischia. Basal ankylosaurians are regarded as the most primitive ornithischians above the lesothosaurian level (Sereno, 1986), so there is indeed some chance that they retained the parasagittal dermal armor of as-yet-unknown ancestral proterosuchians. Dermal armor may also have been present in some ornithopods, such as *Hypsilophodon* and *Thescelosaurus*, but the evidence is weak (Galton, 1974a, 1974b; Sues & Norman, 1990).

Within the Ankylosauria, neither the Nodosauridae nor the Ankylosauridae has any known higher-level descendant taxa (although the Ankylosauridae might be derived from as-yet-unknown early nodosaurids). The basal family Scelidosauridae, however, is thought to be a sister group to the order Stegosauria and the other two ankylosaurian families, and may be regarded as ancestral to them. The resemblance of scelidosaurid genera, such as *Scelidosaurus* and *Emausaurus*, to the primitive stegosaurian genus *Huayangosaurus* is quite apparent and serves to confirm their common ancestry. The deep morphological differences between the later stegosaurians and the later ankylosaurians are what prompted me to retain the Stegosauria as a separate order instead of making it an ankylosaurian suborder. Otherwise, the Ankylosauria is organized mainly according to Coombs & Maryanska, 1990.

Order Stegosauria

Stegosaurians comprise a small monophyletic order of closely related armored dinosaurs. They had a worldwide distribution and probably originated sometime shortly before or during the Middle Jurassic, and they may have endured as a relict group to the end of the Late Cretaceous. Known forms are most numerous from Middle and Late Jurassic faunas of China.

In stegosaurians, the dermal armor was arranged parasagittally as paired spikes or thin plates parellel to the spine. Apart from paired shoulder spines, caudal spikes, and occasional regions of dermal ossicles, stegosaurians were essentially unarmored. Ankylosaurians possessed dermal ossicles and keeled scutes over most of their bodies, ventrally as well as dorsally in some forms. If spines were present, they were situated laterally along the neck and shoulders; the tail possessed a club in ankylosaurids, but otherwise it was unarmed. Stegosaurian hind limbs were generally much longer and straighter than the front limbs, but in ankylosaurians, the limbs were of roughly equal length. The stegosaurian pelvis possessed a large pubis with a well-developed prepubic process; the ankylosaurian pubis had a poorly developed or absent prepubic process, and in later forms the pubis itself was highly reduced. Later ankylosaurians possessed a broad, splayed-out pelvis that matched their low, broad bodies, but later stegosaurians possessed tall, narrow bodies with significantly narrower pelves. Stegosaurian vertebrae were tall with elevated neural spines and arches, which contributed to the overall tallness and narrowness of their bodies; ankylosaurian vertebrae had shorter neural spines and arches. Stegosaurian skulls tended to be long and narrow, and ankylosaurian skulls tended to be short and broad. Comparing figures in Galton (1990b) and Coombs & Maryanska (1990) discloses many other differences between stegosaurian and ankylosaurian skeletons.

I follow Galton (1990b) in retaining two families of stegosaurians, the more primitive parafamily Huayangosauridae and its descendant family, Stegosauridae.

Paraorder Pachycephalosauria

The pachycephalosaurians constitute a small but widespread group of ornithischians that were until recently classified as an orithopod subgroup. Maryanska & Osmólska (1974) established them in a separate ornithischian suborder, and Sereno (1986) noted their affinities with ceratopsians and established the clade Marginocephalia for the two groups.

One of the biggest departures of this list from previous taxonomies is to include the heterodontosaurids within this paraorder rather than as the most primitive ornithopod group. Santa Luca (1980) described the postcranial anatomy of *Heterodontosaurus*, the only well-known heterodontosaurid, and noted that the ischium lacked an obturator process. This, he asserted, mandated removal of the Heterodontosauridae from the Ornithopoda. Subsequent studies of the ornithischians (*cf.* the cladograms cited in Benton, 1990a) seem to have ignored this observation, and the heterodontosaurids continue to appear as a basal outgroup within the Ornithopoda in published classifications.

Shortly after Santa Luca's paper, the description of the primitive pachycephalosaur *Goyocephale lattimorei* by Perle, Maryanska & Osmólska (1982) noted the existence of a fanglike premaxillary tooth in that species, and a diastema at the premaxillary-maxillary junction in many pachycephalosaurs that may have accommodated a dentary fang. Such teeth were homologous to the maxillary and dentary fangs of *Heterodontosaurus*. It was those observations that convinced me that the heterodontosaurids had been persistently misclassified among the ornithopods. They should instead be thought of as basal pachycephalosaurians in which the skull had not yet developed the characteristic thick bony dome.

Norman (1984) and Norman & Weishampel (1985) inadvertently noted another significant difference between heterodontosaurids and other ornithopods when they described the kinds of cranial kinesis found in the Ornithopoda. Heterodontosaurids differed from all ornithopods in having had akinetic skulls; ornithopods possessed pleurokinetic skulls as part of their intricate adaptations for chewing resistant plant matter. Cranial akinesis, however, is an obvious character common to pachycephalosaurians and ceratopsians. It further strengthens the hypothesis that heterodontosaurids were basal pachycephalosaurians.

Weishampel & Witmer (1990b) recently reviewed the Heterodontosauridae. As might be expected of any basal ornithischian group, the heterodontosaurids were found to be similar to hypsilophodontids overall. But interestingly, they noted the presence of a jugal boss in *Heterodontosaurus* that is not known in ornithopods but could well be regarded as incipient to the prominent, hornlike jugals present in later pachycephalosaurians and ceratopsians. I believe that further study will disclose a suite of characters further increasing the gap between heterodontosaurids and ornithopods and diminishing the gap between heterodontosaurids and pachycephalosaurians.

Otherwise, my classification of the Pachycephalosauria follows that of Maryanska (1990). I consider the group, with the Heterodontosauridae included, to be a paraorder ancestral to the order Ceratopsia, but at present there is no described pachycephalosaurian family that convincingly bridges the morphological gap between the orders. I have included the poorly known Triassic parafamily Pisanosauridae as the most basal pachycephalosaurians primarily because the mandible of *Pisanosaurus* conforms to my idea of a heterodontosaurid mandible prior to the development of the autapomorphic dentary fang (Weishampel & Witmer, 1990a). Sereno (1986) clearly demonstrated that the Homalocephalidae ("flat-headed" pachycephalosaurians) were ancestral to the Pachycephalosauridae ("dome-headed" pachycephalosaurians), so the Homalocephalidae comprise another pachycephalosaurian parafamily. Finally, Chao (1983: name spelled Zhao then) noted the existence of a Chinese form (*Chaoyoungosaurus*) that some popular Chinese publications place at the base of the pachycephalosaurian-ceratopsian divergence. Until a formal description is published, however, the parafamily Chaoyoungosauridae is a *nomen nudum*.

Order Ceratopsia

The ceratopsians, or horned dinosaurs, form a well-defined monophyletic group of restricted distribution that evidently arose during the Early Cretaceous. It includes two parafamilies and one family that form an ancestor-descendant series: the Psittacosauridae was ancestral to the Protoceratopsidae, which was in turn ancestral to the Ceratopsidae. Furthermore, within the Ceratopsidae, the parasubfamily Eucentrosaurinae was ancestral to the Chasmosaurinae. In this fairly straightforward progression, the forms that lacked frill and horns (Psittacosauridae) first developed frills (Protoceratopsidae) and then horns (Ceratopsidae). Within the Ceratopsidae, the Eucentrosaurinae possessed short frills, short, deep skulls, large nasal horns, and small frontal horns, which was clearly closer to the protoceratopsid condition than the long frills, long skulls, small nasal horns, and large frontal horns found in the Chasmosaurinae.

I have organized the Ceratopsia according to Sereno (1990), Dodson & Currie (1990), and Lehman (1990), although I have not used the clade Neoceratopsia for Protoceratopsidae plus Ceratopsidae. I used the American spellings of the names Ceratopsia, Protoceratopsidae, and Ceratopsidae, even though the British spellings Ceratopia, Protoceratopia, and Ceratopidae are etymologically correct. In fact, calling the group "Ceratopsia" is as egregious as calling the family Tyrannosauridae "Tyrannosaurusidae," but this inapt usage has thus far prevailed on this side of the Atlantic Ocean.

Order Ornithopoda

The ornithopods were the most diverse ornithischian order, comprising obligatory and facultatively bipedal forms ranging from 1 to 15 or more meters in length. They enjoyed a worldwide distribution from some time before the Middle Jurassic through the end of the Late Cretaceous. The key autapomorphy that characterizes the Ornithopoda is the obturator process on the ischium, a character whose function I have not been able to determine, but which is derived within the Ornithischia.

Of all the ornithischians, the ornithopods are the most-studied group, and cladograms relating its families and genera abound in the literature. Most cladistic studies of the group are in broad agreement with each other, and I simply follow the ornithopod taxonomy presented in *The Dinosauria* (Sues & Norman, 1990; Norman & Weishampel, 1990; Weishampel & Horner, 1990). As noted above, however, I have removed the Heterodontosauridae from the Ornithopoda, leaving the Hypsilophodontidae as the most primitive (para)family. Also, I follow Horner concerning the separate origination of the families Lambeosauridae and Hadrosauridae from within the parafamily Iguanodontidae (Horner, 1988, 1990). As he notes, the postcranial anatomy of the iguanodontid *Ouranosaurus* is closer to that of the lambeosaurids than to that of any hadrosaurid.

Sereno (1986) partitioned the Ornithopoda into two major clades, the Hypsilophodontia and the Iguanodontia, each of which was further divided into subclades. The Iguanodontia in particular contained a nested series of clades five deep converging on the Hadrosauridae. I have abandoned this kind of cladistic microtaxonomy in favor of simply listing the families and parafamilies and their included genera serially. The debate over the detailed relationships among the ornithopod genera is quite hearty—and for the most part beyond the scope of this work.

I regard the Hypsilophodontidae as a parafamily because it is probably ancestral to the Dryosauridae, Camptosauridae, and Iguanodontidae, and the Iguanodontidae as a parafamily because it was almost certainly ancestral to the Hadrosauridae and Lambeosauridae. This is an expanion of the scope of the Hypsilophodontidae over what is given by Sues & Norman (1990), who restrict it to the monophyletic clade containing only the better known genera. Further comments that I have on the ornithopods may be found as notes in that section of the table, and also in the subsections on the Stem-Group Problem and the Too-Deep-Hierarchy Problem in the Taxonomic Considerations section. The hypsilophodontids, as noticed by several authors (*e.g.*, Galton, 1972), comprised a "plexus" of difficult-to-distinguish lineages. This impression results from their somewhat tachytelic core-group role within the Ornithopoda.

The listing of hadrosaurid genera given by Weishampel & Horner (1990) notes four evolutionary lineages ("gryposaurs," "brachylophosaurs," "saurolophs," and "edmontosaurs") of advanced hadrosaurids in addition to an unnamed basal group. I have refrained from creating subfamilies within the Hadrosauridae pending the forthcoming revision of the Hadrosauridae and Lambeosauridae by Horner.

Notes

Parasuperorder: Theropodomorpha nov.

Census: 4 orders, 34 families, 159 genera (42 doubtful), 221 species (80 doubtful)

Paraorder: Basitheropoda nov.

Census: 2 families, 3 genera, 3 species

Family: MEGALANCOSAURIDAE nov.

Census: 2 genera, 2 species

Genus: *Cosesaurus* Ellenberger & de Villalta, 1974
  C. aviceps Ellenberger & de Villalta, 1974 (Type)

NOTE: Originally classified as a thecodontian and thought to be a possible ancestral avian, this genus was identified as an eosuchian by Olsen (1979) and was classified as a prolacertiform reptile by Sanz & López-Martínez (1984). Molnar (1985), however, noted the presence of an antorbital fenestra in the type specimen as well as a general morphological similarity to *Megalancosaurus*, so the genus may be provisionally classified in this family.

Genus: *Megalancosaurus* Calzavara, Muscio & Wild, 1980
  M. preonensis Calzavara, Muscio & Wild, 1980 (Type)

Family: LONGISQUAMIDAE Sharov, 1970

Census: 1 genus, 1 species

Genus: *Longisquama* Sharov, 1970
  = *Longisquamata* McLoughlin, 1979 [*sic*]
  L. insignis Sharov, 1970 (Type)

Order: Lagosuchia Paul, 1988

Census: 2 families, 3 genera, 3 species

Family: LAGOSUCHIDAE Bonaparte, 1975

Census: 2 genera, 2 species

= Lagosuchinae Paul, 1988

Genus: *Lagosuchus* Romer, 1971
  L. talampayensis Romer, 1971 (Type)
    = *Lagosuchus lilloensis* Romer, 1972

Genus: *Pseudolagosuchus* Arcucci, 1987
  P. major Arcucci, 1987 (Type)

NOTE: This genus is referred to the Staurikosauridae by Paul (1988).

Family: LAGERPETONIDAE Arcucci, 1987

Census: 1 genus, 1 species

Genus: *Lagerpeton* Romer, 1971

L. chanarensis Romer, 1971 (Type)
= *Lagerpeton canarensis* Paul, 1988 [*sic*]

Genus: [To be described from the Upper Triassic of New Mexico: a new kind of "thecodont similar to a small dinosaur"; *cf.* New Mexico Museum of Natural History publication *Timetracks 8*(4): p. 4]

Order: Herrerasauria Galton, 1985

Census: 2 families, 8 genera (1 doubtful), 8 species (1 doubtful)

Family: STAURIKOSAURIDAE Galton, 1977

Census: 3 genera (1 doubtful), 3 species (1 doubtful)

Genus: "Chindesaurus" Murry & Long, 1989 [to be described; listed in several articles in *Dawn of the Age of Dinosaurs in the American Southwest*, S. G. Lucas & A. P. Hunt, eds., 1989]
= *Chindesaurus* [Anonymous] 1985 [*nomen nudum*, in *Science News 127*(21): 325, May 25, 1985]
"C. bryansmalli" Murry & Long, 1989 [to be described]
= *Chindesaurus smalli* [Anonymous] 1985 [*nomen nudum*, in *San Diego Union*, June 2, 1985]

Genus: *Frenguellisaurus* Novas, 1986
F. ischigualastensis Novas, 1986 (Type)
NOTE: This genus, originally described as a primitive theropod, may be a staurikosaurid (Molnar, 1990). It is classified in the Herrerasauridae in Paul, 1988. Referred to this family provisionally.

Genus: *Spondylosoma* von Huene, 1942 [*nomen dubium*]
= *Spondylosma* Hunt, 1991 [*sic*]
S. absconditum von Huene, 1942 (Type)
NOTE: This genus, originally described as a primitive saurischian, may be a staurikosaurid. Listed as Dinosauria *incertae sedis* by Sues (1990); referred to this family provisionally.

Genus: *Staurikosaurus* Colbert, 1970
= *Starikosaurus* Parrish, 1989 [*sic*]
S. pricei Colbert, 1970 (Type)

Family: HERRERASAURIDAE Benedetto, 1973

Census: 3 genera, 3 species

= Herrarasauridae Gauthier & Padian, 1985 [*sic*]

Genus: *Herrerasaurus* Reig, 1963
= *Herrarasaurs* Gauthier, 1986 [*sic*]
= *Herrarasaurus* Gauthier & Padian, 1985 [*sic*]
H. ischigualastensis Reig, 1963 (Type)

Genus: *Ischisaurus* Reig, 1963
I. cattoi Reig, 1963 (Type)

Genus: *Sinosaurus* Young, 1948
S. triassicus Young, 1948 (Type)
NOTE: The type specimen of this species (a left maxilla with teeth and associated fragments) may belong to a herrerasaurid, but postcranial material referred to this species is prosauropod (Rozhdestvensky, 1965; Charig, Attridge & Crompton, 1965; van Heerden 1975, 1980). Norman (1990) lists it as a *nomen dubium*, Theropoda *incertae sedis*. P. J. Currie (pers. comm.) suggests it may be a ceratosaur. Classified in this family provisionally.

HERRERASAURIA *incertae sedis*

Census: 2 genera, 2 species

Genus: *Aliwalia* Galton, 1985
A. rex Galton, 1985 (Type)
NOTE: Listed as Dinosauria *incertae sedis* by Sues (1990).

Genus: *Walkeria* Chatterjee, 1986
W. maleriensis Chatterjee, 1986 (Type)
NOTE: Initially described as a podokesaurid theropod, the above genus is classified in the Herrerasauridae in Paul, 1988 and as a herrerasaurian in Novas, 1989. Listed as Theropoda *incertae sedis* by Norman (1990).

Paraorder: Theropoda Marsh, 1881

Census: 9 suborders, 28 families, 145 genera (41 doubtful), 207 species (79 doubtful)

Parasuborder: Ceratosauria Marsh, 1884

Census: 6 families, 41 genera (12 doubtful), 61 species (28 doubtful)

Family: PODOKESAURIDAE von Huene, 1914

Census: 6 genera (2 doubtful), 8 species (3 doubtful)

= Coelophysidae Paul, 1988
= Coelophysinae Nopcsa, 1928
= Podokesaurinae Nopcsa, 1923
= Segisauridae Camp, 1936

Genus: *Coelophysis* Cope, 1889 [*nomen dubium* in Hunt & Lucas, 1991]
= *Coelophyses* Stokes, 1988 [*sic*]
C. bauri (Cope, 1887) (Type)
= *Coelurus bauri* Cope, 1887 [*nomen dubium*]
= *Tanystrophaeus bauri* (Cope, 1887) [*nomen dubium*]
C. willistoni (Cope, 1887) [*nomen dubium*]
= *Tanystrophaeus willistoni* Cope, 1887 [*nomen dubium*]
NOTE: See note for *Rioarribasaurus*.

Genus: *Longosaurus* Welles, 1984 [*nomen dubium* in Hunt & Lucas, 1991]
L. longicollis Welles, 1984 (Type)
= *Coelurus longicollis* Cope, 1887 [*nomen dubium*]
= *Coelophysis longicollis* (Cope, 1887) [*nomen dubium*]
= *Tanystrophaeus longicollis* (Cope, 1887) [*nomen dubium*]
= *Coelophysis collis* Haughton, 1932 [*sic*]
NOTE: Hunt & Lucas, 1991 indicate that the type specimen of *Longosaurus longicollis* is not part of the lectotype of *Coelurus longicollis*, so the synonymy between the two taxa is only subjective. See also note for *Rioarribasaurus*.

Genus: *Podokesaurus* Talbot, 1911
P. holyokensis Talbot, 1911 (Type)
= *Coelophysis holyokensis* (Talbot, 1911)

Genus: *Rioarribasaurus* Hunt & Lucas, 1991
R. colberti Hunt & Lucas, 1991 (Type)
NOTE: This genus and species were proposed for the Ghost Ranch theropods previously referred to *Coelophysis*. Hunt & Lucas (1991) regard *Coelophysis bauri* and *Longosaurus longicollis* as *nomina dubia* based on inadequate or incorrectly identified material and so unsuitable as names for the Ghost Ranch theropods.

Genus: *Segisaurus* Camp, 1936
S. halli Camp, 1936 (Type)

Genus: *Syntarsus* Raath, 1969
S. rhodesiensis Raath, 1969 (Type)
= *Coelophysis rhodesiensis* (Raath, 1969)
S. kayentakatae Rowe, 1989

Genus: [To be described from the *Rutiodon zunii* zone of the lower portion of the Petrified Forest Member of the Chinle Formation of Arizona; R. A. Long, pers. comm.]

Genus: [To be described from the Ghost Ranch quarry: a theropod with a skull resembling that of *Rioarribasaurus* but possessing a prominent sagittal crest; specimen presently housed at the Carnegie Museum; R. A. Long, pers. comm.]

Genus: [To be described from the Chinle Formation near Lacey Point, Petrified Forest; UCMP specimen 129618, similar to but differing in anatomical details from *Rioarribasaurus*; Padian, 1986; Hunt & Lucas, 1991]

Genus: [To be described; a "small ceratosaur" from the Lower Chinle Formation; Murry & Long, 1989; Colbert, 1989]

Family: HALTICOSAURIDAE von Huene, 1956

Census: 6 genera (3 doubtful), 7 species (3 doubtful)

= Halticosaurinae Paul, 1988

Genus: *Dandakosaurus* Yadagiri, 1982?
  D. indicus Yadagiri, 1982? (Type)

NOTE: This is one of two "carnosaurs" reported by Yadagiri (1979) from the Kota Formation of India. Reference not yet seen, so year is uncertain, but the genus and species are reported as having "certain similarities with *Sinosaurus triassicus*" in *Geological Survey of India Annual General Report for 1982–83, 117* (1990): 223. Provisionally classified as a halticosaurid, pending receipt of a copy of the paper that explains just which parts of the composite *Sinosaurus triassicus* this genus is similar to.

Genus: *Dilophosaurus* Welles, 1970
  D. wetherilli (Welles, 1970) (Type)
    = *Megalosaurus wetherilli* Welles, 1970
  [New large species to be described; Welles, 1984]

Genus: *Dolichosuchus* von Huene, 1932 [*nomen dubium*; = *Halticosaurus* or *Liliensternus*?]
  D. cristatus von Huene, 1932 (Type)

NOTE: Listed as Theropoda *incertae sedis* by Norman (1990).

Genus: *Halticosaurus* von Huene, 1908 [*nomen dubium*]
  H. longotarsus von Huene, 1908 (Type)
  ?H. orbitoangulatus von Huene, 1932

Genus: *Liliensternus* Welles, 1984
  L. liliensterni (von Huene, 1934) (Type)
    = *Halticosaurus liliensterni* von Huene, 1934

Genus: *Tanystrosuchus* Kuhn, 1963 [*nomen dubium*; = *Halticosaurus* or *Liliensternus*?]
  T. posthumus (von Huene, 1908) (Type)
    = *Tanystrophaeus posthumus* von Huene, 1908 [*nomen dubium*]
    = *Coelophysis posthumus* (von Huene, 1908) [*nomen dubium*]

NOTE: Wild (1973) removed this species from synonymy with *Tanystropheus conspicuus*, where it was previously classified. Kuhn (1963) created a separate generic name for the species after deciding that it is not referable to the genus *Tanystropheus*, and also (1965) noted that the species might be protorosaurid and not dinosaurian. Steel (1970) noted that the species might be referable to the genus *Halticosaurus*. Listed as Theropoda *incertae sedis* by Norman (1990).

Genus: [To be described; a "large ceratosaur" from the Lower Chinle Formation; Parrish & Carpenter, 1986]

Genus: [To be described; a double-crested Lower Jurassic theropod from Kunming, Yunnan, China illustrated in *Asahi Shinbun* May 29, 1989; M. Tanimoto, pers. comm.; similar to *Dilophosaurus*: P. Currie, pers. comm.]

Genus: [To be described from Airel, Normandy; originally referred to *Halticosaurus* sp. in Larsonneur & Lapparent, 1966; presently being restudied as a possible new genus by G. Cuny and P. M. Galton; Buffetaut, Cuny & Le Loeuff, 1991]

Family: CERATOSAURIDAE Marsh, 1884 emend. Gilmore, 1920

Census: 2 genera, 4 species (2 doubtful)

Genus: *Ceratosaurus* Marsh, 1884
  C. nasicornis Marsh, 1884 (Type)
    = *Megalosaurus nasicornis* (Marsh, 1884)
    = *Labrosaurus sulcatus* Marsh, 1896 [*nomen dubium*]

= *Ceratosaurus nasicornus* Chabli, 1985 [*sic*]
?*C. ingens* (Janensch, 1920) [*nomen dubium*]
= *Megalosaurus ingens* Janensch, 1920 [*nomen dubium*]
?*C. roechlingi* Janensch, 1925 [*nomen dubium*]
= *Labrosaurus stechowi* Janensch, 1925 [*nomen dubium*]
= *Antrodemus steschowi* Chabli, 1985 [*sic*]
= *Ceratosaurus roechlinqi* Chabli, 1985 [*sic*]
[New large species to be described by Madsen & Welles from the Cleveland-Lloyd Quarry in Utah; Madsen, 1978]

Genus: *Sarcosaurus* Andrews, 1921
= *Sacrosaurus* Glut, 1972 [*sic*]
S. woodi Andrews, 1921 (Type)
= *Magnosaurus woodwardi* von Huene, 1932

Family: MEGALOSAURIDAE Huxley, 1869

Census: 11 genera (2 doubtful), 26 species (15 doubtful)

= Erectopodidae von Huene, 1932
= Iliosuchidae Paul, 1988
= Megalosauri Fitzinger, 1843
= Megalosaurinae Paul, 1988
= Megalosauroides Gervais, 1853
= Torovosauridae Kurzanov, 1989 [*sic*]
= Torvosauridae Jensen, 1985

NOTE: This family has become a "grab-bag" for large theropod genera based on fragmentary remains. British megalosaurids are currently being restudied by S. P. Welles & H. P. Powell, and continental European megalosaurids are being restudied by P. Taquet & H. P. Powell (manuscripts in preparation). These studies should greatly aid the classification of many problematic large-theropod taxa. Meanwhile, Britt (1991) has recently restudied the genus *Torvosaurus* and other theropods from the Morrison Formation and has concluded that the Megalosauridae are probably derived ceratosaurians (*sensu* Gauthier, 1986). Following Britt's recommendation, the family Megalosauridae is here included in the suborder Ceratosauria.

Genus: *Embasaurus* Riabinin, 1931 [*nomen dubium*]
= *Embasasaurus* Carroll, 1987 [*sic*]
E. minax Riabinin, 1931 (Type)

Genus: *Erectopus* von Huene, 1922
E. sauvagei von Huene, 1932 (Type)
= *Megalosaurus superbus* Sauvage, 1882 (in part)
= *Erectopus superbus* (Sauvage, 1882)
NOTE: The above genus may be an abelisaurid or may belong in its own family (R. E. Molnar, pers. comm.; Molnar, 1990; Buffetaut, Cuny & Le Loeuff, 1991). The collection that includes the type specimens is apparently lost.

Genus: *Kaijiangosaurus* He, 1984
K. lini He, 1984 (Type)

Genus: *Kelmayisaurus* Dong, 1973 [*nomen dubium*]
= *Kelmaysaurus* Dong, 1987 [*sic*]
K. petrolicus Dong, 1973 (Type)

Genus: *Magnosaurus* von Huene, 1932
M. nethercombensis (von Huene, 1926) (Type)
= *Megalosaurus nethercombensis* von Huene, 1926
?*M. lydekkeri* (von Huene, 1926) [*nomen dubium*]
= *Megalosaurus lydekkeri* von Huene, 1926 [*nomen dubium*]

Genus: *Megalosaurus* Buckland, 1824
= *Gressylosaurus* Lapparent, 1967 [*sic*, for *Gresslyosaurus* Rütimeyer, 1857]
= *Megalasaurus* von Huene, 1926 [*sic*]
= *Megalosaurns* von Huene, 1926 [*sic*]
= *Megalosaurus* Parkinson, 1822 [*nomen nudum*]
= *Megalosausus* von Huene, 1926 [*sic*]
= *Megalousaurus* Ameghino, 1913 [*sic*]
= *Megolosaurus* von Huene, 1926 [*sic*]
= *Meqalosaurus* Walker, 1964 [*sic*]
= *Scrotum* Brookes, 1763 [*nomen oblitum*]
M. bucklandii Ritgen, 1826 (Type)
= *Megalosaurus bucklandi* Mantell, 1827 [*sic*]

= *Scrotum humanum* Brookes, 1763 [*nomen oblitum*]
= *Megalosaurus conybearei* Ritgen, 1826 [*nomen oblitum*]
?*M. cloacinus* Quenstedt, 1858 [*nomen dubium*]
= *Gresslyosaurus cloacinus* (Quenstedt, 1858) [*nomen dubium*]
= *Plateosaurus cloacinus* (Quenstedt, 1858) [*nomen dubium*]

NOTE: The above species is probably based on rauisuchian teeth (Benton, 1986).

?*M. insignis* Eudes-Deslongchamps & Lennier *vide* Lennier, 1870 [*nomen dubium*]
= *Erectopus insignis* (Eudes-Deslongchamps & Lennier *vide* Lennier, 1870) [*nomen dubium*]
= *Morosaurus marchei* Sauvage, 1897/8 [*nomen dubium*]

NOTE: A tooth referred to *Morosaurus marchei* in Sauvage, 1897/8 is indeed a sauropod tooth, but the type specimen, a caudal centrum, is apparently referable to *Megalosaurus insignis* (de Lapparent & Zbyszewski, 1957).

?*M. obtusus* Henry, 1876 [*nomen dubium*]
= *Plateosaurus obtusus* (Henry, 1876) [*nomen dubium*]

NOTE: The above species is probably based on rauisuchian teeth (Benton, 1986).

?*M. pannoniensis* Seeley, 1881 [*nomen dubium*]
= *Megalosaurus pannonicus* von Huene, 1926 [*sic*]
= Gen. indet. *pannonicus* Huene, 1932 [*sic*]
?*M. superbus* Sauvage, 1882 [*nomen dubium*; in part – see also *Erectopus*]
?*M. cambrensis* (Newton, 1899) [*nomen dubium*]
= *Zanclodon cambrensis* Newton, 1899 [*nomen dubium*]
= *Gresslyosaurus cambrensis* (Newton, 1899) [*nomen dubium*]
?*M. hungaricus* Nopcsa, 1902 [*nomen dubium*]
?*M. terquemi* von Huene, 1926 [*nomen dubium*]
= *Gressylosaurus terquemi* (von Huene, 1962) Lapparent, 1967 [*sic*]

NOTE: Buffetaut, Cuny & Le Loeuff (1991) consider this species to be based on parasuchian teeth, the only post-Triassic record of a parasuchian.

M. andrewsi (von Huene, 1932)
= *Sarcosaurus andrewsi* von Huene, 1932
?*M. pombali* de Lapparent & Zbyszewski, 1957 [*nomen dubium*]
?*M. inexpectatus* del Corro, 1966 [*nomen dubium*]
?*M. chubutensis* del Corro, 1974 [*nomen dubium*]
?*M. tibetensis* Zhao, 1986 [*nomen nudum*]
?*M. dapukaensis* Zhao, 1986 [*nomen nudum*]
[New species to be described by S. P. Welles & H. P. Powell]

Genus: *Piveteausaurus* Taquet & Welles, 1977
P. divesensis (Walker, 1964) (Type)
= *Eustreptospondylus divesensis* Walker, 1964
= *Proceratosaurus divesensis* (Walker, 1964)

Genus: *Poekilopleuron* Eudes-Deslongchamps, 1838
= *Peukilopleuron* Stromer, 1934 [*sic*]
= *Poecilopleuron* Bronn, 1837 [*nomen nudum*]
= *Poecilopleuron* Fitzinger, 1843 [*sic*]
= *Poecilopleurum* Agassiz, 1846 [*sic*]
= *Poekilipleuron* Kuhn, 1965 [*sic*]
= *Poelicopleurum* Kuhn, 1965 [*sic*]
= *Poikilopleuron* Owen, 1841 [*sic*]
P. bucklandii Eudes-Deslongchamps, 1838 (Type)
= *Poecilopleuron bucklandi* (Eudes-Deslongchamps, 1838)
= *Poecilopleurum bucklandi* (Eudes-Deslongchamps, 1838)
= *Poikilopleuron bucklandi* (Eudes-Deslongchamps, 1838)
= *Laelaps gallicus* Cope, 1867
= *Dryptosaurus gallicus* (Cope, 1867)
= *Poecilopleurum gallicum* (Cope, 1867)
= *Megalosaurus poikilopleuron* von Huene, 1923
?*P. schmidti* Kiprijanov, 1883 [*nomen dubium*]
= *Megalosaurus schmidti* (Kiprijanov, 1883) [*nomen dubium*]

NOTE: The above species may be a ceratosaurid, but is probably indeterminate (R. E. Molnar, pers. comm.).

Genus: *Torvosaurus* Galton & Jensen, 1979
 = *Torovosaurus* Kurzanov, 1989 [*sic*]
 T. tanneri Galton & Jensen, 1979 (Type)
  = *Megalosaurus tanneri* (Galton & Jensen, 1979)

Genus: *Unquillosaurus* J. Powell, 1979
 U. ceibalii J. Powell, 1979 (Type)
  = *Unquillosaurus ceibalensis* Stipanicic & Bonaparte, 1979 [*sic*]

Genus: *Xuanhanosaurus* Dong, 1984
 = *Xuanhangosaurus* Haubold, 1990 [*sic*]
 = *Xuanhonosaurus* Dong & Tang, 1985 [*sic*]
 X. qilixiaensis Dong, 1984 (Type)
  = *Xuanhanosaurus qilixiaenensis* Dong, 1987 [*sic*]
  = *Xuanhonosaurus qilixian* Kurzanov, 1989 [*sic*]

Genus: [To be described by S. P. Welles & H. P. Powell]
 [Type species to be described]
  = *Megalosaurus hesperis* Waldman, 1974
  = *Megalosaurus bucklandi* von Meyer, 1883 *non* Ritgen, 1826

Genus: [To be described by S. P. Welles & H. P. Powell, based on the lectotype knee joint of *Scelidosaurus harrisoni*; the generic name *Scelidosaurus* is to be conserved for the ankylosaurian; R. A. Long, pers. comm.]

Genus: [To be described from the Kota Formation of India; Yadagiri, 1979]

Genus: [To be described by D. B. Norman, D. B. Weishampel and D. Grigorescu; a new large theropod from Romania; Grigorescu, Seclamen, Norman & Weishampel, 1990]

Family: ABELISAURIDAE
Bonaparte & Novas, 1985

Census: 9 genera (1 doubtful), 9 species (1 doubtful)

= Abelisaurinae Paul, 1988

Genus: *Abelisaurus* Bonaparte & Novas, 1985
 A. comahuensis Bonaparte & Novas, 1985 (Type)

Genus: *Carnotaurus* Bonaparte, 1985
 = *Carnotosaurus* Kricher, 1990 [*sic*]
 C. sastrei Bonaparte, 1985 (Type)

Genus: *Genyodectes* Woodward, 1901 [*nomen dubium*]
 = *Geniodectes* Bonaparte, Novas & Coria, 1990 [*sic*]
 = *Genyodetes* Ameghino, 1913 [*sic*]
 G. serus Woodward, 1901 (Type)

NOTE: The above genus is referred to this family provisionally. R. E. Molnar believes it is not an abelisaurid (pers. comm.), Bonaparte, Novas & Coria (1990) consider it indeterminate.

Genus: *Indosaurus* von Huene, 1932
 I. matleyi von Huene, 1932 (Type)
  = *Megalosaurus matleyi* (von Huene, 1932)

NOTE: The above genus is considered a probable abelisaurid by Molnar (1990) but not by Bonaparte, Novas & Coria (1990).

Genus: *Indosuchus* von Huene, 1932
 I. raptorius von Huene, 1932 (Type)

NOTE: The above genus is considered a probable abelisaurid by Molnar, 1990 and Bonaparte, Novas & Coria, 1990.

Genus: *Labocania* Molnar, 1974
 L. anomala Molnar, 1974 (Type)

NOTE: The above genus is referred to this family provisionally (G. Leahy, pers. comm.).

Genus: *Majungasaurus* Lavocat, 1955
 M. crenatissimus (Deperet, 1896) (Type)
  = *Megalosaurus crenatissimus* Deperet, 1896

NOTE: The above genus is considered a possible abelisaurid by Molnar (1990).

Genus: *Tarascosaurus* Le Loeuff & Buffetaut, 1991
 T. salluvicus Le Loeuff & Buffetaut, 1991 (Type)

Genus: *Xenotarsosaurus* Martínez, Giménez, Rodríguez & Bochatey, 1986
 X. bonapartei Martínez, Giménez, Rodríguez & Bochatey, 1986 (Type)

Family: NOASAURIDAE
Bonaparte & J. Powell, 1980

Census: 1 genus, 1 species

= Noasaurinae Paul, 1988

Genus: *Noasaurus* Bonaparte & J. Powell, 1980
N. leali Bonaparte & J. Powell, 1980 (Type)

CERATOSAURIA *incertae sedis*

Census: 6 genera (4 doubtful),
6 species (4 doubtful)

= Procompsognathidae von Huene, 1929
= Procompsognathinae Nopcsa, 1923

Genus: *Avipes* von Huene, 1932 [*nomen dubium*]
A. dillstedtianus von Huene, 1932 (Type)

Genus: *Lukousaurus* Young, 1948
= *Loukousaurus* Romer, 1966 [*sic*]
= *Lucousaurus* Rozhdestvensky, 1977 [*sic*]
= *Lukosaurus* Camp, Welles & Green, 1953 [*sic*]
L. yini Young, 1948 (Type)

Genus: *Procompsognathus* E. Fraas, 1913
P. triassicus E. Fraas, 1913 (Type)

Genus: *Pterospondylus* Jaekel, 1913 [*nomen dubium*; = *Procompsognathus*?]
P. trielbae Jaekel, 1913 (Type)

Genus: *Saltopus* von Huene, 1910 [*nomen dubium*]
S. elginensis von Huene, 1910 (Type)

Genus: *Velocipes* von Huene, 1932 [*nomen dubium*]
V. guerichi von Huene, 1932 (Type)
= *Velocipes gürichi* von Huene, 1932*

Suborder: Spinosauria nov.

Census: 2 familes, 3 genera, 3 species

Family: BARYONYCHIDAE
Charig & Milner, 1986

Census: 1 genus, 1 species

Genus: *Baryonyx* Charig & Milner, 1986
B. walkeri Charig & Milner, 1986 (Type)

NOTE: The above genus (and family) is referred to this suborder provisionally, based on the near identity of the premaxilla of *Baryonyx* with material referred to *Spinosaurus* by Taquet, 1984 and on the similarity of the dentaries of the two genera. It should be noted that Charig & Milner (1986, 1990) maintain that *Baryonyx* shows no clear relationship with *Spinosaurus* and argue for its placement elsewhere within the Theropoda.

Family: SPINOSAURIDAE Stromer, 1915

Census: 2 genera, 2 species

Genus: *Siamosaurus* Buffetaut & Ingavat, 1986
S. suteethorni Buffetaut & Ingavat, 1986 (Type)

NOTE: The above genus is referred to this family provisionally.

Genus: *Spinosaurus* Stromer, 1915
S. aegyptiacus Stromer, 1915 (Type)
[Species noted as *Spinosaurus* B in Stromer, 1934; specimens destroyed in 1944 during a World War II bombing raid, so it is unlikely that this species will ever be formally described]
[Possible new species to be described from Niger, Algeria, and Morocco, noted by Taquet, 1984]

Suborder: Carnosauria von Huene, 1920

Census: 6 families, 38 genera (10 doubtful), 56 species (19 doubtful)

Parafamily: EUSTREPTOSPONDYLIDAE Paul, 1988

Census: 7 genera, 8 species

= Eustreptospondylinae Paul, 1988
= Iliosuchidae Paul, 1988
= Metriacanthosaurinae Paul, 1988

Genus: *Becklespinax* nov.
B. altispinax (Paul, 1988) (Type)
= *Acrocanthosaurus altispinax* Paul, 1988
NOTE: Type specimen of the above species is BMNH R1828, a series of three caudal dorsal vertebrae with very tall neural spines from the Lower Wealden of Battle-near-Hastings, East Sussex. These vertebrae are the source of the name *Altispinax* von Huene, 1923.

Genus: *Eustreptospondylus* Walker, 1964
E. oxoniensis Walker, 1964 (Type)
= *Streptospondylus cuvieri* Owen, 1842
= *Megalosaurus cuvieri* (Owen, 1842)
[New species to be described by S. P. Welles & H. P. Powell; R. A. Long, pers. comm.]

Genus: *Gasosaurus* Dong, 1985
G. constructus Dong, 1985 (Type)

Genus: *Iliosuchus* von Huene, 1932
I. incognitus von Huene, 1932 (Type)
= *Megalosaurus incognitus* (von Huene, 1932)

Genus: "Kagasaurus" [a large theropod from Japan; Hisa, 1988, *Utan Scientific Magazine* #4, p. 24; to be described]

Genus: *Metriacanthosaurus* Walker, 1964
= *Metricanthosaurus* Swinton, 1970 [*sic*]
M. parkeri (von Huene, 1926) (Type)
= *Megalosaurus parkeri* von Huene, 1926

Genus: "Mifunesaurus" [a large theropod from Japan; Hisa, 1988, *Utan Scientific Magazine* #4, p. 24; to be described]

Genus: *Piatnitzkysaurus* Bonaparte, 1979
= *Piatnitzkisaurus* Kurzanov, 1989 [*sic*]
P. floresi Bonaparte, 1979 (Type)

Genus: *Yangchuanosaurus* Dong, Chang, Li & Zhou, 1978
= *Youngchuanosaurus* Zhao, 1986 [*sic*]
= *Yuangchuanosaurus* Buffetaut & Suteethorn, 1989 [*sic*]
= *Yungchuanosaurus* Dong, 1979 [*sic*]
Y. shangyouensis Dong, Chang, Li & Zhou, 1978 (Type)
= *Metriacanthosaurus shangyouensis* (Dong, Chang, Li & Zhou, 1978)
= *Yangchuanosaurus shangyauensis* Dong, Chang, Li & Zhou, 1978 [*sic*]
= *Yangchuanosaurus shangyuensis* Dong, 1987 [*sic*]
= *Yangchuanosaurus shanguyensis* Kurzanov, 1989 [*sic*]
= *Yangchuanosaurus shanyuensis* Kurzanov, 1989 [*sic*]
Y. magnus Dong, Zhou & Zhang, 1983
= *Yangchuanosaurus magnum* Dong, 1980 [*nomen nudum*]
= *Yangchuanosaurus maganus* Dong, Zhou & Zhang 1983 [*sic*]

Genera: [To be described; as many as five new theropods, known from five distinctive humeri from Colorado; Jensen, 1985]

Family: ALLOSAURIDAE Marsh, 1878

Census: 11 genera (4 doubtful), 18 species (8 doubtful)

= Allosaurinae Paul, 1988
= Antrodemidae Stromer, 1934
= Bahariasauridae von Huene, 1948
= Baharisauridae Maleev, 1968 [*sic*]
= Carcharodontosauridae Stromer, 1931
= Labrosauridae Marsh, 1882
= Streptospondilidae Kurzanov, 1989 [*sic*]
= Streptospondylidae Kurzanov, 1989

Genus: *Acrocanthosaurus* Stovall & Langston, 1950
= *Arcocanthosaurus* Stovall & Langston, 1950 [*sic*]

= *Arcocantosaurus* Bonaparte, 1978 [*sic*]
A. atokensis Stovall & Langston, 1950 (Type)

Genus: *Allosaurus* Marsh, 1877
= *Apatodon* Marsh, 1877 [*nomen dubium*]
= *Creosaurus* Marsh, 1878
= *Empaterius* White, 1973 [*sic*]
= *Epanterias* Cope, 1878
= *Epantherias* Romer, 1966 [*sic*]
= *Labradosaurus* Bonaparte, 1978 [*sic*]
= *Labrosaurus* Marsh, 1879
= *Laerosaurus* Glut, 1972 [*sic*]
?*A. meriani* (Greppin, 1870) [*nomen dubium*]
= *Megalosaurus meriani* Greppin, 1870 [*nomen dubium*]
= *Antrodemus meriani* (Greppin, 1870) [*nomen dubium*]
= *Labrosaurus meriani* (Greppin, 1870) [*nomen dubium*]
A. fragilis Marsh, 1877 (Type)
= *Labrosaurus fragilis* (Marsh, 1877)
= *Apatodon mirus* Marsh, 1877 [*nomen dubium*]
= *Allosaurus lucaris* Marsh, 1878
= *Antrodemus lucaris* (Marsh, 1878)
= *Labrosaurus lucaris* (Marsh, 1878)
= *Creosaurus atrox* Marsh, 1878
= *Allosaurus atrox* (Marsh, 1878)
= *Antrodemus atrox* (Marsh, 1878)
= *Camptonotus amplus* Marsh, 1879
= *Camptosaurus amplus* (Marsh, 1879)
= *Labrosaurus ferox* Marsh, 1884 (provisionally)
= *Allosaurus ferox* (Marsh, 1884) (provisionally)
= *Allosaurus agilis* Zittel, 1887 [*sic*]
= *Allosaurus ferox* Marsh, 1896/(Marsh, 1884) [*sic*]
= *Labrosaurus fragilis* Marsh, 1896 [*sic*]
= *Allosaurus gracilis* von Huene, 1929 [*sic*]
?*A. amplexus* (Cope, 1878)
= *Epanterias amplexus* Cope, 1878
?*A. tendagurensis* Janensch, 1925 [*nomen dubium*]
= *Antrodemus tendagurensis* (Janensch, 1925) [*nomen dubium*]
[New small species to be described from the Morrison Formation by J. Madsen and S. P. Welles]
[New species to be described from the Morrison Formation by R. T. Bakker]

Genus: *Antrodemus* Leidy, 1870 [*nomen dubium*; = *Allosaurus*?]
= *Anthrodemus* von Huene, 1926 [*sic*]
= *Antrodesmus* Mook, 1916 [*sic*]
= *Poicilopleuron* Leidy, 1870 [*sic*; for *Poekilopleuron* Eudes-Deslongchamps, 1838]
A. valens (Leidy, 1870) (Type)
= *Poicilopleuron valens* Leidy, 1870 [*nomen dubium*]
= *Allosaurus valens* (Leidy, 1870) [*nomen dubium*]

NOTE: This genus is probably a senior synonym of *Allosaurus*, but it is best left isolated until comparative work on all the Morrison allosaurid specimens is completed.

Genus: *Bahariasaurus* Stromer, 1934
B. ingens Stromer, 1934 (Type)

NOTE: This genus is referred to this family provisionally.

Genus: *Carcharodontosaurus* Stromer, 1931
= *Carcharodonsauris* Romer, 1966 [*sic*]
= *Carchrodontosaurus* White, 1973 [*sic*]
C. saharicus (Deperet & Savornin, 1925) (Type)
= *Megalosaurus saharicus* Deperet & Savornin, 1925
= *Megalosaurus (Dryptosaurus) saharicus* (Deperet & Savornin, 1925)
= *Megalosaurus africanus* von Huene, 1956

NOTE: The above genus is referred to this family provisionally.

Genus: *Chilantaisaurus* Hu, 1964
= *Chilantaiosaurus* Romer, 1966 [*sic*]
= *Chilanthiosaurus* Glut, 1972 [*sic*]
= *Chlilantaisaurus* Dong, 1980 [*sic*]
?*C. sibiricus* (Riabinin, 1914) Molnar, 1990 [*nomen dubium*]
= *Allosaurus sibiricus* Riabinin, 1914 [*nomen dubium*]
= *Antrodemus sibiricus* (Riabinin, 1914) [*nomen dubium*]
C. tashuikouensis Hu, 1964 (Type)
C. maortuensis Hu, 1964

Genus: *Compsosuchus* von Huene, 1932 [*nomen dubium*]

C. solus von Huene, 1932 (Type)

NOTE: The above genus, usually classified as a coelurid, is probably an allosaurid (Molnar, 1990).

Genus: "Futabasaurus" Lambert, 1990 [a large ?carnosaur to be described from Japan]

Genus: "Jiangjunmiaosaurus" [Anonymous] 1987 [a large, primitive allosaurid to be described in 1992 from a nearly complete skeleton discovered in 1987 by the Canada-China Dinosaur Project; Dong Z., pers. comm.; D. Lambert, pers. comm.; Currie, 1991 SVP annual meeting abstracts; see also "Monolophosaurus"]

Genus: "Katsuyamasaurus" Lambert, 1990 [a large ?carnosaur to be described from Japan]

Genus: "Madsenius" Lambert, 1990 [to be described from the Morrison Formation by R. T. Bakker; based on distinctive skull material and other remains previously referred to *Allosaurus* and *Creosaurus*]

Genus: "Monolophosaurus" Lambert, 1990 [to be described in 1992; a crested ?allosaurid from China previously referred to in *New Scientist*, November 12, 1987: 28, 29 and *Alberta Report*, January 4, 1988: 28–32 as "Jiangjunmiaosaurus"; Dong Z., pers. comm.; P. J. Currie, pers. comm.]

Genus: *Ornithomimoides* von Huene, 1932 [*nomen dubium*]

O. mobilis von Huene, 1932 (Type)

O. barasimlensis von Huene, 1932 [*nomen dubium*]

NOTE: This genus is not an ornithomimid as usually classified (R. E. Molnar, pers. comm.), but is probably an allosaurid (Kurzanov, 1989).

Genus: *Saurophagus* Stovall *vide* Ray, 1941/Swainson 1831

S. maximus Stovall *vide* Ray, 1941 (Type)

NOTE: As shown in Hunt & Lucas, 1987, the description of this large theropod in Ray, 1941 conforms to proper nomenclatural practice, and the genus and species are validly designated. The generic name is, however, preoccupied (R. E. Molnar, pers. comm.), while the species may be referable to *Allosaurus* (R. A. Long, pers. comm.), perhaps to the species *Allosaurus amplexus* (as in Paul, 1988).

Genus: *Streptospondylus* von Meyer, 1830

S. altdorfensis von Meyer, 1832 (Type)

NOTE: The above genus, often classified as crocodilian, is definitely a theropod (S. Pickering, pers. comm.), probably allosaurid. Other species referred to this genus are crocodilian and are not listed here.

Genus: *Szechuanosaurus* Young, 1942 [*nomen dubium*]

= *Szechaunosaurus* Dong, 1979 [*sic*]

= *Szechusanosaurus* Romer, 1966 [*sic*]

S. campi Young, 1942 (Type)

= *Metriacanthosaurus carpenteri* Paul, 1988 [*sic*]

S. yandonensis Dong, Chang, Li & Zhou, 1978 [*nomen nudum*]

Genus: *Valdoraptor* nov.

V. oweni (Lydekker, 1889) (Type)

= *Megalosaurus oweni* Lydekker, 1889

= *Altispinax oweni* (Lydekker, 1889)

= *Altipinax oweni* von Huene, 1932 [*sic*]

NOTE: Type specimen of the above species is BMNH R2559, a partial left metatarsus from the Upper Wealden of Cuckfield, West Sussex, originally described by Owen (1857) as a *Hylaeosaurus* metapodium. Referred to this family provisionally.

Genus: [To be described from the Wealden Formation of the Isle of Wight; Hutt, Simmonds & Hullman, 1989]

Family: ITEMIRIDAE Kurzanov, 1976

Census: 1 genus, 1 species

Genus: *Itemirus* Kurzanov, 1976

I. medullaris Kurzanov, 1976 (Type)

NOTE: This genus is referred to the Carnosauria by Kurzanov (1989). It is probably indeterminate (P. J. Currie, pers. comm.).

Family: DRYPTOSAURIDAE Marsh, 1890

Census: 4 genera (2 doubtful),
7 species (5 doubtful)

Genus: *Altispinax* von Huene, 1923
= *Altipinax* von Huene, 1932 [*sic*]
= *Altispanax* Stovall & Langston, 1950 [*sic*]
A. dunkeri (Dames, 1884) (Type)
= *Megalosaurus dunkeri* Dames, 1884

NOTE: The type specimen of the above species is a tooth from the Lower Wealden of Hanover presently in the University of Marburg collection (it may be lost: S. Pickering, pers. comm.). It resembles teeth referred to the genus *Dryptosaurus* in having no denticles on the mesial carina (Denton, 1990, and pers. comm.), so *Altispinax* is provisionally referred to the family Dryptosauridae; see also *Becklespinax* and *Valdoraptor*.

Genus: *Diplotomodon* Leidy, 1868 [*nomen dubium*; = *Dryptosaurus*?]
= *Tomodon* Leidy, 1865/Dumeril 1853
D. horrificus (Leidy, 1865) (Type)
= *Tomodon horrificus* Leidy, 1865 [*nomen dubium*]

NOTE: Originally described as mosasaurian, the tooth that constitutes the type specimen of the above species was provisionally referred to the Megalosauridae by Welles, 1952, but it most closely resembles the teeth of *Dryptosaurus aquilunguis* (R. E. Molnar, pers. comm.).

Genus: *Dryptosauroides* von Huene, 1932 [*nomen dubium*]
D. grandis von Huene, 1932 (Type)

Genus: *Dryptosaurus* Marsh, 1877
= *Dryptosausus* von Huene, 1922 [*sic*]
= *Laelaps* Cope, 1866/Koch, 1839
D. aquilunguis (Cope, 1866) (Type)
= *Laelaps aquilunguis* Cope, 1866
?*D. trihedrodon* (Cope, 1877) [*nomen dubium*]
= *Laelaps trihedrodon* Cope, 1877 [*nomen dubium*]
= *Antrodemus trihedrodon* (Cope, 1877) [*nomen dubium*]

NOTE: The above species may be referable to *Allosaurus* (R. E. Molnar, pers. comm.).

?*D. medius* (Marsh, 1888) [*nomen dubium*]
= *Allosaurus medius* Marsh, 1888 [*nomen dubium*]
= *Antrodemus medius* (Marsh, 1888) [*nomen dubium*]
?*D. potens* (Lull, 1911) [*nomen dubium*]
= *Creosaurus potens* Lull, 1911 [*nomen dubium*]

Parafamily: AUBLYSODONTIDAE Nopcsa, 1928

Census: 3 genera, 4 species

= Aublysodontinae Nopcsa, 1928
= Shanshanosauridae Dong, 1977

Genus: *Alectrosaurus* Gilmore, 1933
A. olseni Gilmore, 1933 (Type)
= *Albertosaurus (Alectrosaurus) olseni* (Gilmore, 1933)

NOTE: The large forelimb referred to this genus probably belongs to a segnosaurid (Perle, 1977; Mader & Bradley, 1989). A new *Alectrosaurus* specimen recently recovered from Mongolia (P. Currie, pers. comm.; D. McInnes, pers. comm.) shows close affinity to the "Jordan theropod" (*Aublysodon molnari*) but not to the Tyrannosauridae, the family in which *Alectrosaurus* had previously been classified.

Genus: *Aublysodon* Leidy, 1868
= *Deinodon* Leidy, 1856 (in part)
A. mirandus Leidy, 1868 (Type)
= *Deinodon horridus* Leidy, 1856 (in part)
A. amplus Marsh, 1892
= *Deinodon amplus* (Marsh, 1892)
= *Manospondylus amplus* (Marsh, 1892)
= *Tyrannosaurus amplus* (Marsh, 1892)
= *Aublysodon cristatus* Marsh, 1892 [*nomen dubium*]
= *Deinodon cristatus* (Marsh, 1892) [*nomen dubium*]
= *Aublysodon molnari* Paul, 1988
= *Aublysodon molnaris* Paul, 1988*

NOTE: *Aublysodon molnari* was originally described as the "Jordan theropod" (Molnar, 1978). It is more fully described in Molnar & Carpenter, 1989, who tentatively refer it to Leidy's species *Aublysodon mirandus*. Because its provenance is Lance rather than Judith River, however, it and *A. cristatus* are instead referred to the Lance species *Aublysodon amplus* here.

Genus: *Shanshanosaurus* Dong, 1977
S. huoyanshanensis Dong, 1977
= *Aublysodon huoyanshanensis* (Dong, 1977) Paul, 1988
= *Shanshanosaurus houyanshanensis* Dong, 1987 [*sic*]

Genus: [To be described from Dinosaur Provincial Park; D. McInnes, pers. comm.]

Family: TYRANNOSAURIDAE Osborn, 1905

Census: 10 genera (2 doubtful), 16 species (4 doubtful)

= Deinodontidae Brown, 1914
= Deinodontinae Matthew & Brown, 1922
= Dinodontidae Cope, 1866 [*nomen oblitum*]
= Tyrannosaurinae Matthew & Brown, 1922

Genus: *Albertosaurus* Osborn, 1905
= *Albeltosaurus* Molnar & Carpenter, 1989 [*sic*]
A. sarcophagus Osborn, 1905 (Type)
= *Albertosaurus arctunguis* Parks, 1928
= *Deinodon arctunguis* (Parks, 1928)
A. megagracilis Paul, 1988

Genus: *Alioramus* Kurzanov, 1976
A. remotus Kurzanov, 1976 (Type)

Genus: *Chingkankousaurus* Young, 1958 (= *Tarbosaurus*?)
= *Chingkankonsaurus* Romer, 1966 [*sic*]
= *Chingkankouensis* Young, 1958 [*sic*]
= *Chingkankousarurus* Young, 1958 [*sic*]
= *Chingkonkousaurus* Dong, 1973 [*sic*]
= *Chinkankousaurus* Rozhdestvensky, 1977 [*sic*]
C. fragilis Young, 1958 (Type)
= *Chingkankouensis fragilis* Young, 1958 [*sic*]

Genus: *Daspletosaurus* D. A. Russell, 1970
D. torosus D. A. Russell, 1970 (Type)
= *Tyrannosaurus torosus* (D. A. Russell, 1970)
= *Tyrannosaurus (Daspletosaurus) torosus* (D. A. Russell, 1970)
[New species to be described by R. T. Bakker: the "stretch-snout" *Daspletosaurus*]

Genus: *Deinodon* Leidy, 1856 [*nomen dubium*]
= *Dinodon* Cope, 1866/Dumeril & Bibron, 1853 [*sic*]
D. horridus Leidy, 1856 (Type)
= *Dinodon horridus* (Leidy, 1856) [*nomen dubium*]
= *Gorgosaurus horridus* (Leidy, 1856) [*nomen dubium*]
= *Megalosaurus horridus* (Leidy, 1856) [*nomen dubium*]
= *Dryptosaurus kenabekides* Hay, 1899 [*nomen dubium*]
?*D. grandis* (Marsh, 1890) [*nomen dubium*]
= *Ornithomimus grandis* Marsh, 1890 [*nomen dubium*]
= *Aublysodon grandis* (Marsh, 1890) [*nomen dubium*]

NOTE: The above species probably represents a distinct but presently undefinable tyrannosaurid genus (Molnar, Kurzanov & Dong, 1990).

Genus: *Gorgosaurus* Lambe, 1914 (= *Albertosaurus*?)
= *Zatomis* Stephenson, 1912 [*sic*, for *Zatomus*; specimen referred to ?*Gorgosaurus* by Miller, 1967]
G. libratus Lambe, 1914 (Type)
= *Albertosaurus libratus* (Lambe, 1914)
= *Deinodon libratus* (Lambe, 1914)
= *Laelaps incrassatus* Cope, 1876 [*nomen dubium*]
= *Deinodon incrassatus* (Cope, 1876) [*nomen dubium*]
= *Dryptosaurus incrassatus* (Cope, 1876) [*nomen dubium*]
= *Laelaps falculus* Cope, 1876 [*nomen dubium*]
= *Deinodon falculus* (Cope, 1876) [*nomen dubium*]
= *Dromaeosaurus falculus* (Cope, 1876) [*nomen dubium*]
= *Dryptosaurus falculus* (Cope, 1876) [*nomen dubium*]

= *Laelaps hazenianus* Cope, 1876 [*nomen dubium*]
= *Deinodon hazenianus* (Cope, 1876) [*nomen dubium*]
= *Dryptosaurus hazenianus* (Cope, 1876) [*nomen dubium*]
G. sternbergi Matthew & Brown, 1923
= *Gorgosaurus sternbergi* Matthew & Brown, 1922 [*nomen nudum*]
= *Albertosaurus sternbergi* (Matthew & Brown, 1923)
= *Deinodon sternbergi* (Matthew & Brown, 1923)

NOTE: The above species may be a juvenile *Gorgosaurus libratus* (D. A. Russell, 1970), but it may also represent a different tyrannosaurid genus altogether (G. Paul, pers. comm.).

Genus: *Nanotyrannus* Bakker, Williams & Currie, 1988
= *Clevelanotyrannus* Bakker, Williams & Currie *vide* Currie, 1987 [*nomen nudum*]
N. lancensis (Gilmore, 1946) (Type)
= *Gorgosaurus lancensis* Gilmore, 1946
= *Albertosaurus lancensis* (Gilmore, 1946)
= *Albertosaurus (Nanotyrannus) lancensis* (Gilmore, 1946)
= *Deinodon lancensis* (Gilmore, 1946)

NOTE: The generic name *Clevelanotyrannus* Bakker, Williams & Currie was published in the bibliography of Currie, 1987, in *Fourth Symp. Mesozoic Terrestrial Ecosystems, Short Papers*, pp. 52–60. It was changed before the genus was formally described.

Genus: *Prodeinodon* Osborn, 1924 [*nomen dubium*; = *Alectrosaurus*?]
= *Prodeidon* Hou, Yeh & Zhao, 1975 [*sic*]
= *Prodinodon* Hu, 1964 [*sic*]
P. mongoliensis Osborn, 1924 (Type)
= *Prodeinodon mongoliense* Osborn, 1924*
= *Deinodon mongoliensis* Bohlin, 1953 [*sic*]
P. kwangshiensis Hou, Yeh & Zhao, 1975 [*nomen dubium*]

Genus: *Tarbosaurus* Maleev, 1955
= *Alectosaurus* Young, 1958 [*sic*, for *Alectrosaurus*]
= *Tarbasaurus* Maleev, 1955 [*sic*]
T. bataar (Maleev, 1955) (Type)
= *Tyrannosaurus bataar* Maleev, 1955
= *Tyrannosaurus (Tyrannosaurus) bataar* (Maleev, 1955)
= *Albertosaurus periculosus* Riabinin, 1930 [*nomen dubium*]
= *Alectosaurus periculosus* (Riabinin, 1930) [*nomen dubium*]
= *Deinodon periculosus* (Riabinin, 1930) [*nomen dubium*]
= *Gorgosaurus lancinator* Maleev, 1955 (juvenile)
= *Aublysodon lancinator* (Maleev, 1955) (juvenile)
= *Tarbosaurus efremovi* Maleev, 1955
?*T. turpanensis* (Zhai, Zheng & Tong, 1978) n. comb. [*nomen nudum*]
= *Tyrannosaurus turpanensis* Zhai, Zheng & Tong, 1978 [*nomen nudum*]
?*T. luanchuanensis* (Dong, 1979) n. comb.
= *Tyrannosaurus luanchuanensis* Dong, 1979
?*T. lanpingensis* (Zhao, 1986) n. comb. [*nomen nudum*]
= *Tyrannosaurus lanpingi* Zhao, 1986 [*nomen nudum*]
= *Tyrannosaurus lanpingensis* Yeh, 1975 [*nomen nudum*]

NOTE: *T. lanpingensis* may be from the Upper Jurassic of China and thus not referable to either *Tarbosaurus* or *Tyrannosaurus* (Yeh, 1975; R. E. Molnar, pers. comm.).

Large teeth and other fragmentary tyrannosaurid specimens from the Upper Cretaceous of Asia are best referred to the Asian genus *Tarbosaurus* instead of the North American genus *Tyrannosaurus* until the presence of *Tyrannosaurus* can be unequivocally documented in Asia.

Genus: *Tyrannosaurus* Osborn, 1905
= *Dynamosaurus* Osborn, 1905
= *Manospondylus* Cope, 1892 [*nomen oblitum*]
= *Monospondylus* Maleev, 1968 [*sic*]
= *Tiranosaurus* Kurzanov & Tumanova, 1978 [*sic*]
= *Tryannosaurus* Parks, 1928 [*sic*]
= *Tyannosaurus* Hu & Cheng, 1988 [*sic*]
= *Tyrannosaurs* Stokes, 1988 [*sic*]
= *Tyrannus* Ulanov, 1978/Lacepede, 1799 [*sic*]

= *Tyranosaurus* Guggisberg, 1966 [*sic*]
T. rex Osborn, 1905 (Type)
= *Tyrannosaurus (Tyrannosaurus) rex* (Osborn, 1905)
= *Manospondylus gigas* Cope, 1892 [*nomen oblitum*]
= *Dynamosaurus imperiosus* Osborn, 1905

NOTE: R. T. Bakker (pers. comm.) believes material referred to *Tyrannosaurus rex* belongs in two distinct species. These may, however, simply be sexual dimorphs (K. Carpenter, pers. comm.).

[New species to be described; originally noted in D. Lawson's doctoral dissertation; based on a dentary from a large theropod that may not be tyrannosaurid; Carpenter, 1990]

Genus: [To be described by Carpenter (in press)]
[Type species to be redescribed]
= *Gorgosaurus novojilovi* Maleev, 1955
= *Albertosaurus novojilovi* (Maleev, 1955)
= *Aublysodon novojilovi* (Maleev, 1955)
= *Deinodon novojilovi* (Maleev, 1955)

Genus: [To be described by Bakker & Currie; based on the tyrannosaurid skeleton on display at the Field Museum in Chicago, presently labeled *Albertosaurus libratus*]

Genus: [To be described from the Horseshoe Canyon Formation of Alberta; may simply be a new species of *Albertosaurus*; Bakker, Williams & Currie 1988]

CARNOSAURIA *incertae sedis*

Census: 2 doubtful genera,
2 doubtful species

Genus: *Rapator* von Huene, 1932 [*nomen dubium*]
R. ornitholestoides von Huene, 1932 (Type)

NOTE: This genus may be an abelisaurid (R. E. Molnar, pers. comm.).

Genus: *Walgettosuchus* von Huene, 1932 [*nomen dubium*]
W. woodwardi von Huene, 1932 (Type)
= *Megalosaurus woodwardi* (von Huene, 1932) [*nomen dubium*]

Notes and New Taxa

Parasuperorder: Theropodomorpha nov. (continued)

Paraorder: Theropoda Marsh, 1881 (continued)

Parasuborder: Protoaviformes Chatterjee, 1991

Census: 1 family, 1 genus, 1 species

Family: PROTOAVIDAE Chatterjee, 1991

Census: 1 genus, 1 species

Genus: *Protoavis* Chatterjee, 1991
= *Protoavis* Chatterjee, 1986 [*nomen nudum*]
P. texensis Chatterjee, 1991 (Type)

Suborder: Coelurosauria von Huene, 1914

Census: 3 families, 20 genera (10 doubtful), 21 species (10 doubtful)

Family: COMPSOGNATHIDAE Cope, 1875

Census: 1 genus, 2 species

= Compsognathinae Nopcsa, 1923

Genus: *Compsognathus* Wagner, 1859
= *Campsognothus* Stokes, 1988 [*sic*]
C. longipes Wagner, 1859 (Type)
C. corallestris Bidar, Demay & Thomel, 1972
= *Compsognathus corralestris* Callison & Quimby, 1984 [*sic*]

NOTE: Ostrom (1978) and Norman (1990) regard the two species of *Compsognathus* as synonymous, but European workers (Fabre, de Broin, Ginsburg & Wenz, 1982; Taquet, 1985) maintain their distinctness.

Genus: [To be described from the Toarcian (upper Lower Jurassic) of Morocco; Jenny, Jenny-Deshusses, la Marrec & Taquet, 1980; Taquet, 1985]

Family: COELURIDAE Marsh, 1881

Census: 18 genera (10 doubtful), 18 species (10 doubtful)

= Coelurosauridae Cope, 1882
= Ornitholestinae Paul, 1988

NOTE: This family, named after a genus of uncertain relationships, has become a "grab-bag" for small theropod genera based on fragmentary remains. Further study of the genera included herein may disclose that many can be classified in other theropod families.

Genus: *Aristosuchus* Seeley, 1887 [*nomen dubium*]
= *Calamospondylus* Fox, 1866 [*nomen nudum*]
A. pusillus (Owen, 1876) (Type)
= *Poikilopleuron pusillus* Owen, 1876 [*nomen dubium*]
= *Calamospondylus oweni* Fox, 1866 [*nomen nudum*]

= *Poecilopleuron minor* Owen *vide* Cope, 1878 [*sic*]

NOTE: The above genus may be a compsognathid (R. E. Molnar, pers. comm.).

Genus: *Calamospondylus* Lydekker, 1889 [*nomen dubium*; = *Aristosuchus*?]
  = *Calamosaurus* Lydekker, 1891 [*nomen dubium*]
  C. foxi Lydekker, 1889 (Type)
    = *Calamosaurus foxi* (Lydekker, 1889) [*nomen dubium*]

Genus: *Chuandongocoelurus* He, 1984
  C. primitivus He, 1984 (Type)

Genus: *Coeluroides* von Huene, 1932 [*nomen dubium*]
  C. largus von Huene, 1932 (Type)

Genus: *Coelurus* Marsh, 1879
  C. fragilis Marsh, 1879 (Type)
    = *Coelurus agilis* Marsh, 1884
    = *Elaphrosaurus agilis* (Marsh, 1884)

Genus: *Inosaurus* de Lapparent, 1960 [*nomen dubium*]
  I. tedreftensis de Lapparent, 1960 (Type)

Genus: *Jubbulpuria* von Huene, 1932 [*nomen dubium*]
  J. tenuis von Huene, 1932 (Type)

Genus: *Kakuru* Molnar & Pledge, 1980
  K. kujani Molnar & Pledge, 1980 (Type)

NOTE: The above genus is included in this family provisionally.

Genus: *Laevisuchus* von Huene, 1932 [*nomen dubium*]
  L. indicus von Huene, 1932 (Type)

NOTE: The above genus has cervical vertebrae similar to those of *Microvenator* and consequently may be an oviraptorosaur (R. E. Molnar, pers. comm.).

Genus: *Marshosaurus* Madsen, 1976
  M. bicentesimus Madsen, 1976 (Type)

NOTE: The above genus is included in this family provisionally (Madsen, 1976; Dodson, Behrensmeyer & Bakker, 1980). It may be a eustreptospondylid (Paul, 1988).

Genus: *Ngexisaurus* Zhao, 1983 [*nomen nudum*]
  N. dapukaensis Zhao, 1986 (Type)

Genus: *Nuthetes* Owen, 1854
  = *Nothetes* Morris, 1854 [*sic*]
  N. destructor Owen, 1854 (Type)
    = *Megalosaurus destructor* (Owen, 1854)
    = *Nuthetes destrictor* Kuhn, 1965 [*sic*]

NOTE: The type specimen of the above species has been described as lacertilian, but it is probably a small theropod. The "granicones" associated with the specimen are likely armor scutes of a basal ankylosaurian (Galton, 1986). *Nuthetes* is referred to this family provisionally.

Genus: *Ornitholestes* Osborn, 1903
  = *Orintholestes* Breed, 1968 [*sic*]
  O. hermanni Osborn, 1903 (Type)
    = *Coelurus hermanni* (Osborn, 1903)

NOTE: This genus is regarded as a small allosaurid by Paul, 1988.

Genus: *Proceratosaurus* von Huene, 1926
  P. bradleyi (Woodward, 1910) (Type)
    = *Megalosaurus bradleyi* Woodward, 1910

NOTE: Paul, 1988 refers the above genus to the subfamily Ornitholestinae of the family Allosauridae.

Genus: *Sinocoelurus* Young, 1942 [*nomen dubium*]
  = *Sinosaurus* Dong, 1979/Young, 1948 [*sic*]
  S. fragilis Young, 1942 (Type)

Genus: *Stokesosaurus* Madsen, 1974
  S. clevelandi Madsen, 1974 (Type)
    = *Iliosuchus clevelandi* (Madsen, 1974)

NOTE: The above genus is included in this family provisionally (Madsen, 1976; Dodson, Behrensmeyer & Bakker, 1980). It may be an allosaurid (R. E. Molnar, pers. comm.).

Genus: *Teinurosaurus* Nopcsa, 1928 emend. 1929 [*nomen dubium*]
  = *Caudocoelus* von Huene, 1932 [*nomen dubium*]
  T. sauvagei (von Huene, 1932) Olshevsky, 1978 (Type)
    = *Caudocoelus sauvagei* von Huene, 1932 [*nomen dubium*]
    = *Iguanodon prestwichii* Sauvage, 1897/8 *non* Hulke, 1880

Genus: *Thecocoelurus* von Huene, 1923 [*nomen dubium*; = *Aristosuchus*?]
  = *Therocoelurus* von Huene, 1956 [*sic*]
  T. daviesi (Seeley, 1888) (Type)
    = *Thecospondylus daviesi* Seeley, 1888 [*nomen dubium*]
    = *Coelurus daviesi* (Seeley, 1888) [*nomen dubium*]

Genus: *Tugulusaurus* Dong, 1973 [*nomen dubium*]
  = *Tugulosaurus* Dong, 1980 [*sic*]
  T. faciles Dong, 1973 (Type)

Genus: [To be described from the Fruita Formation of Colorado; Rasmussen & Callison, 1981]

Family: AVISAURIDAE
Brett-Surman & Paul, 1985

Census: 1 genus, 1 species

Genus: *Avisaurus* Brett-Surman & Paul, 1985
  A. archibaldi Brett-Surman & Paul, 1985 (Type)

NOTE: This genus may be an enantiornithid bird (Bonaparte, 1986). It is included here provisionally.

Suborder: Ornithomimosauria Barsbold, 1976

Census: 2 families, 11 genera (1 doubtful), 20 species (5 doubtful)

Family: ORNITHOMIMIDAE Marsh, 1890

Census: 10 genera (1 doubtful), 19 species (5 doubtful)

= Garudimimidae Barsbold, 1981
= Garudiminae Paul, 1988
= Harpymimidae Barsbold & Perle, 1984
= Ornithomiminae Nopcsa, 1923

Genus: *Anserimimus* Barsbold, 1988
  A. planinychus Barsbold, 1988 (Type)

Genus: *Archaeornithomimus* D. A. Russell, 1972
  = *Archeornithomimus* Kranz, 1989 [*sic*]
  ?*A. affinis* (Gilmore, 1920)
    = *Coelosaurus affinis* Gilmore, 1920
    = *Ornithomimus affinis* (Gilmore, 1920)
    = *Ornithomimus (Archaeornithomimus) affinis* (Gilmore, 1920)
    = *Allosaurus medius* Marsh, 1888 (in part)
    = *Dryosaurus grandis* Lull, 1911 [*nomen dubium*]
  A. asiaticus (Gilmore, 1933) (Type)
    = *Ornithomimus asiaticus* Gilmore, 1933
    = *Ornithomimus (Archaeornithomimus) asiaticus* (Gilmore, 1933)
    = *Ornithomimus asistiecus* Dong, 1979 [*sic*]

Genus: "Arkansaurus" [to be described; a primitive ornithomimid from Arkansas; may prove to be a species of *Archaeornithomimus*; D. Chure, pers. comm.]
  = *Arkanosaurus* Sattler, 1983 [*sic*]
  "A. fridayi" [to be described]

Genus: *Betasuchus* von Huene, 1932 [*nomen dubium*]
  = *Ornithomimidorum* gen. b von Huene, 1926 [*nomen oblitum*]
  B. bredai (Seeley, 1883) (Type)
    = *Megalosaurus bredai* Seeley, 1883 [*nomen dubium*]
    = *Ornithomimidorum* gen. b *bredai* (Seeley, 1883) [*nomen oblitum*]

Genus: *Dromiceiomimus* D. A. Russell, 1972
  D. brevetertius (Parks, 1926) (Type)
    = *Struthiomimus brevetertius* Parks, 1926
    = *Ornithomimus brevetertius* (Parks, 1926)
    = *Dromiceiomimus brevitertius* D. A. Russell, 1972 [*sic*]
    = *Struthiomimus ingens* Parks, 1933
    = *Ornithomimus ingens* (Parks, 1933)
  D. samueli (Parks, 1928)
    = *Struthiomimus samueli* Parks, 1928
    = *Ornithomimus samueli* (Parks, 1928)

Genus: *Elaphrosaurus* Janensch, 1920
  = *Elephrosaurus* Paul, 1988 [*sic*]
  E. bambergi Janensch, 1920 (Type)

?*E. iguidiensis* de Lapparent, 1960 [*nomen dubium*]
?*E. gautieri* de Lapparent, 1960 [*nomen dubium*]

NOTE: The above genus is referred to the Podokesauridae (as the Coelophysidae) by Paul (1988).

Genus: *Gallimimus* Osmólska, Roniewicz & Barsbold, 1972
= *Callimimus* Barsbold, 1983 [*sic*]
G. bullatus Osmólska, Roniewicz & Barsbold, 1972 (Type)
= *Ornithomimus bullatus* (Osmólska, Roniewicz & Barsbold, 1972)

Genus: *Garudimimus* Barsbold, 1981
G. brevipes Barsbold, 1981 (Type)

Genus: *Harpymimus* Barsbold & Perle, 1984
= *Harpimimus* Currie, 1989 [*sic*]
H. okladnikovi Barsbold & Perle, 1984 (Type)

Genus: *Ornithomimus* Marsh, 1890
= *Coelosaurus* Leidy, 1865/[Anonymous, but known to be Owen] 1854
= *Coelurosaurus* White, 1973 [*sic*]
= *Ornithomimidorum* gen. a von Huene, 1926 [*nomen oblitum*]
= *Ornithominus* Nopcsa, 1918 [*sic*]
?*O. antiquus* (Leidy, 1865)
= *Coelosaurus antiquus* Leidy, 1865
= *Struthiomimus antiquus* (Leidy, 1865)
= *Laelaps macropus* Cope, 1868 [*nomen dubium*]
= *Dryptosaurus macropus* (Cope, 1868) [*nomen dubium*]

NOTE: Recent work by T. R. Holtz, Jr. (doctoral dissertation) indicates that *Coelosaurus* is probably not an ornithomimid (reported in *BVP* #152).

?*O. lonzeensis* (Dollo, 1883) [*nomen dubium*]
= *Megalosaurus lonzeensis* Dollo, 1883 [*nomen dubium*]
= *Ornithomimidorum* gen. a *lonzeensis* (Dollo, 1883) [*nomen oblitum*]

NOTE: The above species may not be an ornithomimid (R. E. Molnar, pers. comm.).

O. velox Marsh, 1890 (Type)
?*O. tenuis* Marsh, 1890 [*nomen dubium*]
O. sedens Marsh, 1892
O. edmontonensis C. M. Sternberg, 1933
= *Ornithomimus edmontonicus* C. M. Sternberg, 1933*
= *Struthiomimus currelli* Parks, 1933
= *Ornithomimus edmontonianus* Kuhn, 1965 [*sic*]
[New species to be described; Leahy, 1987]

Genus: "Sanchusaurus" Hisa, 1988 [in *Utan Scientific Magazine* #4: 24; based on a fragmentary caudal vertebra from Japan; possibly the oldest and largest-known ornithomimid (Manabe & Hasegawa, 1991)]

Genus: *Struthiomimus* Osborn, 1916
S. altus (Lambe, 1902) (Type)
= *Ornithomimus altus* Lambe, 1902

Genus: [To be described from Argentina; with unfused metatarsals; J. F. Bonaparte, pers. comm.; J. S. McIntosh, pers. comm.]

Genus: [To be described from Argentina; with fused metatarsals and a metatarsal III that is almost pinched out of existence; J. F. Bonaparte, pers. comm.; J. S. McIntosh, pers. comm.]

Genus: [To be described from the Dockum Formation of Texas; based on a nearly complete skull; Chatterjee, 1991 SVP annual meeting abstracts]

Family: DEINOCHEIRIDAE Osmólska & Roniewicz, 1970

Census: 1 genus, 1 species

= Deinocheirinae Paul, 1988

Genus: *Deinocheirus* Osmólska & Roniewicz, 1970
D. mirificus Osmólska & Roniewicz, 1970 (Type)

Suborder: Deinonychosauria Colbert & D. A. Russell, 1969

Census: 3 families, 18 genera (5 doubtful), 29 species (14 doubtful)

Parafamily: ARCHAEOPTERYGIDAE Huxley, 1871

Census: 3 genera (1 doubtful), 4 species (2 doubtful)

Genus: *Archaeopteryx* von Meyer, 1861
- = *Archaeopterix* [Anonymous] 1861 [*sic*]
- = *Archaeornis* Petronievics *vide* Petronievics & Woodward, 1917
- = *Archeopteryx* Owen, 1864 [*sic*]
- = *Griphornis* Woodward, 1962 [*sic*]
- = *Griphosaurus* Wagner, 1861
- = *Gryphornis* Lambrecht, 1933 [*sic*]
- = *Gryphosaurus* Marschall, 1873 [*sic*]

A. lithographica von Meyer, 1861 (Type)
- = *Pterodactylus crassipes* von Meyer, 1857 [*nomen oblitum*]
- = *Archaeopteryx crassipes* (von Meyer, 1857) [*nomen oblitum*]
- = *Rhamphorhynchus crassipes* (von Meyer, 1857) [*nomen oblitum*]
- = *Scaphognathus crassipes* (von Meyer, 1857) [*nomen oblitum*]
- = *Griphosaurus problematicus* Wagner, 1861
- = *Archaeopteryx macrura* Owen, 1862
- = *Griphosaurus longicaudatus* Owen, 1862
- = *Griphosaurus longicaudatum* Owen, 1862 [*sic*]
- = *Gryphornis longicaudatus* (Owen, 1862)
- = *Archaeopteryx macrurus* Owen, 1863 [*sic*]
- = *Archaeopteryx macroura* Vogt, 1879 [*sic*]
- = *Archaeopteryx siemensii* Dames, 1897
- = *Archaeornis siemensii* (Dames, 1897)
- = *Archaeopteryx oweni* Petronievics, 1917

?*A. vicensensis* [Anonymous] *vide* Lambrecht, 1933 [*nomen dubium*]

NOTE: The above species is a pterosaur, according to O. Kleinschmidt (Brodkorb, 1978).

Genus: *Jurapteryx* Howgate, 1985

J. recurva (Howgate, 1984) (Type)
- = *Archaeopteryx recurva* Howgate, 1984

NOTE: Most workers regard this species as a synonym of *Archaeopteryx lithographica*.

Genus: *Palaeopteryx* Jensen, 1981 [*nomen dubium*]

P. thomsoni Jensen, 1981 (Type)

NOTE: Originally described as a primitive avian, the above genus may represent a small deinonychosaur, probably an archaeopterygid—although the type specimen is indeterminate (Jensen & Padian, 1989).

Family: DROMAEOSAURIDAE D. A. Russell, 1969

Census: 10 genera (3 doubtful), 17 species (10 doubtful)

= Bradycnemidae Harrison & C. A. Walker, 1975
= Dromaeosaurinae Matthew & Brown, 1922
= Velociraptorinae Barsbold, 1978

Genus: *Adasaurus* Barsbold, 1983
- = *Adasaurus* Barsbold, 1978 [*nomen nudum*]

A. mongoliensis Barsbold, 1983 (Type)

Genus: *Bradycneme* Harrison & C. A. Walker, 1975 [*nomen dubium*]

B. draculae Harrison & C. A. Walker, 1975 (Type)

NOTE: Described as a genus of large owls, the above "almost certainly represents a theropod dinosaur" (Brodkorb, 1978). Based on the structure of the astragalus, it is a dromaeosaurid (R. E. Molnar, pers. comm.).

Genus: *Deinonychus* Ostrom, 1969
- = *Daptosaurus* Brown, 1933 *vide* Chure & McIntosh, 1989
- = *Deynonychus* Bonaparte, 1978 [*sic*]
- = *Dienynochus* Dong, 1980 [*sic*]
- = *Koreanosaurus* Kim, 1979 [*nomen nudum*]
- = *Koreasaurus* Kim, 1979 [*sic*]

D. antirrhopus Ostrom, 1969 (Type)
- = *Velociraptor antirrhopus* (Ostrom, 1969)
- = *Daptosaurus agilis* Brown, 1933 *vide* Chure & McIntosh, 1989

NOTE: *Koreanosaurus*, based on a femur, was initially described as a deinodontid (tyrannosaurid), but Kim (1983) referred to the femur as possibly hypsilophodontid, and recently (pers. comm., 1986) he states it may be referable to *Deinonychus*. Lacking a type species, the genus *Koreanosaurus* is a *nomen nudum*. Paul (1988) synonymizes *Deinonychus* with *Velociraptor*, but Ostrom (1990) rejects this as unwarranted.

Genus: *Dromaeosaurus* Matthew & Brown, 1922
  ?*D. cristatus* (Cope, 1876) [*nomen dubium*]
    = *Laelaps cristatus* Cope, 1876 [*nomen dubium*]
    = *Dryptosaurus cristatus* Cope, 1876 [*nomen dubium*]
  ?*D. explanatus* (Cope, 1876) [*nomen dubium*]
    = *Laelaps explanatus* Cope, 1876 [*nomen dubium*]
    = *Deinodon explanatus* (Cope, 1876) [*nomen dubium*]
    = *Dryptosaurus explanatus* (Cope, 1876) [*nomen dubium*]
  ?*D. laevifrons* (Cope, 1876) [*nomen dubium*]
    = *Laelaps laevifrons* Cope, 1876 [*nomen dubium*]
    = *Dryptosaurus laevifrons* (Cope, 1876) [*nomen dubium*]
  ?*D. lateralis* (Cope, 1876) [*nomen dubium*]
    = *Aublysodon lateralis* Cope, 1876 [*nomen dubium*]
    = *Deinodon lateralis* (Cope, 1876) [*nomen dubium*]
  ?*D. gracilis* (Marsh, 1888) [*nomen dubium*]
    = *Coelurus gracilis* Marsh, 1888 [*nomen dubium*]
  ?*D. minutus* (Marsh, 1892) [*nomen dubium*]
    = *Ornithomimus minutus* Marsh, 1892 [*nomen dubium*]
  D. albertensis Matthew & Brown, 1922 (Type)

Genus: *Euronychodon* Telles Antunes & Sigogneau-Russell, 1991
  E. portucalensis Telles Antunes & Sigogneau-Russell, 1991 (Type)

Genus: *Hulsanpes* Osmólska, 1982
  H. perlei Osmólska, 1982 (Type)

Genus: "Kitadanisaurus" Lambert, 1990 [an indeterminate dromaeosaurid from Japan; Manabe & Hasegawa, 1991]

Genus: *Paronychodon* Cope, 1876 [*nomen dubium*]
  = *Triprotodon* Chure & McIntosh, 1989 [*sic*]
  = *Zapsalis* Cope, 1876 [*nomen dubium*]
  P. lacustris Cope, 1876 (Type)
    = *Zapsalis abradens* Cope, 1876 [*nomen dubium*]
  P. caperatus (Marsh, 1889) [*nomen dubium*]
    = *Tripriodon caperatus* Marsh, 1889 [*nomen dubium*]
    = *Meniscoessus caperatus* (Marsh, 1889) [*nomen dubium*]
    = *Triprotodon caperatus* ((Marsh, 1889) Chure & McIntosh, 1989 [*sic*]

Genus: *Phaedrolosaurus* Dong, 1973 [*nomen dubium*]
  P. ilikensis Dong, 1973 (Type)

Genus: *Sauromitholestes* Sues, 1978
  S. langstoni Sues, 1978 (Type)
    = *Velociraptor langstoni* (Sues, 1978) Paul, 1988

Genus: *Velociraptor* Osborn, 1924
  = *Ovoraptor* Osborn, 1924 [*nomen nudum*]
  = *Velociraptoe* Dong, 1977 [*sic*]
  V. mongoliensis Osborn, 1924 (Type)
    = *Ovoraptor djadochtari* Osborn, 1924 [*nomen nudum*]

Genus: [To be described from the Lower Cretaceous Cedar Mountain Formation of Utah; noted by Chure in the June 1984 *SVP Bulletin*]

Genus: [To be described from the Late Cretaceous of Mongolia; a large dromaeosaurid about 4 meters long; P. Currie, pers. comm.; D. McInnes, pers. comm.]

Genus: [To be described from the Late Cretaceous of Provence, France; material includes teeth and postcrania, and more than one taxon may be present; Buffetaut, Cuny & Le Loeuff, 1991]

Family: TROODONTIDAE Gilmore, 1924

Census: 5 genera (1 doubtful),
8 species (3 doubtful)

= Sauromithoididae Barsbold, 1974
= Troödontidae Gilmore, 1924*

Genus: *Borogovia* Osmólska, 1987
  B. gracilicrus Osmólska, 1987 (Type)

Genus: *Heptasteomis* Harrison & C. A. Walker, 1975 [*nomen dubium*]
  H. andrewsi Harrison & C. A. Walker, 1975 (Type)
    = *Troodon andrewsi* (Harrison & C. A. Walker, 1975) [*nomen dubium*]

NOTE: Described as a genus of large owls, the above "almost certainly represents a theropod dinosaur" (Brodkorb, 1978). Based on the structure of the astragalus, it is a troodontid (Paul, 1988).

Genus: *Sauromithoides* Osborn, 1924 (= *Troodon*?)
  = *Omithoides* Osborn, 1924 [*nomen nudum*]
  = *Sauronithoides* Maryanska, 1977 [*sic*]
  S. mongoliensis Osborn, 1924 (Type)
    = *Troodon mongoliensis* (Osborn, 1924)
    = *Omithoides oshiensis* Osborn, 1924 [*nomen nudum*]
  S. junior Barsbold, 1974
  ?*S. asiamericanus* (Nessov, 1985) n. comb. [*nomen dubium*]
    = *Pectinodon asiamericanus* Nessov, 1985 [*nomen dubium*]

NOTE: Synonymy of *Pectinodon* with *Troodon* (Currie, 1987) indicates that the above species is best placed provisionally in the genus *Sauromithoides*.

Genus: "Sinornithoides" [Anonymous] 1990 [to be described by D. A. Russell & Dong Z. from a Lower Cretaceous formation in the Ordos Basin of Inner Mongolia; name published in *Update*, an Ex Terra Foundation publication]

Genus: *Tochisaurus* Kurzanov & Osmólska, 1991
  T. nemegtensis Kurzanov & Osmólska, 1991 (Type)

Genus: *Troodon* Leidy, 1856
  = *Troödon* Leidy, 1856*
  = *Pectinodon* Carpenter, 1982
  = *Polydontosaurus* Glut, 1972 [*sic*]
  = *Polyodontosaurus* Sternberg, 1932
  = *Stenonychosaurus* Sternberg, 1932
  T. formosus Leidy, 1856 (Type)
    = *Troödon formosus* Leidy, 1856*
    = *Stegoceras formosum* (Leidy, 1856)
    = *Stegoceras formosus* (Leidy, 1856)*
    = *Stenonychosaurus inequalis* Sternberg, 1932
    = *Sauromithoides inequalis* (Sternberg, 1932)
    = *Polyodontosaurus grandis* Sternberg, 1932
  T. bakkeri (Carpenter, 1982) n. comb. [*nomen dubium*]
    = *Pectinodon bakkeri* Carpenter, 1982 [*nomen dubium*]

NOTE: The above species is provisionally retained for Lance *Troodon* teeth.

Suborder: Oviraptorosauria Barsbold, 1976

Census: 4 families, 7 genera, 10 species

Family: CAENAGNATHIDAE R. M. Sternberg, 1940

Census: 1 genus, 2 species

= Caenagnathinae Paul, 1988

Genus: *Caenagnathus* R. M. Sternberg, 1940
  = *Caegnathus* Molnar & Carpenter, 1989 [*sic*]
  = *Caenognathus* Langston, 1965 [*sic*]
  = *Chaenagnathus* Gregory, 1951 [*sic*]
  = *Coenagnathus* Gradzinski, Kielan-Jaworowska & Maryanska, 1977 [*sic*]
  C. collinsi R. M. Sternberg, 1940 (Type)
  C. stembergi Cracraft, 1971

Family: ELMISAURIDAE Osmólska, 1981

Census: 3 genera, 4 species

Genus: *Chirostenotes* Gilmore, 1924
= *Cheirostenotes* Nopcsa, 1928 [*sic*]
= *Macrophalangia* C. M. Sternberg, 1932
C. pergracilis Gilmore, 1924 (Type)
= *Macrophalangia canadensis* C. M. Sternberg, 1932

NOTE: A newly described partial skeleton effectively establishes the synonymy of the two genera *Chirostenotes* and *Macrophalangia* (Currie & D. A. Russell, 1988).

Genus: *Elmisaurus* Osmólska, 1981
E. rarus Osmólska, 1981 (Type)
= *Chirostenotes rarus* (Osmólska, 1981)
E. elegans (Parks, 1933)
= *Ornithomimus elegans* Parks, 1933
= *Chirostenotes elegans* (Parks, 1933)
= *Macrophalangia elegans* (Parks, 1933)

Genus: *Microvenator* Ostrom, 1970
= *Megadontosaurus* Brown, 1933 *vide* Chure & McIntosh, 1989
= *Microventer* Stokes, 1988 [*sic*]
M. celer Ostrom, 1970 (Type)
= *Megadontosaurus ferox* Brown, 1933 *vide* Chure & McIntosh, 1989
?*M. chagyabi* Zhao, 1986 [*nomen nudum*]

Family: OVIRAPTORIDAE Barsbold, 1976

Census: 2 genera, 3 species

= Oviraptorinae Barsbold, 1981

Genus: *Conchoraptor* Barsbold, 1986
C. gracilis Barsbold, 1986 (Type)

Genus: *Oviraptor* Osborn, 1924
= *Fenestrosaurus* Osborn, 1924 [*nomen nudum*]
O. philoceratops Osborn, 1924 (Type)
= *Oviraptor (Oviraptor) philoceratops* (Osborn, 1924)
= *Fenestrosaurus philoceratops* Osborn, 1924 [*nomen nudum*]
O. mongoliensis Barsbold, 1986

Genus: [To be described from the Late Cretaceous of Mongolia; possesses a didactyl manus and may represent a new family; D. McInnes, pers. comm.]

Family: INGENIIDAE Barsbold, 1986

Census: 1 genus, 1 species

= Ingeniinae Barsbold, 1981

Genus: *Ingenia* Barsbold, 1981
I. yanshini Barsbold, 1981 (Type)
= *Oviraptor (Ingenia) yanshini* (Barsbold, 1981)

Suborder: Avimimiformes Chatterjee, 1991

Census: 1 family, 1 genus, 1 species

Family: AVIMIMIDAE Kurzanov, 1981

Census: 1 genus, 1 species

Genus: *Avimimus* Kurzanov, 1981
A. portentosus Kurzanov, 1981 (Type)

Genus: [To be described from the Late Cretaceous Erenhot Formation of Mongolia; may be merely a new species of *Avimimus*; P. J. Currie, pers. comm.]

Theropoda *incertae sedis*

Census: 5 genera (3 doubtful), 5 species (3 doubtful)

Genus: *Macrodontophion* Zborzewski, 1834 [*nomen dubium*]

No type species named

NOTE: This genus is based on a tooth usually considered to be megalosaurid. It could well belong to a crocodilian or a plesiosaur (R. E. Molnar, pers. comm.).

Genus: *Ornithodesmus* Seeley, 1887

O. cluniculus Seeley, 1887 (Type)

NOTE: This genus, usually classified in its own pterosaur family, **Ornithodesmidae** Hooley, 1913, was recently determined to be a small theropod dinosaur by S. Howse & Andrew Milner (*SVP Bulletin* #145: 43; Wellnhofer, 1991).

Genus: *Orthogoniosaurus* Das-Gupta, 1931 [*nomen dubium*]

O. rawesi (Lydekker, 1890) n. comb. [*nomen dubium*]

= *Massospondylus rawesi* Lydekker, 1890 [*nomen dubium*]

= *Megalosaurus rawesi* (Lydekker, 1890) Vianey-Liaud, Jain & Sahni, 1987 [*nomen dubium*]

O. matleyi Das-Gupta, 1931 (Type)

NOTE: The tooth that is the type specimen of *Massospondylus rawesi* resembles the type tooth of *Orthogoniosaurus matleyi* in a number of features that suggest it is from a different part of the jaw of the same genus, if not the same species.

Genus: *Patricosaurus* Seeley, 1887 [*nomen dubium*]

P. merocratus Seeley, 1887 (Type)

NOTE: The above genus, based on the proximal end of a femur, is not lacertilian as originally classified but is probably an indeterminate small theropod (R. E. Molnar, pers. comm.).

Genus: *Richardoestesia* Currie, Rigby & Sloan, 1990

= *Ricardoestesia* Currie, Rigby & Sloan, 1990 [*sic*]

R. gilmorei Currie, Rigby & Sloan, 1990 (Type)

NOTE: The above genus is based on a small dentary originally referred to *Chirostenotes* in Gilmore, 1924.

Genus: [To be described from the Late Cretaceous of Mongolia; represents a new family of small theropods with a monodactyl manus; P. J. Currie, pers. comm.]

Notes and New Taxa

Superorder: Sauropodomorpha von Huene, 1932

Census: 2 orders, 18 families, 96 genera (19 doubtful), 151 species (41 doubtful)

Order: Brontosauria nov.

Census: 2 suborders, 16 families, 91 genera (19 doubtful), 145 species (41 doubtful)

Parasuborder: Prosauropoda von Huene, 1920

Census: 7 families, 18 genera (3 doubtful), 23 species (6 doubtful)

Family: THECODONTOSAURIDAE Lydekker, 1890

Census: 3 genera (2 doubtful), 5 species (4 doubtful)

Genus: *Agrosaurus* Seeley, 1891 [*nomen dubium*]
  A. macgillivrayi Seeley, 1891 (Type)
    = *Thecodontosaurus macgillivrayi* (Seeley, 1891)

Genus: *Azendohsaurus* Dutuit, 1972 [*nomen dubium*]
  = *Azandohosaurus* Galton, 1978 [*sic*]
  = *Azandohsaurus* Dutuit, 1972 [*sic*]
  A. laaroussii Dutuit, 1972 (Type)

Genus: *Thecodontosaurus* Riley & Stutchbury, 1836
  T. antiquus Morris, 1843 (Type)
  ?T. elizae (Sauvage, 1907) von Huene, 1908 [*nomen dubium*]
    = *Plateosaurus elizae* Sauvage, 1907 [*nomen dubium*]

NOTE: This species is based on the teeth of a carnivore (rauisuchid, herrerasaurid, ornithosuchid, or theropod) and is not a prosauropod (Galton, 1985).

  ?T. minor Haughton, 1918 [*nomen dubium*]
    = *Thecodontosaurus browni* von Huene, 1932 *non* Seeley, 1895 [*nomen dubium*]
    = *Thecodontosaurus minimus* Ellenberger, 1970 [*sic*; probably an error for *Thecodontosaurus minor*]

Family: ANCHISAURIDAE Marsh, 1885

Census: 1 genus, 3 species

= Amphisauridae Marsh, 1882

Genus: *Anchisaurus* Marsh, 1885
  = *Amphisaurus* Marsh, 1877 [*nomen nudum*]
  = *Amphisaurus* Marsh, 1882/Barkas, 1870
  = *Gyposaurus* Broom, 1911
  = *Megadactylus* Hitchcock, 1865/Fitzinger, 1843
  = *Yaleosaurus* von Huene, 1932
  A. polyzelus (Hitchcock, 1865) (Type)
    = *Megadactylus polyzelus* Hitchcock, 1865
    = *Amphisaurus polyzelus* (Hitchcock, 1865)
    = *Thecodontosaurus polyzelus* (Hitchcock, 1865)

- = *Palaeosaurus fraserianus* Cope, 1878 [*nomen dubium*]
- = *Clepsysaurus fraserianus* (Cope, 1878) [*nomen dubium*]
- = *Palaeosauriscus fraserianus* (Cope, 1878) [*nomen dubium*]
- = *Thecodontosaurus fraserianus* (Cope, 1878) [*nomen dubium*]
- = *Anchisaurus colurus* Marsh, 1891
- = *Yaleosaurus colurus* (Marsh, 1891)

A. capensis (Broom, 1911)

- = *Gyposaurus capensis* Broom, 1911
- = *Hortalotarsus skirtopodus* Broom, 1906 *non* Seeley, 1894

A. sinensis (Young, 1941) Dong n. comb.

- = *Gyposaurus sinensis* Young, 1941

NOTE: The above genus is organized according to Galton, 1976, Galton & Cluver, 1976, and Dong Z. (pers. comm.). Galton, 1976 regards the differences between *Anchisaurus polyzelus* and *Yaleosaurus colurus* as due to sexual dimorphism, with *A. polyzelus* the male and *Y. colurus* the female.

Genus: [To be described from the Lower Chinle Formation; Murry & Long, 1989]

Family: MASSOSPONDYLIDAE von Huene, 1914

Census: 1 genus, 2 species (1 doubtful)

= Gryponichidae Tatarinov, 1964 [*sic*]
= Gryponychidae von Huene, 1932

Genus: *Massospondylus* Owen, 1854

- = *Aetonyx* Broom, 1911
- = *Aristosaurus* van Hoepen, 1920
- = *Dromicosaurus* van Hoepen, 1920
- = *Gryponyx* Broom, 1911
- = *Leptospondylus* Owen, 1854 [*nomen dubium*]
- = *Messospondylus* Chinsamy, 1991 [*sic*]
- = *Pachyspondylus* Owen, 1854 [*nomen dubium*]

M. carinatus Owen, 1854 (Type)

- = *Plateosaurus carinatus* (Owen, 1854)
- = *Leptospondylus capensis* Owen, 1854 [*nomen dubium*]
- = *Pachyspondylus orpenii* Owen, 1854 [*nomen dubium*]
- = *Hortalotarsus skirtopodus* Seeley, 1894
- = *Gyposaurus skirtopodus* (Seeley, 1894)
- = *Thecodontosaurus skirtopodus* (Seeley, 1894)
- = *Massospondylus browni* Seeley, 1895 [*nomen dubium*]
- = *Thecodontosaurus browni* (Seeley, 1895) [*nomen dubium*]
- = *Massospondylus harriesi* Broom, 1911
- = *Aetonyx palustris* Broom, 1911
- = *Gryponyx africana* Broom, 1911
- = *Gryponyx africanus* Broom, 1911*
- = *Gryponyx transvaalensis* Broom, 1912 [*nomen dubium*]
- = *Aristosaurus erectus* van Hoepen, 1920
- = *Gyposaurus erectus* (van Hoepen, 1920)
- = *Dromicosaurus gracilis* van Hoepen, 1920
- = *Gryponyx taylori* Haughton, 1924 [*nomen dubium*]
- = *Massospondylus schwarzi* Haughton, 1924 [*nomen dubium*]
- = *Thecodontosaurus dubius* Haughton, 1924
- = *Thecodontosaurus minor* Haughton, 1924 *non* Haughton, 1918
- = *Gyposaurus capensis* von Huene, 1932 *non* Broom, 1911
- = *Gryponyx transvalensis* von Huene, 1932 [*sic*]

?*M. hislopi* Lydekker, 1890 [*nomen dubium*]

[New species to be described from the Kayenta Formation of Arizona; skull described in Crompton & Attridge, 1986]

Family: YUNNANOSAURIDAE Young, 1942

Census: 1 genus, 1 species

Genus: *Yunnanosaurus* Young, 1942

- = *Yuannanosaurus* Young, 1982 [*sic*]

Y. huangi Young, 1942 (Type)

- = *Yunnanosaurus robustus* Young, 1951
- = *Yuannanosaurus robustas* Young, 1982 [*sic*]

Family: PLATEOSAURIDAE Marsh, 1895

Census: 8 genera (1 doubtful),
8 species (1 doubtful)

= Ammosauridae von Huene, 1914
= Fulengidae Carroll & Galton, 1977
= Plateosauriden von Huene, 1929
= Sellosauridae von Huene, 1908

Genus: *Ammosaurus* Marsh, 1891
= *Ammorsaurus* Stokes & Madsen, 1978 [*sic*]
A. major (Marsh, 1889) (Type)
= *Anchisaurus major* Marsh, 1889
= *Anchisaurus solus* Marsh, 1892 (juvenile)
= *Ammosaurus solus* (Marsh, 1892) (juvenile)

Genus: *Coloradisaurus* Lambert, 1983
= *Coloradia* Bonaparte, 1978/Blake, 1863
C. brevis (Bonaparte, 1978) (Type)
= *Coloradia brevis* Bonaparte, 1978

Genus: *Euskelosaurus* Huxley, 1866
= *Enskelosaurus* Nopcsa, 1926 [*sic*]
= *Entelosaurus* D. E. Russell, 1971 [*sic*]
= *Eucnemesaurus* van Hoepen, 1920 [*nomen dubium*]
= *Euscelesaurus* Lydekker, 1890 [*sic*]
= *Euscelidosaurus* Lydekker *vide* Nicholson & Lydekker, 1889 [*sic*]
= *Euscellosaurus* Lydekker, 1890 [*sic*]
= *Euscelosaurus* Zittel, 1890 [*sic*]
= *Euskelesaurus* Huxley, 1867 [*sic*]
= *Euskelosaurs* van Heerden, 1980 [*sic*]
= *Gigantoscelis* von Huene, 1932 [*sic*]
= *Gigantoscelus* van Hoepen, 1916 [*nomen dubium*]
= *Gigantoskelis* Glut, 1972 [*sic*]
= *Orinosaurus* Lydekker, 1889 [*nomen dubium*]
= *Orosaurus* Huxley, 1867/Peters, 1862
= *Plateosauravus* von Huene, 1932
E. browni Huxley, 1866 (Type)
= *Orinosaurus capensis* Lydekker, 1889 [*nomen dubium*]
= *Euskelosaurus capensis* (Lydekker, 1889) [*nomen dubium*]
= *Orosaurus capensis* (Lydekker, 1889) [*nomen dubium*]
= *Plateosaurus stormbergensis* Broom, 1915 [*nomen dubium*]
= *Plateosauravus stormbergensis* (Broom, 1915) [*nomen dubium*]
= *Gigantoscelus molengraaffi* van Hoepen, 1916 [*nomen dubium*]
= *Euskelosaurus molengraaffi* (van Hoepen, 1916) [*nomen dubium*]
= *Eucnemesaurus fortis* van Hoepen, 1920 [*nomen dubium*]
= *Euskelosaurus africanus* Haughton, 1924
= *Plateosaurus cullingworthi* Haughton, 1924
= *Plateosauravus cullingworthi* (Haughton, 1924)

Genus: *Fulengia* Carroll & Galton, 1977 [*nomen dubium* in Sereno, 1991]
F. youngi Carroll & Galton, 1977 (Type)

NOTE: Originally classified as a "modern" lizard in its own family **Fulengidae**, the above genus and species are probably based on a hatchling or extremely young prosauropod (Dong Z., pers. comm.; Sereno, 1991).

Genus: *Lufengosaurus* Young, 1941
= *Lufengocephalus* Young, 1974
= *Lugengosaurus* Carroll, 1987 [*sic*]
= *Lunfengosaurus* Rozhdestvensky, 1965 [*sic*]
= *Tawasaurus* Young, 1982 (juvenile)
L. huenei Young, 1941 (Type)
= *Lufengosaurus magnus* Young, 1942
= *Lufengocephalus tawae* Young, 1974
= *Tawasaurus minor* Young, 1982 (juvenile)
?*L. changduensis* Zhao, 1986 [*nomen nudum*]

NOTE: The genus *Lufengocephalus*, formerly classified as a rhynchosaur, is apparently a senior synonym of *Tawasaurus* (Dong Z., pers. comm.) and thus a junior synonym of *Lufengosaurus*. Sereno (1991) considers *Tawasaurus* to be a *nomen dubium* classifiable only as Prosauropoda indet.

Genus: *Mussaurus* Bonaparte & Vince, 1979
= *Mussasaurus* Olshevsky, 1978 [*sic*]
= *Mussaurus* Bonaparte, 1978 [*nomen nudum*]
M. patagonicus Bonaparte & Vince, 1979 (Type)

= *Mussaurus patagonicus* Bonaparte, 1978 [*nomen nudum*]

NOTE: The type specimen is a hatchling prosauropod. An adult individual of this genus was described as *Plateosaurus* sp. by Casamiquela, 1980.

Genus: *Plateosaurus* von Meyer, 1837
= *Dimodosaurus* Pidancet & Chopard, 1862
= *Dinosaurus* Rütimeyer, 1856/Fischer de Waldheim, 1847
= *Greeslyosaurus* Yadagiri, 1988 [*sic*]
= *Greslyosaurus* Heilmann, 1927 [*sic*]
= *Gresslyosaurus* Rütimeyer, 1857
= *Pachysauriscus* Kuhn, 1959 [*nomen dubium*]
= *Pachysaurops* von Huene, 1961 [*sic*]
= *Pachysaurus* von Huene, 1908/Fitzinger, 1843
= *Plataeosaurus* von Meyer, 1845 [*sic*]
= *Plateosaums* Yadagiri, 1988 [*sic*]
= *Platysaurus* Agassiz, 1846/Smith, 1844 [*sic*]
P. engelhardti von Meyer, 1837 (Type)
= *Zanclodon laevis* Plieninger, 1847 *non* Plieninger, 1846
= *Dinosaurus gresslyi* Rütimeyer, 1856
= *Gresslyosaurus ingens* Rütimeyer, 1857
= *Dimodosaurus poligniensis* Pidancet & Chopard, 1862
= *Plateosaurus poligniensis* (Pidancet & Chopard, 1862) von Huene, 1908
= *Zanclodon quenstedti* Koken, 1900
= *Plateosaurus quenstedti* (Koken, 1900)
= *Gresslyosaurus robustus* von Huene, 1908 [*nomen dubium*]
= *Plateosaurus robustus* (von Huene, 1908) von Huene, 1932 [*nomen dubium*]
= *Pachysaurus ajax* von Huene, 1908 [*nomen dubium*]
= *Gresslyosaurus ajax* (von Huene, 1908) [*nomen dubium*]
= *Pachysauriscus ajax* (von Huene, 1908) Kuhn, 1959 [*nomen dubium*]
= *Pachysaurus magnus* von Huene, 1908 [*nomen dubium*]
= *Gresslyosaurus magnus* (von Huene, 1908) Steel, 1970 [*nomen dubium*]
= *Pachysauriscus magnus* (von Huene, 1908) Kuhn, 1959 [*nomen dubium*]
= *Plateosaurus erlenbergiensis* von Huene, 1905
= *Plateosaurus ornatus* von Huene, 1905 [*nomen dubium*]
= *Plateosaurus plieningeri* von Huene, 1905
= *Gresslyosaurus plieningeri* (von Huene, 1905) von Huene, 1926
= *Plateosaurus reinigeri* von Huene, 1905 [*nomen dubium*]
= *Gresslyosaurus reinigeri* (von Huene, 1908) von Huene, 1926 [*nomen dubium*]
= *Pachysauriscus reinigeri* (von Huene, 1908) Kuhn, 1959 [*nomen dubium*]
= *Pachysaurus reinigeri* (von Huene, 1908) von Huene, 1932 [*nomen dubium*]
= *Gresslyosaurus torgeri* Jaekel, 1911 [*nomen dubium*]
= *Plateosaurus longiceps* Jaekel, 1913
= *Plateosaurus trossingensis* E. Fraas, 1913
= *Plateosaurus integer* E. Fraas *vide* von Huene, 1915 [*nomen nudum*]
= *Pachysaurus giganteus* von Huene, 1932 [*nomen dubium*]
= *Gresslyosaurus giganteus* (von Huene, 1932) Steel, 1970 [*nomen dubium*]
= *Pachysauriscus giganteus* (von Huene, 1932) Kuhn, 1959 [*nomen dubium*]
= *Pachysaurus wetzelianus* von Huene, 1932 [*nomen dubium*]
= *Gresslyosaurus wetzelianus* (von Huene, 1932) Steel, 1970 [*nomen dubium*]
= *Pachysauriscus wetzelianus* (von Huene, 1932) Kuhn, 1959 [*nomen dubium*]
= *Plateosaurus fraasianus* von Huene, 1932

NOTE: Synonymy within this genus is mainly according to Galton (1984, 1985). Preliminary morphometric analysis by Weishampel & Chapman (1990) indicates that two or more species may be present. Further work is needed before they can be correctly named.

Paragenus: *Sellosaurus* von Huene, 1908
= *Efraasia* Galton, 1973 (juvenile)
S. gracilis von Huene, 1908 (Type)
= *Plateosaurus gracilis* (von Huene, 1908)
= *Thecodontosaurus diagnosticus* E. Fraas, 1905 [*nomen nudum*]
= *Sellosaurus fraasi* von Huene, 1908
= *Plateosaurus fraasi* (von Huene, 1908)
= *Teratosaurus minor* von Huene, 1908

= *Teratosaurus trossingensis* von Huene, 1908
= *Thecodontosaurus hermannianus* von Huene, 1908
= *Sellosaurus hermannianus* (von Huene, 1908)
= *Thecodontosaurus diagnosticus* von Huene, 1932
= *Palaeosaurus diagnosticus* (von Huene, 1932)
= *Palaeosauriscus diagnosticus* (von Huene, 1932)
= *Efraasia diagnostica* (von Huene, 1932)

Genus: [To be described from the Upper Triassic Dharmaram Formation of India; Kutty, 1969]

Family: MELANOROSAURIDAE von Huene, 1929

Census: 3 genera, 3 species

= Plateosauravidae von Huene, 1932

Genus: *Camelotia* Galton, 1985
  C. borealis Galton, 1985 (Type)
    = *Gresslyosaurus ingens* Seeley, 1898 non Rütimeyer, 1857

Genus: *Likhoelesaurus* Ellenberger, 1972 [*nomen nudum*]
  L. ingens Ellenberger, 1972 (Type)
    = *Likhoelesaurus ferox* Ellenberger, 1972 [*nomen nudum*]

Genus: *Melanorosaurus* Haughton, 1924
  = *Malanorosaurus* Yadagiri, 1988 [*sic*]
  = *Melanosaurus* von Huene, 1954/Gilmore, 1927 [*sic*]
  = *Melanososaurus* Yadagiri, 1988 [*sic*]
  M. readi Haughton, 1924 (Type)

Genus: *Microdontosaurus* Zhao, 1983 [*nomen nudum*]
  M. dayensis Zhao, 1986 (Type)

Genus: *Riojasaurus* Bonaparte, 1969
  = *Strenusaurus* Bonaparte, 1969 (juvenile)
  R. incertus Bonaparte, 1969 (Type)
    = *Strenusaurus procerus* Bonaparte, 1969 (juvenile)

Genus: *Roccosaurus* van Heerden *vide* Anderson & Cruickshank, 1978 [*nomen nudum*]
  R. tetrasacralis van Heerden *vide* Kitching & Raath, 1984 (Type)

NOTE: The above genus and species have thus far been published only in faunal lists. The species may be a junior synonym of *Melanorosaurus readi* (P. Galton, pers. comm.).

Genus: *Thotobolosaurus* Ellenberger, 1972 [*nomen nudum*]
  T. mabeatae Ellenberger, 1972 (Type)

NOTE: The above genus is the "Maphutseng dinosaur" of Crompton & Charig, 1965. It is probably not a synonym of *Euskelosaurus* as some workers have reported (J. S. McIntosh, pers. comm.).

Genus: [To be described from China; based on material originally referred to *Sinosaurus*; van Heerden, 1978, 1980]

Genus: [To be described from Argentina; Bonaparte, 1986]

Family: BLIKANASAURIDAE Galton & van Heerden, 1985

Census: 1 genus, 1 species

= Blikanosauridae Hunt, 1991 [*sic*]

Genus: *Blikanasaurus* Galton & van Heerden, 1985
  = *Blikanosaurus* Hunt, 1991 [*sic*]
  B. cromptoni Galton & van Heerden, 1985 (Type)

Notes and New Taxa

Superorder: Sauropodomorpha von Huene, 1932 (continued)

Order: Brontosauria nov. (continued)

Suborder: Sauropoda Marsh, 1878

Census: 9 families, 73 genera (16 doubtful), 122 species (35 doubtful)

Family: BARAPASAURIDAE L. B. Halstead & J. Halstead, 1981

Census: 5 genera, 5 species

= Vulcanodontidae Cooper, 1984

Genus: *Barapasaurus* Jain, Kutty, Roy-Chowdhury & Chatterjee, 1975
  = *Barapasurus* Yadagiri, 1988 [*sic*]
  = *Basapasaurus* Chow, 1979 [*sic*]
  B. tagorei Jain, Kutty, Roy-Chowdhury & Chatterjee, 1975 (Type)

Genus: *Chinshakiangosaurus* Zhao, 1986 [*nomen nudum*]
  = *Chinshakiangosaurus* Yeh, 1975 [*nomen nudum*]
  C. zhongheensis Zhao, 1986 (Type)
    = *Chinshakiangosaurus chunghoensis* Yeh, 1975 [*nomen nudum*]
    = *Chinshakiangosaurus zhonghonensis* Zhao, 1986 [*sic*]

NOTE: The above genus remains undescribed, but a photograph of its femur was published by Zhao (1986). Referred to this family provisionally.

Genus: *Kotasaurus* Yadagiri, 1988
  = *Kotasaurus* Yadagiri, 1986 [*nomen nudum*]
  = *Kotasautus* Yadagiri, 1988 [*sic*]
  = *Kotasurus* Yadagiri, 1988 [*sic*]
  K. yamanpalliensis Yadagiri, 1988 (Type)
    = *Kotasaurus yamanpalliensis* Yadagiri, 1986 [*nomen nudum*]
    = *Kotasaurus yemanpalliensis* Yadagiri, 1988 [*sic*]

Genus: *Kunmingosaurus* Zhao, 1986 [*nomen nudum*]
  = *Kunmingosaurus* Zhen, Li & Rao, 1986 [*nomen nudum*]
  K. utingensis Zhao, 1986 (Type)
    = *Kunmingosaurus utingensjs* Zhao, 1986 [*sic*]
    = *Kunmingosaurus utingi* Zhen, Li & Rao, 1986 [*nomen nudum*]
    = *Kunmingosaurus wudingi* Zhao, 1986 [*sic*]
    = *Kunmingosaurus wudingensis* [Anonymous] 1990 [*nomen nudum*]

NOTE: The above genus remains undescribed, but a photograph of its hind limb and pelvis was published by Zhao (1986), and its entire skeleton appeared in *The Age of Dinosaurs in Japan and China* (Dong, Hasegawa & Azuma, 1990), a Japanese dinosaur exhibition guidebook (title transliterated by M. Tanimoto, pers. comm.). Referred to this family provisionally.

Genus: *Ohmdenosaurus* Wild, 1978
  O. liasicus Wild, 1978 (Type)
    = *Ohmdenosaurus liassicus* Yadagiri, 1988 [*sic*]

Genus: *Vulcanodon* Raath, 1972
= *Volcondon* Dong, 1990 [*sic*]
= *Vulcanadon* Yadagiri, 1988 [*sic*]
= *Vulcandon* Yadagiri, 1988 [*sic*]
V. karibaensis Raath, 1972 (Type)

Genus: *Zizhongosaurus* Dong, Zhou & Zhang, 1983
= *Zizhangosaurus* McIntosh, 1990 [*sic*]
Z. chuanchengensis Dong, Zhou & Zhang, 1983 (Type)
= *Zizhongosaurus chuanchensis* Dong, Zhou & Zhang, 1983 [*sic*]

Parafamily: CETIOSAURIDAE Lydekker, 1888

Census: 11 genera (1 doubtful), 14 species (1 doubtful)

= Bellusaurinae Dong, 1986 [*nomen nudum*]
= Bellusaurinae Dong, 1990
= Cardiodontidae Lydekker, 1895
= Cetiosaurinae Janensch, 1929
= Shunosaurinae McIntosh, 1990

Genus: *Amygdalodon* Cabrera, 1947
= *Amigdalodon* Bonaparte, 1978 [*sic*]
A. patagonicus Cabrera, 1947 (Type)

Genus: *Austrosaurus* Longman, 1933
A. mckillopi Longman, 1933 (Type)

NOTE: The above genus is referred to this family provisionally (R. E. Molnar, pers. comm.).

Genus: *Bellusaurus* Dong, 1990
= *Bellusaurus* Dong, 1986 [*nomen nudum*]
B. sui Dong, 1990 (Type)
= *Bellusaurus sui* Dong, 1986 [*nomen nudum*]

NOTE: Initially classified as a brachiosaurid, the above genus is probably a cetiosaurid (J. S. McIntosh, pers. comm.).

Genus: *Cardiodon* Owen, 1841 [*nomen dubium*; = *Cetiosaurus*?]
C. rugulosus Owen, 1845 (Type)
= *Cetiosaurus rugulosus* (Owen, 1845) [*nomen dubium*]

NOTE: The above genus and species are based on a sauropod tooth probably but not certainly referable to *Cetiosaurus*.

Genus: *Cetiosaurus* Owen, 1842
= *Ceteosaurus* Phillips, 1871 [*sic*]
C. medius Owen, 1842
= *Cetiosaurus hypoolithicus* Owen, 1842 [*nomen oblitum*]
= *Cetiosaurus hypooolithicus* Olshevsky, 1978 [*sic*]
C. oxoniensis Phillips, 1871 (Type)
= *Cetiosaurus giganteus* Owen *vide* Huxley, 1870 [*nomen oblitum*]
?*C. mogrebiensis* de Lapparent, 1955

Genus: *Dachungosaurus* Zhao, 1986 [*nomen nudum*]
= *Dachongosaurus* Zhao, 1986 [*sic*]
D. yunnanensis Zhao, 1986 (Type)

NOTE: The above genus remains undescribed, but a photograph of its remains *in situ* was published by Zhao (1986). Referred to this family provisionally.

Genus: *Datousaurus* Dong & Tang, 1984
= *Datousaurus* Dong, 1983 [*nomen nudum*]
= *Lancangosaurus* Dong, Zhou & Zhang, 1983 [*nomen nudum*]
D. bashanensis Dong & Tang, 1984 (Type)
= *Datousaurus bashanensis* Dong, 1983 [*nomen nudum*]

Genus: *Haplocanthosaurus* Hatcher, 1903
= *Haplacanthosaurus* von Huene, 1909 [*sic*]
= *Haplocanthus* Hatcher, 1903/Agassiz, 1845 (as *Haplacanthus*; *Haplocanthosaurus* conserved in Lucas & Hunt, 1989 [ICZN Case #2684] and ICZN Opinion #1633)
= *Harlocanthosaurus* Yadagiri, 1988 [*sic*]
H. priscus (Hatcher, 1903) (Type)
= *Haplocanthus priscus* Hatcher, 1903
= *Morosaurus agilis* Marsh, 1889 [*nomen dubium*]
= *Camarasaurus agilis* (Marsh, 1889) [*nomen dubium*]
= *Haplocanthosaurus utterbacki* Hatcher, 1903
= *Haplocanthus utterbacki* Olshevsky, 1978 [*sic*]
= *Haplocanthosaurus piscus* Yadagiri, 1988 [*sic*]

H. delfsi McIntosh & Williams, 1988

Genus: *Lancangjiangosaurus* Zhao, 1983 [*nomen nudum*]
= *Lancanjiangosaurus* Zhao, 1986 [*nomen nudum*]
L. cachuensis Zhao, 1986 (Type)
NOTE: The above genus remains undescribed, but a photograph of its remains *in situ* was published by Zhao (1986). Referred to this family provisionally.

Genus: *Oshanosaurus* Zhao, 1986 [*nomen nudum*]
O. youngi Zhao, 1986 (Type)
NOTE: The above genus remains undescribed, appearing in a faunal list in Zhao, 1986. Referred to this family provisionally.

Genus: *Patagosaurus* Bonaparte, 1979
P. fariasi Bonaparte, 1979 (Type)

Genus: *Protognathosaurus* nov.
= *Protognathus* Zhang, 1988/Basilewsky, 1950
P. oxyodon (Zhang, 1988) n. comb. (Type)
= *Protognathus oxyodon* Zhang, 1988
NOTE: The generic name *Protognathosaurus* is proposed to replace the name *Protognathus*, which is preoccupied by the name of a beetle.

Genus: *Rhoetosaurus* Longman, 1925
= *Rhaetosaurus* de Lapparent & Lavocat, 1955 [*sic*]
= *Rheteosaurus* Yadagiri, Prasad & Satsangi, 1979 [*sic*]
R. brownei Longman, 1925 (Type)

Genus: *Shunosaurus* Dong, Zhou & Zhang, 1983
= *Shunasaurus* Dong, 1980 [*sic*]
= *Shunosaurus* Dong, 1981 [*nomen nudum*]
= *Shuosaurus* Chow, 1979 [*nomen nudum*]
S. lii Dong, Zhou & Zhang, 1983 (Type)
= *Shuosaurus lii* Dong, 1980 [*nomen nudum*]
S. ziliujingensis [Anonymous] 1986 [*nomen nudum*; to be described by Zhang]

Genus: [To be described from the Bathonian of Morocco; a large cetiosaurid presently referred to *Cetiosaurus mogrebiensis*; Taquet & Monbaron, 1981; McIntosh, 1990]

Family: BRACHIOSAURIDAE
Riggs, 1904

Census: 12 genera (2 doubtful),
21 species (9 doubtful)

= Astrodontidae von Huene, 1948
= Astrodontinae von Huene, 1932
= Bothriospondylidae Lydekker, 1895 [*nomen oblitum*]
= Brachiosaurinae Janensch, 1929
= Pleurocoelidae Marsh, 1888 [*nomen oblitum*]

Genus: *Astrodon* Johnston, 1859
= *Astrodonius* Kuhn, 1961
= *Astrodontonius* Steel, 1970 [*sic*]
= *Astrond* Dong, 1990 [*sic*]
= *Astrood* Dong, 1990 [*sic*]
A. johnstoni Leidy, 1865 (Type)
= *Astrodonius johnstoni* (Leidy, 1865)

Genus: *Bothriospondylus* Owen, 1875
= *Marmarospondylus* Owen, 1875 [*nomen dubium*]
B. suffosus Owen, 1875 (Type)
= *Pleurocoelus suffosus* (Owen, 1875) Marsh, 1897
?*B. robustus* (Owen, 1875) [*nomen dubium*]
= *Marmarospondylus robustus* Owen, 1875 [*nomen dubium*]
?*B. madagascariensis* Lydekker, 1895 [*nomen dubium*]
NOTE: Material referred to this species, considered indeterminate by McIntosh, 1990, was made the type specimen of the cetiosaurid *Lapparentosaurus madagascariensis*.

Genus: *Brachiosaurus* Riggs, 1903
= *Brachyosaurus* Langston, 1974 [*sic*]
= *Branchiosaurus* Yadagiri, 1988 [*sic*]
B. altithorax Riggs, 1903 (Type)
= *Brachiosaurus (Brachiosaurus) altithorax* (Riggs, 1903)
= *Brachiosaurus altus* Jensen, 1986 [*sic*]

- ?*B. atalaiensis* de Lapparent & Zbyszewski, 1957
  - = *Brachiosaurus ataliensis* Paul, 1988 [*sic*]
  - = *Branchiosaurus atalaiensis* Yadagiri, 1988 [*sic*]
- ?*B. nougaredi* de Lapparent, 1960

NOTE: See note for *Giraffatitan*.

Genus: *Damalasaurus* Zhao, 1983 [*nomen nudum*]
- = *Damalasaurus* Zhao, 1986 [*nomen nudum*]
- *D. laticostalis* Zhao, 1986 (Type)
- *D. magnus* Zhao, 1986 [*nomen nudum*]

Genus: *Dinodocus* Owen, 1884 [*nomen dubium*; = *Pelorosaurus*?]
- *D. mackesoni* Owen, 1884 (Type)
  - = *Pelorosaurus mackesoni* (Owen, 1884) [*nomen dubium*]

NOTE: Referred to this family provisionally; may be a synonym of *Pelorosaurus* or some other brachiosaurid (R. E. Molnar, pers. comm.; McIntosh, 1990).

Genus: *Dystylosaurus* Jensen, 1985
- *D. edwini* Jensen, 1985 (Type)

NOTE: This genus is referred to the Brachiosauridae in Paul, 1988 and McIntosh, 1990. J. A. Jensen (pers. comm.), however, considers it distinctive enough to warrant its own family.

Genus: *Giraffatitan* Paul, 1988 [*nomen novum ex subgenero*]
- = *Giraffatitan* Paul, 1987 [*nomen nudum*]
- *G. brancai* (Janensch, 1914) n. comb. (Type)
  - = *Brachiosaurus brancai* Janensch, 1914
  - = *Brachiosaurus (Giraffatitan) brancai* (Janensch, 1914) Paul, 1988
  - = *Cetiosaurus brancai* (Janensch, 1914) Yadagiri, 1988 [*sic*]
  - = *Dicraeosaurus brancai* (Janensch, 1914) Lambrecht, 1933 [*sic*]
  - = *Brachiosaurus fraasi* Janensch, 1914

NOTE: The above genus, initially described as a subgenus of *Brachiosaurus*, is separable therefrom on the basis of the vertebral column figured by Paul (1988). J. S. McIntosh (pers. comm.) does not believe the differences are generically significant.

Genus: *Lapparentosaurus* Bonaparte, 1986
- *L. madagascariensis* Bonaparte, 1986 (Type)

NOTE: See note for *Bothriospondylus madagascariensis*.

Genus: *Pelorosaurus* Mantell, 1850
- = *Gigantosaurus* Seeley, 1869 [*nomen dubium*]
- = *Hoplosaurus* Lydekker, 1890/Seeley, 1881 [*sic*]
- = *Ischyrosaurus* Hulke, 1874/Cope, 1869 [*nomen dubium*]
- = *Morinosaurus* Sauvage, 1874 [*nomen dubium*]
- = *Neosodon* de la Moussaye, 1885 [*nomen dubium*]
- = *Nesodon* Dollo, 1885 *vide* Nopcsa, 1926/Owen, 1840 [*sic*]
- = *Oplosaurus* Gervais, 1852 [*nomen dubium*]
- = *Ornithopsis* Sauvage, 1897/8 [*sic*]
- = *Ornithopsis* Seeley, 1870 [*nomen dubium*]
- = *Pelerosaurus* Galton, 1980 [*sic*]
- = *Pelosaurus* Fischer, 1989 [*sic*]
- = *Pelrorosaurus* Delair, 1959 [*sic*]
- = *Polorosaurus* Seeley, 1869 [*sic*]
- = *Telorosaurus* Baur, 1891 [*sic*]
- *P. conybearei* Mantell, 1850 (Type)
  - = *Cetiosaurus brevis* Owen, 1842 [*nomen dubium*]
  - = *Morosaurus brevis* (Owen, 1842) [*nomen dubium*]
  - = *Cetiosaurus conybearei* Melville, 1849–50 [*nomen dubium*]
  - = *Oplosaurus armatus* Gervais, 1852 [*nomen dubium*]
  - = *Hoplosaurus armatus* (Gervais, 1852) [*nomen dubium*]
  - = *Oplosaurus arcuatus* Gervais, 1853 [*sic*]
  - = *Ornithopsis hulkei* Seeley, 1870 [*nomen dubium*]
  - = *Pelorosaurus hulkei* (Seeley, 1870) [*nomen dubium*]
  - = *Bothriospondylus elongatus* Owen, 1875 [*nomen dubium*]
  - = *Bothriospondylus magnus* Owen, 1875 [*nomen dubium*]
  - = *Chondrosteosaurus magnus* (Owen, 1875) [*nomen dubium*]

= *Pleurocoelus valdensis* Lydekker, 1889 [*nomen dubium*]
= *Astrodon valdensis* (Lydekker, 1889) [*nomen dubium*]
?*P. becklesii* Mantell, 1852 [*nomen dubium*]
= *Pelorosaurus becklesi* Mantell, 1852 [*nomen dubium*]*
= *Morosaurus becklesi* (Mantell, 1852) Marsh, 1889
?*P. megalonyx* (Seeley, 1869) [*nomen dubium*]
= *Gigantosaurus megalonyx* Seeley, 1869 [*nomen dubium*]
?*P. humerocristatus* (Hulke, 1874) [*nomen dubium*]
= *Cetiosaurus humerocristatus* Hulke, 1874 [*nomen dubium*]
= *Ornithopsis humerocristatus* (Hulke, 1874) [*nomen dubium*]
= *Pelosaurus humerocristatus* (Hulke, 1874) Fischer, 1989 [*sic*]
= *Iguanodon praecursor* Sauvage, 1876 [*nomen dubium*]
= *Caulodon praecursor* (Sauvage, 1876) [*nomen dubium*]
= *Neosodon praecursor* (Sauvage, 1876) [*nomen dubium*]
= *Pelorosaurus praecursor* (Sauvage, 1876) [*nomen dubium*]
= *Neosodon* de la Moussaye, 1885 (no specific name assigned)
?*P. manseli* (Hulke, 1874) [*nomen dubium*]
= *Ischyrosaurus manseli* Hulke, 1874 *vide* Lydekker, 1888 [*nomen dubium*]
= *Ornithopsis manseli* (Hulke, 1874) [*nomen dubium*]
= *Morinosaurus typus* Sauvage, 1874 [*nomen dubium*]
?*P. leedsi* (Hulke, 1887) [*nomen dubium*]
= *Ornithopsis leedsi* Hulke, 1887 [*nomen dubium*]
= *Cetiosauriscus leedsi* (Hulke, 1887) [*nomen dubium*]
= *Cetiosaurus leedsi* (Hulke, 1887) [*nomen dubium*]

Genus: *Pleurocoelus* Marsh, 1888 (= *Astrodon*?)
= *Plaurocoelus* Langston, 1974 [*sic*]
= *Pleurocaelus* Sauvage, 1897/8 [*sic*]
P. nanus Marsh, 1888 (Type; juvenile)
= *Astrodon nanus* (Marsh, 1888) (juvenile)
= *Pleurocoelus altus* Marsh, 1888 (adult)
= *Astrodon altus* (Marsh, 1888) (adult)

Genus: *Ultrasauros* nov.
= *Ultrasaurus* Jensen, 1978 [*nomen nudum*]
= *Ultrasaurus* Jensen, 1985/Kim, 1983
U. macintoshi (Jensen, 1985) n. comb. (Type)
= *Ultrasaurus macintoshi* Jensen, 1985
= *Ultrasaurus mcintoshi* Miller, Baer, Stadtman & Britt, 1991 [*sic*]

NOTE: The above generic name is proposed to replace *Ultrasaurus* Jensen, 1985, which is preoccupied by *Ultrasaurus* Kim, 1983. Paul, 1988 synonymizes this genus with *Brachiosaurus*, but the type dorsal vertebra of *Ultrasauros* as figured therein is too dissimilar from the dorsal vertebrae of *Brachiosaurus altithorax* to warrant synonymy. The genera are best kept separate pending further work.

Genus: *Ultrasaurus* Kim, 1983 [*nomen dubium*]
= *Ultrasaurus* Kim, 1979 [*nomen nudum*]
U. tabriensis Kim, 1983 (Type)

NOTE: The above genus is referred to this family provisionally.

Genus: *Volkheimeria* Bonaparte, 1979
= *Voekeimeria* Yadagiri, 1988 [*sic*]
= *Volkherimeria* Czerkas & Czerkas, 1990 [*sic*]
V. chubutensis Bonaparte, 1979 (Type)
= *Voekeimeria chulbutensis* Yadagiri, 1988 [*sic*]

Genus: [To be described; the "Hughenden sauropod," a large Lower Cretaceous ?brachiosaurid from Australia; Molnar, 1980]

Genus: [To be described from the Morrison Formation; a "sauropod with four pedal unguals," perhaps just a new species of *Pleurocoelus*; Galton & Jensen, 1973]

Genus: [To be described from the Lower Cretaceous of Montana; the "Cloverly sauropod," perhaps just a new species of *Pleurocoelus*; Ostrom, 1970]

Genus: [To be described from France; initially referred to *Bothriospondylus madagascariensis*

(Dorlodot, 1934; Lapparent, 1943) but probably represents a new genus; McIntosh, 1990]

Family: CAMARASAURIDAE Cope, 1877

Census: 7 genera (2 doubtful),
11 species (3 doubtful)

= Camarasaurinae Nopcsa, 1928
= Morosauridae Marsh, 1882
= Opisthocoelicaudiinae McIntosh, 1990

Genus: *Algoasaurus* Broom, 1904
A. bauri Broom, 1904 (Type)

Genus: *Aragosaurus* Sanz, Buscalioni, Casanovas & Santafe, 1987
A. ischiaticus Sanz, Buscalioni, Casanovas & Santafe, 1987 (Type)

Genus: *Asiatosaurus* Osborn, 1924 [*nomen dubium*]
= *Asitosaurus* Kalandadze & Kurzanov, 1973 [*sic*]
A. mongoliensis Osborn, 1924 (Type)
= *Asiatosaurus mongolicus* Young, 1937 [*sic*]
A. kwangshiensis Hou, Yeh & Zhao, 1975 [*nomen dubium*]

Genus: *Camarasaurus* Cope, 1877
= *Camacasaurus* Young, 1958 [*sic*]
= *Camaeosaurus* Cope, 1877 [*sic*]
= *Camarasuarus* Berman & McIntosh, 1978 [*sic*]
= *Camarosaurus* Riggs, 1901 [*sic*]
= *Camasaurus* McIntosh, 1977 [*sic*]
= *Camerasaurus* Colbert, 1951 [*sic*]
= *Caulodon* Cope, 1877 [*nomen dubium*]
= *Monosaurus* Berman & McIntosh, 1978 [*sic*]
= *Morasaurus* Riggs, 1904 [*sic*]
= *Morosaurus* Marsh, 1878
= *Uintasaurus* Holland, 1919
C. supremus Cope, 1877 (Type)
= *Amphicoelias latus* Cope, 1877 (juvenile?)
= *Caulodon diversidens* Cope, 1877 [*nomen dubium*]
= *Caulodon leptoganus* Cope, 1878 [*nomen dubium*]
= *Camarasaurus leptodirus* Cope, 1879 [*nomen dubium*]
= *Pleurocoelus montanus* Marsh, 1896 (juvenile)
= *Astrodon montanus* (Marsh, 1896) (juvenile)
= *Amphicoelias altus* Berman & McIntosh, 1978 [*sic*; err. for *Amphicoelias latus* Cope, 1877]
C. grandis (Marsh, 1877)
= *Apatosaurus grandis* Marsh, 1877
= *Morosaurus grandis* (Marsh, 1877)
= *Morosaurus impar* Marsh, 1878
= *Camarasaurus impar* (Marsh, 1878)
= *Morosaurus robustus* Marsh, 1878 [*nomen dubium*]
= *Camarasaurus robustus* (Marsh, 1878) [*nomen dubium*]
C. lentus (Marsh, 1889)
= *Morosaurus lentus* Marsh, 1889
= *Uintasaurus douglassi* Holland, 1919
= *Camarasaurus douglassi* (Holland, 1919)
= *Camarosaurus annae* Ellinger, 1950
= *Camarasaurus annae* (Ellinger, 1950)
?*C. alenquerensis* (de Lapparent & Zbyszewski, 1957)
=*Apatosaurus alenquerensis* de Lapparent & Zbyszewski, 1957
= *Atlantosaurus alenquerensis* (de Lapparent & Zbyszewski, 1957)
= *Brontosaurus alenquerensis* (de Lapparent & Zbyszewski, 1957)

Genus: *Cathetosaurus* Jensen, 1988 (= *Camarasaurus*?)
= *Cathetosaurus* Jensen, 1987 [*nomen nudum*]
C. lewisi Jensen, 1988 (Type)
= *Cathetosaurus lewisi* Jensen, 1987 [*nomen nudum*]

Genus: *Chondrosteosaurus* Owen, 1876 [*nomen dubium*]
= *Chondrosteus* von Huene, 1907/8 [*sic*]/Agassiz, 1833–44
= *Eucamarotus* von Huene, 1909 [*sic*]
= *Eucamerotes* Rozhdestvensky & Tatarinov, 1964 [*sic*]
= *Eucamerotus* Hulke, 1872 [*nomen dubium*]
C. gigas Owen, 1876 (Type)

= *Chondrosteus gigas* (Owen, 1876) [*sic*]
= *Eucamerotus* Hulke, 1872 [*nomen dubium*; no specific name assigned]
= *Ornithopsis eucamerotus* Hulke, 1882 [*nomen dubium*]
= *Titanosaurus valdensis* von Huene, 1929 [*nomen dubium*]
= *Chondrosteosaurus megalus* Fox *vide* Blows, 1983 [*nomen oblitum*]

Genus: *Opisthocoelicaudia* Borsuk-Bialynicka, 1977
= *Opisthocoelocaudia* Carroll, 1987 [*sic*]
O. skarzynskii Borsuk-Bialynicka, 1977 (Type)

Family: EUHELOPODIDAE Kuhn, 1965

Census: 5 genera (1 doubtful), 10 species (1 doubtful)

= Euhelopodinae Romer, 1956
= Helopodinae von Huene, 1932
= Mamenchisauridae Young & Chao, 1972
= Mamenchisaurinae McIntosh, 1990

Genus: *Chiayusaurus* Bohlin, 1953 [*nomen dubium*]
= *Chiayüsaurus* Bohlin, 1953 [*nomen dubium*]*
= *Chiayasaurus* Dong, 1977 [*sic*]
= *Chiayausaurus* Dong, 1977 [*sic*]
= *Chiayiisaurus* Rozhdestvensky & Tatarinov, 1964 [*sic*]
= *Chiayuesaurus* Young, 1958 [*sic*]
= *Chiryuesaurus* Young, 1958 [*sic*]
C. lacustris Bohlin, 1953 (Type)
= *Chiayüsaurus lacustris* Bohlin, 1953 [*nomen dubium*]*
= *Chiayasaurus laciatain* Dong, 1977 [*sic*]

Genus: *Euhelopus* Romer, 1956
= *Eohelopus* Rozhdestvensky, 1977 [*sic*]
= *Helopus* Wiman, 1929/Wagler, 1832
E. zdanskyi (Wiman, 1929) (Type)
= *Helopus zdanskyi* Wiman, 1929

Genus: "Klamelisaurus" [to be described by Zhao C. C. from the Late Jurassic of the Dzungar Basin, Xinjiang; known from a skeleton about 80% complete; *SVP Bulletin* #149: 45]
"K. gobiensis" [type species to be described]

Genus: *Mamenchisaurus* Young, 1954
= *Mamenchiosaurus* Dong, 1980 [*sic*]
= *Mammenchisaurus* Czerkas & Czerkas, 1990 [*sic*]
= *Manenchisaurus* Young, 1954 [*sic*]
= "Moshisaurus" Hisa, 1988 [*nomen nudum* in *Utan Scientific Magazine* #4: 24]
M. constructus Young, 1954 (Type)
?*M. hochuanensis* Young & Chao, 1972
= *Mamenchisaurus hochuanensis* [Anonymous] 1965 [*nomen nudum*]

NOTE: This species of *Mamenchisaurus* could well belong to a different genus. Its postcranial skeleton, reconstructed in Young & Chao, 1972, shows numerous differences from that of the type species.

[New species to be described from the Upper Jurassic of Chengdu; M. Tanimoto, pers. comm.]

NOTE: Sauropod remains nicknamed "Moshisaurus" or "Moshi-ryu" in a Japanese popular-science article were referred to *Mamenchisaurus* sp. by Hasegawa, Manabe, Hanai, Kase & Oji (1991).

Genus: *Omeisaurus* Young, 1939
= *Omeiosaurus* Galton, 1986 [*sic*]
= *Zigongosaurus* Hou, Chao & Chu, 1976
O. junghsiensis Young, 1939 (Type)
= *Omeisaurus yunghsiensis* Young, 1939 [*sic*]
= *Omeisaurus junghsienensis* Young, 1958 [*sic*]
= *Omeisaurus jungshiensis* Dong, 1987 [*sic*]
O. changshouensis Young, 1958
O. fuxiensis (Hou, Chao & Chu, 1976)
= *Zigongosaurus fuxiensis* Hou, Chao & Chu, 1976
= *Omeisaurus fuxiensis* Dong, Zhou & Zhang, 1983
O. tianfuensis He, Li, Cai & Gao, 1984
?*O. zigongensis* Tanimoto, 1988 [*nomen nudum*]
O. luoquanensis Li *vide* He, Li & Cai, 1988

Genus: *Tienshanosaurus* Young, 1937
= *Teinshanosaurus* Dong, 1979 [*sic*]
= *Tienschanosaurus* Rozhdestvensky, 1977 [*sic*]
T. chitaiensis Young, 1937 [*sic*]

Genus: [To be described from China by D. A. Russell and Zheng Z.; one or more very large (some estimated to be over 30 meters long) sauropods, including one new genus with associated cranial material and distinctive, slender posterior cervical vertebrae with a cervical ribs over 3 meters long; D. A. Russell, pers. comm.]

Family: DIPLODOCIDAE Marsh, 1884

Census: 10 genera (3 doubtful),
21 species (6 doubtful)

= Amphicoeliidae Cope, 1877 [*nomen oblitum*]
= Apatosauridae von Huene, 1927
= Apatosaurinae Janensch, 1929
= Atlantosauridae Marsh, 1877 [*nomen oblitum*]
= Atlantosaurinae Steel, 1970
= Diplodocinae Janensch, 1929
= Titanosauridae Marsh, 1895/ Lydekker, 1885

Genus: *Amphicoelias* Cope, 1877
= *Amphicdelias* Hou, Yeh & Zhao, 1975 [*sic*]
A. altus Cope, 1877 (Type)
= *Amphicoelias fragillimus* Cope, 1878
= *Amphicoelias fragillissimus* Cope, 1881 [*sic*]

Genus: *Apatosaurus* Marsh, 1877
= *Apatosanrus* Yadagiri, 1988 [*sic*]
= *Apatosausus* Dong, 1979 [*sic*]
= *Bronotosaurus* Langston, 1974 [*sic*]
= *Brontasaurus* McIntosh & Berman, 1975 [*sic*]
= *Brontosaurus* Marsh, 1879
= *Brontsaurus* Stokes, 1988 [*sic*]
= *Elosaurus* Peterson & Gilmore, 1902 (juvenile)
A. ajax Marsh, 1877 (Type)
= *Atlantosaurus ajax* (Marsh, 1877)
= *Atlantosaurus immanis* Marsh, 1878
= *Apatosaurus laticollis* Marsh, 1879
= *Atlantosaurus laticollis* (Marsh, 1879)
A. excelsus (Marsh, 1879)
= *Brontosaurus excelsus* Marsh, 1879
= *Atlantosaurus excelsus* (Marsh, 1879)
= *Brontosaurus amplus* Marsh, 1881
= *Apatosaurus amplus* (Marsh, 1881)
= *Atlantosaurus amplus* (Marsh, 1881)
= *Elosaurus parvus* Peterson & Gilmore, 1902 (juvenile)
A. louisae Holland, 1915
= *Atlantosaurus louisae* (Holland, 1915)
= *Brontosaurus louisae* (Holland, 1915)
?*A. minimus* Mook, 1917
= *Atlantosaurus minimus* (Mook, 1917)

NOTE: The above species may represent a new genus of cetiosaurid (McIntosh, 1990).

Genus: *Atlantosaurus* Marsh, 1877 [*nomen dubium*]
= *Titanosaurus* Marsh, 1877/Lydekker, 1877
A. montanus (Marsh, 1877) (Type)
= *Titanosaurus montanus* Marsh, 1877 [*nomen dubium*]

Genus: *Barosaurus* Marsh, 1890 (= *Amphicoelias*?)
B. lentus Marsh, 1890 (Type)
= *Barosaurus affinis* Marsh, 1899 [*nomen dubium*]

Genus: *Cetiosauriscus* von Huene, 1927
?*C. longus* (Owen, 1842) [*nomen dubium*]
= *Cetiosaurus longus* Owen, 1842 [*nomen dubium*]
= *Cetiosaurus epioolithicus* Owen, 1842 [*nomen oblitum*]
?*C. glymptonensis* (Phillips, 1871) [*nomen dubium*]
= *Cetiosaurus glymptonensis* Phillips, 1871 [*nomen dubium*]
?*C. greppini* (von Huene, 1922)
= *Ornithopsis greppini* von Huene, 1922
= *Cetiosaurus greppini* (von Huene, 1922)
C. stewarti Charig, 1980 (Type)

= *Cetiosaurus leedsi* von Huene, 1927 *non* (Hulke, 1887)

Genus: *Diplodocus* Marsh, 1878
= *Dipiodocus* Yadagiri, 1988 [*sic*]
D. longus Marsh, 1878 (Type)
D. lacustris Marsh, 1884 [*nomen dubium*]
D. carnegii Hatcher, 1901
= *Diplodocus carnegiei* Holland, 1906 [*sic*]
D. hayi Holland, 1924

Genus: *Dystrophaeus* Cope, 1877 [*nomen dubium*]
D. viaemalae Cope, 1877 (Type)

Genus: *Megacervixosaurus* Zhao, 1983 [*nomen nudum*]
M. tibetensis Zhao, 1986 (Type)

Genus: *Mongolosaurus* Gilmore, 1933 [*nomen dubium*]
M. haplodon Gilmore, 1933 (Type)
= *Mongolosaurus hoplodon* Young, 1937 [*sic*]

Genus: "Seismosaurus" Gillette, 1986 [to be described from the Morrison Formation of New Mexico; a very large diplodocid; the generic name was published in numerous newspaper accounts in 1986 and in an article by I. Anderson in *New Scientist*, April 23, 1987: 24]

Genus: *Supersaurus* Jensen, 1985
= *Supersaurus* Jensen, 1972 [*nomen nudum*]
S. vivianae Jensen, 1985 (Type)
NOTE: Paul, 1988 suggests that this genus is a junior synonym of *Barosaurus*.

Genus: *Tornieria* Sternfeld, 1911
= *Gigantosaurus* E. Fraas, 1908/Seeley, 1869
T. africana (E. Fraas, 1908) Sternfeld, 1911 (Type)
= *Gigantosaurus africanus* E. Fraas, 1908
= *Barosaurus africanus* (E. Fraas, 1908)
T. gracilis (D. A. Russell, Beland & McIntosh, 1980) n. comb.
= *Barosaurus gracilis* D. A. Russell, Beland & McIntosh, 1980
= *Barosaurus africanus* var. *gracilis* Janensch, 1961
?*T. dixeyi* (Haughton, 1928)
= *Gigantosaurus dixeyi* Haughton, 1928

NOTE: *Tornieria africana* is almost certainly a diplodocid, but *Tornieria dixeyi* probably represents a new genus of titanosaurid (R. E. Molnar, pers. comm.; McIntosh, 1990). McIntosh (1990), however, conservatively retains *Tornieria* in the Titanosauridae. Wild (1991) proposed the genus *Janenschia* for the species *Tornieria robusta*, presently regarded as a titanosaurid.

Genus: [To be described from the Morrison Formation by J. A. Jensen; the description may not appear in the near future; J. S. McIntosh, pers. comm.]

Family: DICRAEOSAURIDAE
von Huene, 1956

Census: 5 genera, 8 species (1 doubtful)

= Dicraeosaurinae Janensch, 1929

Genus: *Amargasaurus* Salgado & Bonaparte, 1991
= *Amargasaurus* Bonaparte, 1984 [*nomen nudum*]
= *Amargasaurus* Bonaparte, 1990 [*nomen nudum*]
= *Amargosaurus* McIntosh, 1989 [*sic*]
A. cazaui Salgado & Bonaparte, 1991 (Type)
= *Amargasaurus groeberi* Bonaparte, 1984 [*nomen nudum*]
= *Amargasaurus cazaui* Bonaparte, 1990 [*nomen nudum*]

Genus: *Dicraeosaurus* Janensch, 1914
= *Dicraeosaurns* Yadagiri, 1988 [*sic*]
= *Dicreaosaurus* Swinton, 1970 [*sic*]
= *Dicreosaurus* Borsuk-Bialynicka, 1977 [*sic*]
= *Dikraeosaurus* Lull, 1924 [*sic*]
D. hansemanni Janensch, 1914 (Type)
D. sattleri Janensch, 1914

Genus: *Nemegtosaurus* Nowinski, 1971
N. mongoliensis Nowinski, 1971 (Type)
N. pachi Dong, 1977 [*nomen dubium*]

Genus: *Quaesitosaurus* Kurzanov & Bannikov, 1983 (= *Nemegtosaurus*?)
= *Questiosaurus* Tatarinov, 1982 [*sic*]
= *Questosaurus* Carroll, 1987 [*sic*]

Q. orientalis Kurzanov & Bannikov, 1983 (Type)

Genus: *Rebbachisaurus* Lavocat, 1954
R. garasbae Lavocat, 1954 (Type)
R. tamesnensis de Lapparent, 1960

NOTE: The above genus probably represents a new family of sauropods (McIntosh, 1990) and is referred to this family provisionally.

Genus: [To be described from the Late Cretaceous of Mongolia; based on postcranial remains presently on display at the Paleontological Institute of the USSR Academy of Sciences; may prove to be *Quaesitosaurus* or *Nemegtosaurus*; P. Currie, pers. comm.]

Family: TITANOSAURIDAE Lydekker, 1885

Census: 16 genera (6 doubtful), 30 species (13 doubtful)

= Antarctosauridae Olshevsky, 1978
= Antarctosaurinae J. Powell, 1986 ***vide*** **Bonaparte, 1987**
= Argyrosaurinae J. Powell, 1986 ***vide*** **Bonaparte, 1987**
= Saltasaurinae J. Powell, 1986 ***vide*** **Bonaparte, 1987**
= Titanosaurinae Nopcsa, 1928

NOTE: This family has become a "grab-bag" for Cretaceous sauropod genera based on fragmentary remains. Work in progress by J. Powell (Ph. D. dissertation) will greatly aid classification of the South American forms. The names of all of the new genera, as well as of the new subfamilies, introduced in Powell's dissertation have been published elsewhere and are not new to this listing.

Genus: *Aegyptosaurus* Stromer, 1932
A. baharijensis Stromer, 1932 (Type)

Genus: *Aeolosaurus* J. Powell, 1987
= *Aelosaurus* BVP 1987 [*sic*]
= *Aeolosaurus* J. Powell, 1986 [*nomen nudum*]
= *Eolosaurus* J. Powell *vide* Bonaparte, 1985 [*sic*]
A. rionegrinus J. Powell, 1987 (Type)
= *Aeolosaurus rionegrinus* J. Powell, 1986 [*nomen nudum*]
= *Eolosaurus rionegrinus* J. Powell *vide* Bonaparte, 1985 [*sic*]

NOTE: The above genus and species were described in J. Powell's doctoral dissertation; a brief description was published by Powell in 1987.

Genus: *Aepisaurus* Gervais, 1852 [*nomen dubium*]
= *Aeposaurus* Romer, 1966 [*sic*]
= *Aepyosaurus* von Huene, 1932 [*sic*]
= *Aepysaurus* Gervais, 1859 [*sic*]
A. elephantinus Gervais, 1852 (Type)

Genus: *Alamosaurus* Gilmore, 1922
A. sanjuanensis Gilmore, 1922 (Type)

Genus: *Antarctosaurus* von Huene, 1927
= *Anarctosaurus* Janensch, 1935 [*sic*]
= *Anctartosaurus* [Anonymous] 1977 [*sic*; in *Die Geheimnisse der Urzeit 3*, p. 234]
A. wichmannianus von Huene, 1929 (Type)
?*A. giganteus* von Huene, 1929
?*A. septentrionalis* von Huene, 1932
?*A. jaxarticus* Riabinin, 1938 [*nomen dubium*]
= *Antarctosaurus jaxartensis* Kuhn, 1965 [*sic*]
?*A. brasiliensis* Arid & Vizotto, 1972

Genus: *Argyrosaurus* Lydekker, 1893
= *Argirosaurus* Sanz, Casanovas & Santafe, 1982 [*sic*]
A. superbus Lydekker, 1893 (Type)

Genus: *Campylodoniscus* Kuhn, 1961 [*nomen dubium*]
= *Campylodan* Bonaparte, 1978 [*sic*]
= *Campylodon* von Huene, 1929/Cuvier & Valenciennes, 1832
C. ameghinoi (von Huene, 1929) (Type)
= *Campylodon ameghinoi* von Huene, 1929 [*nomen dubium*]

Genus: *Clasmodosaurus* Ameghino, 1898 [*nomen dubium*]
= *Clasmadosaurus* Rozhdestvensky & Tatarinov, 1964 [*sic*]
= *Clasmodon* von Huene, 1929 [*sic*]
= *Clasmosaurus* Romer, 1966 [*sic*]
C. spatula Ameghino, 1898 (Type)

= *Clasmodon spatula* (Ameghino, 1898)
[*sic*]

NOTE: The above genus is probably a sauropod and not a synonym of *Genyodectes* as frequently classified (Molnar, 1980). It is listed as a probable titanosaurid in J. Powell's dissertation (1986).

Genus: *Epachthosaurus* J. Powell, 1986 [*nomen nudum*]
= *Epachtosaurus* J. Powell, 1986 *vide* Martínez, Giménez, Rodríguez & Bochatey, 1986 [*nomen nudum*]
E. sciuttoi J. Powell, 1986 (Type)
= *Epachtosaurus sciuttoi* J. Powell, 1986 *vide* Martínez, Giménez, Rodríguez & Bochatey, 1986 [*nomen nudum*]

NOTE: The above genus and species, described in J. Powell's unpublished doctoral dissertation, were published (and spelled slightly differently) without description in Martínez, Giménez, Rodríguez & Bochatey, 1986.

Genus: *Hypselosaurus* Matheron, 1869
= *Hypselaurus* Villatte, Taquet & Bilotte, 1985 [*sic*]
H. priscus Matheron, 1869 (Type)
[New species from northern Spain; Bataller, 1960]

Genus: *Janenschia* Wild, 1991
J. robusta (E. Fraas, 1908) Wild, 1991 (Type)
= *Gigantosaurus robustus* E. Fraas, 1908
= *Tornieria robusta* (E. Fraas, 1908) Sternfeld, 1911
= *Tornieria gigantea* von Huene, 1956 [*sic*]

NOTE: See note for *Tornieria* (Diplodocidae).

Genus: *Loricosaurus* von Huene, 1929 [*nomen dubium*; = *Neuquensaurus*?]
L. scutatus von Huene, 1929 (Type)

NOTE: The above genus and species, based on dermal armor scutes, has previously been classified as ankylosaurian. The scutes, however, resemble those of the titanosaurid *Saltasaurus*, and the species could well be a junior synonym of *Neuquensaurus australis* (Bonaparte & J. Powell, 1980).

Genus: *Macrurosaurus* Seeley, 1876
= *Macrosaurus* Thenius, 1972 [*sic*]
= *Macrourosaurus* Sauvage, 1879 [*sic*]
M. semnus Seeley, 1876 (Type)

Genus: *Magyarosaurus* von Huene, 1932 [*nomen dubium*]
= *Maggiarosaurus* von Huene, 1956 [*sic*]
= *Magiarosaurus* Rozhdestvensky & Tatarinov, 1964 [*sic*]
M. dacus (Nopcsa, 1915) [*nomen dubium*]
= *Titanosaurus dacus* Nopcsa, 1915 [*nomen dubium*]
M. transsylvanicus (von Huene, 1929) [*nomen dubium*]
= *Titanosaurus transsylvanicus* von Huene, 1929 [*nomen dubium*]
M. hungaricus von Huene, 1932 (Type)
= *Titanosaurus hungaricus* (von Huene, 1932) [*nomen dubium*]

Genus: *Microcoelus* Lydekker, 1893 [*nomen dubium*; = *Saltasaurus*?]
= *Microsaurops* Kuhn, 1963 [*sic*]
= *Microsaurus* Hatcher, 1900 *vide* Lull, 1910/Dejean, 1833 [*sic*]
M. patagonicus Lydekker, 1893 (Type)

NOTE: Synonymy of this genus with *Saltasaurus* is suggested by J. McIntosh (pers. comm.).

Genus: *Neuquensaurus* J. Powell, 1986 *vide* Bonaparte, 1987 [*nomen nudum*]
N. australis (Lydekker, 1893) (Type)
= *Titanosaurus australis* Lydekker, 1893
N. robustus (von Huene, 1929) J. Powell, 1986 [*nomen dubium*]
= *Titanosaurus robustus* von Huene, 1929 [*nomen dubium*]
= *Saltasaurus robustus* (von Huene, 1929) McIntosh, 1990 [*nomen dubium*]

NOTE: The name of the above genus was published without description in Bonaparte, 1987, and its type species appeared in J. Powell, 1987. The description of the genus, in Powell's doctoral dissertation, has not yet been published.

Genus: *Saltasaurus* Bonaparte & J. Powell, 1980
S. loricatus Bonaparte & J. Powell, 1980 (Type)

Genus: *Titanosaurus* Lydekker, 1877
  = *Lametasaurus* Matley, 1923 [*nomen dubium*; in part]
  = *Lametasarus* Colbert, 1977 [*sic*]
  = *Laplatasaurus* von Huene, 1927
  = *Laplatosaurus* Obata & Kanie, 1977 [*sic*]
  = *Titamosaurus* Colbert, 1952 [*sic*]
  = *Titinosaurus* Galton, 1981 [*sic*]
  T. indicus Lydekker, 1877 (Type)
    = *Titanosaurus blanfordi* Lydekker, 1879 [*nomen dubium*]
    = *Lametasaurus indicus* Matley, 1923 [*nomen dubium*; in part]
  T. nanus Lydekker, 1893 [*nomen dubium*]
  ?*T. madagascariensis* Deperet, 1896 [*nomen dubium*]
    = *Laplatasaurus madagascariensis* (Deperet, 1896) [*nomen dubium*]
  T. araukanicus (von Huene, 1929) J. Powell, 1986
    = *Laplatasaurus araukanicus* von Huene, 1929 (Type)
  ?*T. lydekkeri* von Huene, 1929 [*nomen dubium*]

NOTE: The above species may belong to the genus *Chondrosteosaurus* (R. E. Molnar, pers. comm.).

  ?*T. falloti* Hoffet, 1942 [*nomen dubium*]
  ?*T. rahioliensis* Mathur & Srivastava, 1987

Genus: [To be described from Argentina by Calvo & J. F. Bonaparte]

Genus: [To be described from North America; Jensen, 1979]

Genus: [To be described from procoelous caudal vertebrae from the Cenomanian of Argentina; J. F. Bonaparte, pers. comm.; J. S. McIntosh, pers. comm.]

Genus: [To be described from the Cenomanian of Argentina; a huge sauropod with slender limbs, very long pubis and ischium, and strap-like scapula; J. F. Bonaparte, pers. comm.; J. S. McIntosh, pers. comm.]

Genus: [To be described from the Rio Limay Formation of Neuquen, Argentina; a gigantic titanosaurid; Bonaparte, 1989]

Genus: [To be described from the Aptian Matasiete Formation of Chubut, Argentina; a large sauropod; Martínez, Giménez, Rodríguez & Luna, 1989]

Genus: [To be described from China; a possible primitive titanosaurid; D. A. Russell, pers. comm.]

Family: CHUBUTISAURIDAE del Corro, 1974

Census: 1 genus, 1 species

Genus: *Chubutisaurus* del Corro, 1974
  C. insignis del Corro, 1974 (Type)

NOTE: This genus is probably a brachiosaurid (McIntosh, 1990).

SAUROPODA *incertae sedis*

Census: 1 doubtful genus, 1 doubtful species

Genus: "Hisanohamasaurus" Lambert, 1990 [to be described from Japan]

Genus: *Regnosaurus* Mantell, 1848 [*nomen dubium*]
  R. northamptoni Mantell, 1848 (Type)
    = *Hylaeosaurus northamptoni* (Mantell, 1848) [*nomen dubium*]

Genus: "Sugiyamasaurus" Lambert, 1990 [to be described from Japan; noted as having spatulate teeth]

Genus: [To be described from Fergan, Soviet Union; Rozhdestvensky, 1968]

Genus: [To be described from the Toarcian (late Early Jurassic) of Morocco; Jenny, Jenny-Deshusses, la Marrec & Taquet, 1980]

Genus: [To be described from the Toarcian (late Early Jurassic) of Morocco (Jenny, Jenny-Deshusses, la Marrec & Taquet, 1980]

Genus: [To be described from China; based on a tooth; P. C. Sereno, pers. comm.]

Genus: [To be described from the Oagannur Formation of Inner Mongolia; Dong Z., pers. comm.]

Order: Segnosauria Barsbold & Perle, 1980

Census: 2 families, 5 genera, 6 species

Family: SEGNOSAURIDAE Perle, 1979

Census: 3 genera, 3 species

= Enigmosauridae Barsbold, 1983

Genus: *Enigmosaurus* Barsbold & Perle, 1983
  E. mongoliensis Barsbold & Perle, 1983 (Type)

Genus: *Erlikosaurus* Perle, 1980
  = *Erlicosaurus* Perle, 1981 [*sic*]
  E. andrewsi Perle, 1980 (Type)
  [Possible new species to be described from the Judith River Formation of Alberta, Canada; P. J. Currie, pers. comm.]

Genus: *Segnosaurus* Perle, 1979
  S. galbinensis Perle, 1979 (Type)
    = *Segnosaurus ghalbiensis* Barsbold, 1983 [*sic*]

Family: THERIZINOSAURIDAE Maleev, 1954

Census: 1 genus, 1 species

Genus: *Therizinosaurus* Maleev, 1954
  = *Therezinosaurus* Sukhanov, 1964 [*sic*]
  = *Therisinosaurus* Osmolska, 1980 [*sic*]
  T. cheloniformis Maleev, 1954 (Type)

SEGNOSAURIA *incertae sedis*

Census: 1 genus, 2 species

Genus: *Nanshiungosaurus* Dong, 1979
  = *Nanshingosaurus* Dong, 1980 [*sic*]
  = *Nanshungisaurus* Paul, 1987 [*sic*]
  N. brevispinus Dong, 1979 (Type)

Genus: [To be described]
  [Type species to be redescribed]
    = *Chilantaisaurus zheziangensis* Dong, 1979

NOTE: This species is based on probable segnosaurian pedal elements (Barsbold & Maryanska, 1990) and is thus not referable to the carnosaurian genus *Chilantaisaurus*.

Genus: [To be described; based on the large forelimb that was one of the two syntypes of *Alectrosaurus olseni*; Mader & Bradley, 1989]

Genus: [To be described from China; a primitive form that according to D. A. Russell (pers. comm.) displays conclusive evidence that segnosaurians are derived theropods and not sauropodomorphs; when this form is described, it my be necessary to remove the order Segnosauria from the superorder Sauropodomorpha and place it into the Theropodomorpha]

Notes and New Taxa

Superorder: Ornithischia Seeley, 1888

Census: 6 orders, 19 families, 191 genera (42 doubtful), 280 species (83 doubtful)

Paraorder: Lesothosauria nov.

Census: 1 family, 6 genera (4 doubtful), 7 species (5 doubtful)

Family: LESOTHOSAURIDAE
L. B. Halstead & J. Halstead, 1981

Census: 1 genus, 1 species

Genus: *Lesothosaurus* Galton, 1978
  L. diagnosticus Galton, 1978 (Type)
    = *Fabrosaurus australis* Thulborn, 1970
    non Ginsburg, 1964

Genus: [To be described from the Stormberg Series of South Africa; a robust "fabrosaurid"; P. M. Galton, pers. comm.; Crompton & Attridge, 1986]

Genus: [To be described from the Upper Elliot Formation of South Africa; one or more genera may be present; A. P. Santa Luca, 1984; Gow, 1981, 1985]

LESOTHOSAURIA *incertae sedis*

Census: 5 genera (4 doubtful), 6 species (5 doubtful)

= Fabrosauridae Galton, 1972
= Nannosaurinae Nopcsa, 1928 [*sic*]
= Nanosauridae Marsh, 1878
= Nanosaurinae Abel, 1919

Genus: *Alocodon* Thulborn, 1973 [*nomen dubium* in Weishampel & Witmer, 1990]
  A. kuehnei Thulborn, 1973 (Type)
  NOTE: Referred to as Ornithischia *incertae sedis* in Sereno, 1991.

Genus: *Fabrosaurus* Ginsburg, 1964 [*nomen dubium* in Weishampel & Witmer, 1990]
  = *Eabrosaurus* Rozhdestvensky, 1974 [*sic*]
  F. australis Ginsburg, 1964 (Type)

Genus: *Nanosaurus* Marsh, 1877 [*nomen dubium* in Sues & Norman, 1990]
  = *Nannosaurus* Nopcsa, 1928 [*sic*]
  N. agilis Marsh, 1877 (Type)
  NOTE: Sereno (1991) concludes that this genus and species represent an indeterminate small ornithischian; referred to this family provisionally.

Genus: *Technosaurus* Chatterjee, 1984
  T. smalli Chatterjee, 1984 (Type)
  NOTE: Sereno (1991) shows that the holotype specimen is composite and includes both ornithischian and hatchling prosauropod elements. Reference of this genus and species to this family here is provisional.

Genus: *Trimucrodon* Thulborn, 1973 [*nomen dubium* in Weishampel & Witmer, 1990]
  = *Trimurodon* Galton, 1980 [*sic*]
  T. cuneatus Thulborn, 1973 (Type)
  NOTE: Referred to as Ornithischia *incertae sedis* in Sereno, 1991.

Genus: [To be described by P. E. Olsen and P. M. Galton; P. M. Galton, pers. comm.]
  [Type species to be redescribed]

= *Thecodontosaurus gibbidens* Cope, 1878 [*nomen dubium* in Weishampel & Witmer, 1990]

Genus: [To be described from the Late Triassic of the Mendip Hills, England; Long & Welles, 1975]

Genus: [To be described from Nova Scotia; one or more genera may be present; P. E. Olsen, pers. comm.]

Paraorder: Ankylosauria Osborn, 1923

Census: 3 families, 42 genera (12 doubtful), 51 species (18 doubtful)

Parafamily: SCELIDOSAURIDAE Cope, 1869

Census: 5 genera, 5 species

= Scelidosaurididae Nopcsa, 1917 [*sic*]
= Scelidosaurinae Nopcsa, 1923
= Scutellosauridae Lambert, 1990

Genus: *Emausaurus* Haubold, 1991
E. ernsti Haubold, 1991 (Type)

Genus: *Lusitanosaurus* de Lapparent & Zbyszewski, 1957
L. liasicus de Lapparent & Zbyszewski, 1957 (Type)

Genus: *Scelidosaurus* Owen, 1859 [*nomen conservandum*]
= *Scelodosaurus* Gilmore, 1920 [*sic*]
S. harrisonii Owen, 1861 (Type)
= *Scelidosaurus harrisoni* (Owen, 1861)

NOTE: Because no type specimen had been designated in the original description, Lydekker, 1893 made the lectotype specimen of *Scelidosaurus harrisonii* a megalosaurid knee joint that was part of the material originally referred to the species. This specimen will be redescribed in the forthcoming review of British theropod material by S. P. Welles and H. P. Powell as a new megalosaurid genus and species, and the International Commission of Zoological Nomenclature will be petitioned to retain the generic name *Scelidosaurus* for the armored dinosaur under the *nomen conservandum* rule.

Padian (1989) has reported *Scelidosaurus*-like armor scutes from the Kayenta Formation of Arizona.

Genus: *Scutellosaurus* Colbert, 1981
S. lawleri Colbert, 1981 (Type)

NOTE: Previously classified as a "fabrosaurid," the above genus is referred to the "Thyreophora" by Gauthier (1986) and Sereno (1986), but is provisionally referred to the Scelidosauridae here.

Genus: *Tatisaurus* Simmons, 1965
T. oehleri Simmons, 1965 (Type)

NOTE: Simmons, in his description of the type specimen, noted its ankylosaurian affinities but declined to refer the above genus to the Ankylosauria because the order was then thought to be restricted to the Cretaceous. Now that ankylosaurian material is known from the Jurassic (*cf.* various papers by Galton), this stricture no longer applies. Dong (1990), however, refers *Tatisaurus* to the Huayangosauridae.

Genus: [To be described from Great Britain; referred to by Rixon (1968) as a juvenile *Scelidosaurus* but may be a new genus; Coombs, Weishampel & Witmer, 1990]

Family: NODOSAURIDAE Marsh, 1890

Census: 23 genera (9 doubtful), 31 species (15 doubtful)

= Acantholipidae Nopcsa, 1917 [*sic*]
= Acanthopholididae Nopcsa, 1902
= Acanthopholidinae von Huene, 1956
= Acanthopholinae Nopcsa, 1923
= Edmontoniidae Bakker, 1988
= Edmontoniinae L. S. Russell, 1940
= Hylaeosauridae Nopcsa, 1902

= Hylaeosaurididae Nopcsa, 1917 [*sic*]
= Nodosaurinae Abel, 1919
= Palaeoscincidae Nopcsa, 1918
= Panoplosaurinae Nopcsa, 1929
= Panoplosaurines de Lapparent & Lavocat, 1955
= Polacanthidae Wieland, 1911
= Polacanthines Lavocat, 1955
= Struthiosauridae Kuhn, 1966
= Struthiosaurinae Nopcsa, 1923

Genus: *Acanthopholis* Huxley, 1867 [*nomen dubium*]
- *A. horridus* Huxley, 1867 (Type)
- *A. eucercus* Seeley, 1869 [*nomen dubium*]
- *A. macrocercus* Seeley, 1869 [*nomen dubium*]
- ?*A. platypus* Seeley, 1869 [*nomen dubium*; sauropod?]
  - = *Macrurosaurus platypus* (Seeley, 1869) [*nomen dubium*]
- *A. stereocercus* Seeley, 1869 [*nomen dubium*]

Genus: *Brachypodosaurus* Chakravarti, 1934 [*nomen dubium*]
- = *Brachyopodosaurus* Galton, 1981 [*sic*]
- *B. gravis* Chakravarti, 1934 (Type)

NOTE: The above genus is referred to this family provisionally (Coombs, 1978). It may be a stegosaur (K. Carpenter, pers. comm.).

Genus: *Chasstembergia* Bakker, 1988 [*nomen novum ex subgenero*]
- *C. rugosidens* (Gilmore, 1930) n. comb. (Type)
  - = *Palaeoscincus rugosidens* Gilmore, 1930
  - = *Edmontonia rugosidens* (Gilmore, 1930)
  - = *Panoplosaurus rugosidens* (Gilmore, 1930)

NOTE: Although Bakker (1988) introduced *Chasstembergia* as a subgenus of the genus *Edmontonia*, the name was never formally used as a subgenus (that is, in parenthesis following the generic name) in his paper. Further, it is clear from that paper's systematics discussion that if *Denversaurus* is to be removed from *Edmontonia* as a separate genus, so should *Chasstembergia*. This view is adopted here, although Carpenter (1990) and W. Coombs (pers. comm.) regard both *Chasstembergia* and *Denversaurus* as junior synonyms of *Edmontonia*.

Genus: *Cryptodraco* Lydekker, 1889 [*nomen dubium*]
- = *Cryptosaurus* Seeley, 1869/Geoffroy Saint-Hilaire, 1833
- = *Crytodraco* Delair, 1959 [*sic*]
- *C. eumerus* (Seeley, 1869) (Type)
  - = *Cryptosaurus eumerus* Seeley, 18699 [*nomen dubium*]

Genus: *Danubiosaurus* Bunzel, 1871 [*nomen dubium*]
- = *Danubriosaurus* Romer, 1966 [*sic*]
- *D. anceps* Bunzel, 1871 (Type; in part)
  - = *Crataeomus pawlowitschii* Seeley, 1881 (in part)

NOTE: The original type specimen of *Danubiosaurus anceps* is composite (K. Carpenter, pers. comm.). Most of the type material is referable to *Struthiosaurus*, but one scapula may represent a distinct genus. Until a restudy of the Gosau material is carried out, this scapula, once part of the type specimen of *Crataeomus pawlowitschii*, is best separated from the other type material into the available genus *Danubiosaurus* (Coombs, 1978; Molnar, 1980). K. Carpenter (pers. comm.) further notes that *Danubiosaurus* is probably a *nomen oblitum*, and in a forthcoming article will designate lectotype specimens for some species of *Struthiosaurus* and *Crataeomus*.

Genus: *Denversaurus* Bakker, 1988
- *D. schlessmani* Bakker, 1988 (Type)

NOTE: See also *Chasstembergia* and *Edmontonia*.

Genus: *Dracopelta* Galton, 1980
- *D. zbyszewskii* Galton, 1980 (Type)

Paragenus: *Edmontonia* C. M. Sternberg, 1928
- *E. longiceps* C. M. Sternberg, 1928 (Type)
  - = *Panoplosaurus longiceps* (C. M. Sternberg, 1928)

NOTE: This is a paragenus because it is almost certainly ancestral to the genera *Chasstembergia* and *Denversaurus*; but see the note for *Chasstembergia*.

Genus: *Hierosaurus* Wieland, 1909 [*nomen dubium*]
  = *Heirosaurus* Colbert, 1961 [*sic*]
  = *Xierosaurus* Maleev, 1954 [*sic*]
 H. sternbergii Wieland, 1909 (Type)
  = *Nodosaurus sternbergii* (Wieland, 1909)

Genus: *Hoplitosaurus* Lucas, 1902 (= *Polacanthus*?)
  = *Xoplitosaurus* Maleev, 1954 [*sic*]
 H. marshi (Lucas, 1901) (Type)
  = *Stegosaurus marshi* Lucas, 1901
  = *Polacanthus marshi* (Lucas, 1901)

Genus: *Hylaeosaurus* Mantell, 1833
  = *Hyaelosaurus* von Huene, 1909 [*sic*]
  = *Hylacosaurus* del Corro, 1974 [*sic*]
  = *Hyleosaurus* Maryanska, 1977 [*sic*]
  = *Hylosaurus* Fitzinger, 1843 [*sic*]
 H. armatus Mantell, 1833 (Type)
  = *Hylaeosaurus mantelli* Fitzinger, 1843
  = *Hylaeosaurus oweni* Mantell, 1844

Genus: *Nodosaurus* Marsh, 1889
 N. textilis Marsh, 1889 (Type)

Genus: *Palaeoscincus* Leidy, 1856 [*nomen dubium*]
  = *Palaeosincus* Maleev, 1956 [*sic*]
  = *Palaeosynchus* Stokes, 1988 [*sic*]
 P. costatus Leidy, 1856 (Type)
 P. latus Marsh, 1892 [*nomen dubium*]
 P. magoder Hennig, 1914 [*nomen nudum*; name created by typographical error: D. Chure & J. S. McIntosh, pers. comm.]

Genus: *Panoplosaurus* Lambe, 1919
  = *Panaplosaurus* Galton, 1981 [*sic*]
 P. mirus Lambe, 1919 (Type)

Genus: *Polacanthoides* Nopcsa, 1928
 P. ponderosus Nopcsa, 1928 (Type)

NOTE: K. Carpenter (pers. comm.) will redescribe the type scapula of the above species and establish it as a valid nodosaurid quite distinct from *Hylaeosaurus* and *Polacanthus*.

Genus: *Polacanthus* Owen *vide* Huxley, 1867
  = *Polacanthus* Owen *vide* [Anonymous] 1865 [*nomen nudum*]
  = *Polecanthus* McLoughlin, 1979 [*sic*]
  = *Vectensia* Delair, 1982 [*nomen nudum*]
 P. foxii Hulke, 1881 (Type)
  = *Hylaeosaurus foxii* (Hulke, 1881)
  = *Polacanthus becklesi* Hennig, 1924 [*nomen dubium*]

Genus: *Priconodon* Marsh, 1888 [*nomen dubium*]
  = *Princonodon* Lull, 1911 [*sic*]
 P. crassus Marsh, 1888 (Type)
  = *Stegosaurus crassus* (Marsh, 1888) [*nomen dubium*]

Genus: *Priodontognathus* Seeley, 1875 [*nomen dubium*]
  = *Priodontosaurus* Romer, 1966 [*sic*]
 P. phillipsii (Seeley, 1869) (Type)
  = *Iguanodon phillipsi* Seeley, 1869 [*nomen dubium*]
  = *Dacentrurus phillipsi* (Seeley, 1869) [*nomen dubium*]
  = *Omosaurus phillipsi* (Seeley, 1869) [*nomen dubium*]

NOTE: The type specimen of this species is a nodosaurid left maxilla with teeth (Galton, 1980); a femur referred to the species *Omosaurus phillipsi* by Seeley, 1893 is apparently stegosaurian and should remain in the genus *Dacentrurus* (see Stegosauria). It is possible that *Priodontognathus* is a junior synonym of *Hylaeosaurus* or a senior synonym of *Cryptodraco* (Galton, 1980), but it is unlikely to be differentiable from any described nodosaurid (K. Carpenter, pers. comm.).

Genus: *Sarcolestes* Lydekker, 1893
 S. leedsi Lydekker, 1893 (Type)

Genus: *Sauropelta* Ostrom, 1970
  = *Peltosaurus* Glut, 1972/Cope, 1873 [*sic*]
 S. edwardsorum Ostrom, 1970 (Type)
  = *Sauropelta edwardsi* Ostrom, 1970*

NOTE: The specific name of the type species is emended to the genitive plural ending, inasmuch as it is in honor of the entire Edwards family.

Genus: *Silvisaurus* Eaton, 1960
 S. condrayi Eaton, 1960 (Type)

Genus: *Stegopelta* Williston, 1905 (= *Nodosaurus*?)
 S. landerensis Williston, 1905 (Type)
  = *Nodosaurus landerensis* (Williston, 1905)

Genus: *Struthiosaurus* Bunzel, 1870 [*nomen dubium*]
- = *Crataeomus* Seeley, 1881 [*nomen dubium*]
- = *Hoplosaurus* Seeley, 1881 [*nomen dubium*]
- = *Leipsanosaurus* Nopcsa, 1918 [*nomen dubium*]
- = *Lepanosaurus* Romer, 1966 [*sic*]
- = *Plerropeltus* Tumanova, 1987 [*sic*]
- = *Pleuropeltis* Coombs, 1971 [*sic*]
- = *Pleuropeltus* Seeley, 1881 [*nomen dubium*]
- = *Pluropeltus* Rozhdestvensky & Tatarinov, 1964 [*sic*]
- = *Rhodanosaurus* Nopcsa, 1929 [*nomen dubium*]

S. austriacus Bunzel, 1871 (Type)
- = *Danubiosaurus anceps* Bunzel, 1871 [*nomen dubium*; in part]

?*S. transilvanicus* Nopcsa, 1915
- = *Struthiosaurus transylvanicus* Nopcsa, 1915 [*sic*]
- = *Struthiosaurus transsylvanicus* Nopcsa, 1929 [*sic*]
- = *Struthiosaurus transilvaticus* Coombs, 1971 [*sic*]
- = *Crataeomus* Seeley, 1881 (no specific name assigned)
- = *Crataeomus lepidophorus* Seeley, 1881 [*nomen dubium*]
- = *Struthiosaurus lepidophorus* (Seeley, 1881) [*nomen dubium*]
- = *Crataeomus pawlowitschii* Seeley, 1881 [*nomen dubium*; in part]
- = *Struthiosaurus pawlowitschii* (Seeley, 1881) [*nomen dubium*; in part]
- = *Struthiosaurus pawlowitschi* var. *lepidophorus* (Seeley, 1881) Nopcsa, 1918 [*nomen dubium*]
- = *Hoplosaurus ischyrus* Seeley, 1881 [*nomen dubium*]
- = *Nodosaurus ischyrus* (Seeley, 1881) [*nomen dubium*]
- = *Pleuropeltus suessii* Seeley, 1881 [*nomen dubium*]
- = *Hoplosaurus insignis* Sauvage, 1882 [*sic*]
- = *Leipsanosaurus noricus* Nopcsa, 1918 [*nomen dubium*]
- = *Struthiosaurus noricus* (Nopcsa, 1918) [*nomen dubium*]
- = *Crataeomus pavlowitschii* Nopcsa, 1929 [*sic*]

NOTE: Coombs & Maryanska (1990) consider *Struthiosaurus austriacus* (and hence the genus *Struthiosaurus*), based on a single partial basicranium, to be a *nomen dubium* and possibly saurischian. They refer most of the Gosau nodosaurid taxa to an as-yet-unnamed new genus (pending redescription of the Gosau material) whose type species would be *Struthiosaurus transilvanicus*. K. Carpenter (pers. comm.) further notes that this genus is probably distinguishable from *Crataeomus*. See also *Danubiosaurus*.

?*S. ludgunensis* (Nopcsa, 1929) [*nomen dubium*]
- = *Rhodanosaurus ludgunensis* Nopcsa, 1929 [*nomen dubium*]
- = *Struthiosaurus lugdunensis* de Lapparent & Lavocat, 1955 [*sic*]
- = *Struthiosaurus lugundensis* Jeletsky, 1960 [*sic*]

Genus: [To be described by Carpenter, Dilkes & Weishampel]

[Type species to be redescribed]
- = *Hierosaurus coleii* Mehl, 1936
- = *Nodosaurus coleii* (Mehl, 1936)

Genus: [To be described from the Upper Cretaceous of Carlsbad, California; similar to *Nodosaurus*]

Family: ANKYLOSAURIDAE Brown, 1908

Census: 14 genera (3 doubtful),
15 species (3 doubtful)

= Anchylosauridae Lydekker, 1909 [*sic*]
= Ancylosauridae von Huene, 1908 [*sic*]
= Ankylosaurinae Nopcsa, 1918
= Shamosaurinae Tumanova, 1983
= Syrmosauridae Maleev, 1952

Genus: *Ankylosaurus* Brown, 1908
- = *Anchylosaurus* C. H. Sternberg, 1917 [*sic*]
- = *Ancylosaurus* von Huene, 1909 [*sic*]

A. magniventris Brown, 1908 (Type)
- = *Euoplocephalus magniventris* (Brown, 1908)

Genus: *Dyoplosaurus* Parks, 1924

= *Andontosaurus* Bodily, 1969 [*sic*]
= *Anodontosaurus* C. M. Sternberg, 1929
= *Dioplosaurus* Hay, 1929 [*sic*]
= *Dyoplasaurus* Maryanska, 1977 [*sic*]
= *Scalosaurus* Mehl, 1936 [*sic*]
= *Scholosaurus* Minelli, 1987 [*sic*]
= *Scolasaurus* Chevraux, 1980 [*sic*]
= *Scolosaurus* Nopcsa, 1928
= *Skolosaurus* von Huene, 1954 [*sic*]
D. acutosquameus Parks, 1924 (Type)
= *Scolosaurus cutleri* Nopcsa, 1928
= *Anodontosaurus lambei* C. M. Sternberg, 1929

Paragenus: *Euoplocephalus* Lambe, 1910
= *Erroplocephalus* Nopcsa, 1928 [*sic*]
= *Euopliocephalus* [Anonymous] 1979 [*sic*]
= *Euoploasurus* von Huene, 1956 [*sic*]
= *Euoplocophalus* Glut, 1972 [*sic*]
= *Euoplology* Hou, 1977 [*sic*]
= *Euoplosaurus* Maleev, 1956 [*sic*]
= *Euplocephalus* Lambe, 1920 [*sic*]
= *Europlocephalus* C. H. Sternberg, 1915 [*sic*]
= *Europocephalus* Nopcsa, 1923 [*sic*]
= *Sterecephalus* Maleev, 1956 [*sic*]
= *Stereocephalus* Lambe, 1902/Lynch Arribalzaga, 1884
= *Sterocephalus* Maleev, 1956 [*sic*]
E. tutus (Lambe, 1902) (Type)
= *Stereocephalus tutus* Lambe, 1902
= *Palaeoscincus tutus* (Lambe, 1902)
= *Palaeoscincus asper* Lambe, 1902 [*nomen dubium*]
= *Palaeoscincus rugosus* Nopcsa, 1918 [*sic*]

NOTE: The name *Ankylosaurus acinacodens*, coined by Barnum Brown in the early 1930s but never published, appears on file photographs of a *Euoplocephalus* specimen at the American Museum of Natural History.

This is a paragenus because it is almost certainly ancestral to the genera *Dyoplosaurus* and *Ankylosaurus*.

Genus: *Heishansaurus* Bohlin, 1953 [*nomen dubium*]
= *Heischansaurus* Rozhdestvensky, 1977 [*sic*]
= *Heishanasaurus* Glut, 1972 [*sic*]
= *Heishanosaurus* Swinton, 1970 [*sic*]
H. pachycephalus Bohlin, 1953 (Type)

Genus: *Maleevus* Tumanova, 1987
M. disparoserratus (Maleev, 1952) (Type)
= *Syrmosaurus disparoserratus* Maleev, 1952
= *Pinacosaurus disparoserratus* (Maleev, 1952)
= *Talarurus disparoserratus* (Maleev, 1952)
= *Syrmosaurus disparoserrata* Kuhn, 1964 [*sic*]
= *Talarurus disparsoserratus* Maryanska, 1977 [*sic*]

Genus: *Minmi* Molnar, 1980
M. paravertebra Molnar, 1980 (Type)

NOTE: New material of this genus shows nodosaurid, ankylosaurid, and even stegosaurid characters, probably indicating a more basal position (Scelidosauridae or new family) for this taxon (R. E. Molnar, pers. comm.).

Genus: *Peishansaurus* Bohlin, 1953 [*nomen dubium*]
= *Peishanosaurus* Dong, 1979 [*sic*]
P. philemys Bohlin, 1953 (Type)

NOTE: The above genus is referred to this family provisionally. Coombs (1971) indicates that the type specimen, a fragment from a very small jaw, may not be a juvenile ankylosaurian as originally classified; it may actually be a pachycephalosaur (K. Carpenter, pers. comm.). Bohlin's monograph also carries a plate captioned "*Peishansaurus latipons*," but that is a typographical error for *Peishanemys latipons*, a chelonian.

Genus: *Pinacosaurus* Gilmore, 1933
= *Ninghsiasaurus* Young, 1965 [*sic*]
= *Syrmosaurus* Maleev, 1952
= *Viminicaudus* von Huene, 1958 [*sic*]
P. grangeri Gilmore, 1933 (Type)
= *Pinacosaurus ninghsiensis* Young, 1935
= *Syrmosaurus viminocaudus* Maleev, 1952
= *Syrmosaurus viminicaudus* Maleev, 1956 [*sic*]
= *Pinacosaurus ninghsiaensis* Young, 1964 [*sic*]

Genus: *Saichania* Maryanska, 1977
= *Saichana* Maryanska, 1977 [*sic*]
S. chulsanensis Maryanksa, 1977 (Type)

Genus: *Sangonghesaurus* Zhao, 1983 [*nomen nudum*]
No type species named

Genus: *Sauroplites* Bohlin, 1953
S. scutiger Bohlin, 1953 (Type)
= *Sauroplites spiniger* Maryanska, 1971 [*sic*]

Genus: *Shamosaurus* Tumanova, 1983
= *Shamosaurus* Tumanova, 1981 [*nomen nudum*]
S. scutatus Tumanova, 1983 (Type)

Genus: *Stegosaurides* Bohlin, 1953 [*nomen dubium*]
= *Stegosauroides* Colbert, 1961 [*sic*]
S. excavatus Bohlin, 1953 (Type)

Genus: *Talarurus* Maleev, 1952
= *Talararus* Swinton, 1970 [*sic*]
= *Talarusus* Galton, 1970 [*sic*]
T. plicatospineus Maleev, 1952 (Type)

Genus: *Tarchia* Maryanska, 1977
T. gigantea (Maleev, 1956)
= *Dyoplosaurus giganteus* Maleev, 1956
= *Euoplocephalus giganteus* (Maleev, 1956)
T. kielanae Maryanska, 1977 (Type)

Genus: *Tenchisaurus* [Anonymous] 1981 [*nomen nudum*; transliterated from Japanese]
= *Teinchisaurus* Dong, 1987 [*nomen nudum*]
No type species named
NOTE: The name of the above genus was published in Japanese in a dinosaur chart in the guidebook to the Chinese dinosaur exhibition in Japan in 1981; its spelling is a transliteration provided by M. Tanimoto (pers. comm.). Dong Z. (pers. comm.) notes that a description of the genus is in preparation.

Genus: [To be described from Maortu, China; may or may not be *Tenchisaurus*; Rozhdestvensky, 1961]

Genus: [To be described from Shakh-Shakh, Mongolia; Rozhdestvensky, 1972]

Genus: [To be described from the Lower Cretaceous of Khovboor, Mongolia; a primitive ankylosaurid; Kramarenko, 1974]

Genus: [To be described from the Late Cretaceous of Mongolia; a juvenile ankylosaurid similar to but not congeneric with *Pinacosaurus*; P. Currie, pers. comm.]

Order: Stegosauria Marsh, 1877

Census: 2 families, 14 genera (1 doubtful), 23 species (8 doubtful)

Parafamily: HUAYANGOSAURIDAE Galton, 1990

Census: 1 genus, 1 species

= Huayangosaurinae Dong, Tang & Zhou, 1982
= Huoyangosauridae Dodson & Dawson, 1991 [*sic*]

Genus: *Huayangosaurus* Dong, Tang & Zhou, 1982
= *Huangosaurus* Galton, 1986 [*sic*]
H. taibaii Dong, Tang & Zhou, 1982 (Type)

Family: STEGOSAURIDAE Marsh, 1877

Census: 13 genera (1 doubtful), 22 species (8 doubtful)

= Hypsirhophidae Cope, 1898
= Omosauridae Lydekker, 1888
= Stegosaurididae Nopcsa, 1917 [*sic*]
= Stegosaurinae Abel, 1919
= Stegosauroidae Hay, 1930

Genus: *Changdusaurus* Zhao, 1986 [*nomen nudum*]
= *Changtusaurus* Zhao, 1983 [*nomen nudum*]
C. laminaplacodus Zhao, 1986 (Type)

Genus: *Chialingosaurus* Young, 1959
  = *Chialangosaurus* Colbert, 1961 [*sic*]
  C. kuani Young, 1959 (Type)

Genus: *Chungkingosaurus* Dong, Zhou & Zhang, 1983
  C. jiangbeiensis Dong, Zhou & Zhang, 1983 (Type)

Genus: *Craterosaurus* Seeley, 1874 [*nomen dubium*]
  C. pottonensis Seeley, 1874 (Type)

Genus: *Dacentrurus* Lucas, 1902
  = *Dacentrosaurus* Dong, 1990 [*sic*]
  = *Dacentrurosaurus* Hennig, 1925 [*sic*]
  = *Omosaurus* Owen, 1875/Leidy, 1856
  = *Osmosaurus* Galton, 1980 [*sic*]
  D. armatus (Owen, 1875) (Type)
    = *Omosaurus armatus* Owen, 1875
    = *Stegosaurus armatus* (Owen, 1875) *non* Marsh, 1877
    = *Omosaurus lennieri* Nopcsa, 1911
    = *Dacentrurus lennieri* (Nopcsa, 1911)
    = *Astrodon pusillus* de Lapparent & Zbyszewski, 1957 (juvenile)
    = *Pleurocoelus pusillus* (de Lapparent & Zbyszewski, 1957) (juvenile)
    = *Osmosaurus lennieri* Galton, 1980 [*sic*]
  D. hastiger (Owen, 1877) [*nomen dubium*]
    = *Omosaurus hastiger* Owen, 1877 [*nomen dubium*]
  ?*D. phillipsi* (Seeley, 1893) *non* (Seeley, 1869) [*nomen dubium*]
    = *Omosaurus phillipsi* Seeley, 1893 *non* (Seeley, 1869) [*nomen dubium*]

Genus: *Diracodon* Marsh, 1881
  = *Diracondon* Hay, 1901 [*sic*]
  D. laticeps Marsh, 1881 (Type)
    = *Stegosaurus laticeps* (Marsh, 1881)
  D. stenops (Marsh, 1887) Bakker, 1986
    = *Stegosaurus stenops* Marsh, 1887

NOTE: Synonymies within the above genus are organized according to unpublished work by R. T. Bakker as reported at Boulder, Colorado, 1986. See also *Stegosaurus.*

Genus: *Dravidosaurus* Yadagiri & Ayyasami, 1979
  = *Davidosaurus* Galton, 1981 [*sic*]
  D. blanfordi Yadagiri & Ayyasami, 1979 (Type)

Genus: *Kentrosaurus* Hennig, 1915
  = *Centrurosaurus* Nopcsa, 1917 [*sic*]
  = *Doryphorosaurus* Nopcsa, 1916
  = *Kentrurosaurus* Hennig, 1916
  K. aethiopicus Hennig, 1915 (Type)
    = *Doryphorosaurus aethiopicus* (Hennig, 1915)
    = *Kentrurosaurus aethiopicus* (Hennig, 1915)

Genus: *Lexovisaurus* Hoffstetter, 1957
  = *Lexousaurus* Dong, Chang, Li & Zhou, 1978 [*sic*]
  L. durobrivensis (Hulke, 1887) (Type)
    = *Omosaurus durobrivensis* Hulke, 1887
    = *Stegosaurus durobrivensis* (Hulke, 1887)
    = *Omosaurus leedsi* Seeley, 1901 *vide* von Huene, 1901 [*nomen dubium*; in part]
    = *Lexovisaurus leedsi* (Seeley, 1901) [*nomen dubium*]
    = *Stegosaurus priscus* Nopcsa, 1911 [*nomen dubium*; juvenile?]
    = *Lexovisaurus priscus* (Nopcsa, 1911) [*nomen dubium*; juvenile?]
    = *Omosaurus priscus* (Nopcsa, 1911) [*nomen dubium*; juvenile?]
  ?*L. vetustus* (von Huene, 1910) [*nomen dubium*]
    = *Omosaurus vetustus* von Huene, 1910 [*nomen dubium*]
    = *Dacentrurus vetustus* (von Huene, 1910) [*nomen dubium*]

Genus: *Monkonosaurus* Zhao *vide* Dong, 1990
  = *Monkonosaurus* Zhao, 1983 [*nomen nudum*]
  M. lawulacus Zhao *vide* Dong, 1990 (Type)
    = *Monkonosaurus lawulacus* Zhao, 1986 [*nomen nudum*]
    = *Monkonosaurus lawulocus* Dong, 1987 [*sic*]

Genus: *Paranthodon* Nopcsa, 1929
  = *Anthodon* Owen, 1876 (in part)
  = *Paracanthodon* von Huene, 1956 [*sic*]
  P. africanus (Broom, 1910) (Type)

= *Palaeoscincus africanus* Broom, 1910
= *Anthodon serrarius* Owen, 1876 (in part)
= *Paranthodon owenii* Nopcsa, 1929

Genus: *Stegosaurus* Marsh, 1877
= *Hypsirhophus* Cope, 1878 [*sic*]
= *Hypsirophus* Cope, 1878 [*nomen dubium*]
= *Hypsirrhophus* von Huene, 1909 [*sic*]
= *Sregosaurus* Glut, 1972 [*sic*]
= *Stegasaurus* [Anonymous] 1980 [*sic*]
S. armatus Marsh, 1877 (Type)
S. discurus (Cope, 1878) [*nomen dubium*]
= *Hypsirophus discurus* Cope, 1878 [*nomen dubium*; type specimen probably composite]
= *Hypsirophus discursus* Hennig, 1924 [*sic*]
S. seeleyanus (Cope, 1879) [*nomen dubium*]
= *Hypsirhophus seeleyanus* Cope, 1879 [*nomen dubium*]
S. ungulatus Marsh, 1879
= *Stegosaurus duplex* Marsh, 1887
= *Stegosaurus longispinus* Gilmore, 1914
= *Stegosaurus altispinus* Gilmore, 1914 [*sic*]
S. affinis Marsh, 1881 [*nomen dubium*]
S. sulcatus Marsh, 1887 [*nomen dubium*]
[New species to be described from the Morrison Formation of Colorado; R. T. Bakker, pers. comm.]

NOTE: Synonymies within the above genus are organized according to unpublished work by R. T. Bakker as reported at Boulder, Colorado, 1986. Listed as a paragenus because it is almost certainly ancestral to *Diracodon*.

Genus: *Tuojiangosaurus* Dong, Li, Zhou & Zhang, 1977
= *Taojiangosaurus* Dong, Zhou & Zhang, 1983 [*sic*]
= *Tiejiangosaurus* Dong, Li, Zhou & Zhang, 1977 [*sic*]
= *Tuajiangosaurus* Dong, Zhou & Zhang, 1983 [*sic*]
= *Tueojiangosaurus* Dong, Li, Zhou & Zhang, 1977 [*sic*]
= *Tuojiangosaurus* [Anonymous] 1977 [*nomen nudum*]
= *Tuojingosaurus* Galton, 1981 [*sic*]
= *Tuojiongosaurus* Dong, Li, Zhou & Zhang, 1977 [*sic*]
T. multispinus Dong, Li, Zhou & Zhang, 1977 (Type)

Genus: *Wuerhosaurus* Dong, 1973
= *Wuherosaurus* Sereno, 1986 [*sic*]
W. homheni Dong, 1973 (Type)

Genus: *Yingshanosaurus* Zhou, 1984 [*nomen nudum*]
No type species named

Genus: [To be described from the Morrison Formation of Utah, presently referred to as the "Cleveland-Lloyd ankylosaur"; Madsen, 1976]

Genus: [To be described from the Kota Formation of India; Yadagiri, 1979]

Genus: [To be described from the Maastrichtian of India; Yadagiri, 1979]

Genus: [To be described from the Ordos Basin of Inner Mongolia by Dong; similar to *Wuerhosaurus* but has only 12 dorsal vertebrae; collected in 1988; P. J. Currie, pers. comm.]

Paraorder: Pachycephalosauria Maryanska & Osmólska, 1974

Census: 4 families, 22 genera (1 doubtful), 24 species (4 doubtful)

Parafamily: PISANOSAURIDAE Casamiquela, 1967

Census: 1 genus, 1 species

Genus: *Pisanosaurus* Casamiquela, 1967
= *Pisanosauru* Dong, 1979 [*sic*]
P. mertii Casamiquela, 1967 (Type)

Parafamily: HETERODONTOSAURIDAE Kuhn, 1966

Census: 7 genera (1 doubtful), 7 species (3 doubtful)

= Tianchungosauroidea Zhao, 1983 [*nomen nudum*]

= Xiphosauridae Sereno, 1986

Genus: *Abrictosaurus* Hopson, 1975
  A. consors (Thulborn, 1974) (Type)
    = *Lycorhinus consors* Thulborn, 1974

Genus: *Dianchungosaurus* Young, 1982 [*nomen dubium*]
  = *Diachungosaurus* Haubold, 1990 [*sic*]
  = *Tianchungosaurus* Zhao, 1983 [*sic*]
  D. lufengensis Young, 1982 (Type)
  D. elegans Zhao, 1986 [*nomen nudum*]

NOTE: It is possible that *Dianchungosaurus* and *Tianchungosaurus* are distinct genera, with *D. elegans* the type species of *Tianchungosaurus*, but without descriptions of Zhao's taxa this is presently indeterminable. *Tianchungosaurus* is supposed to represent a new family of pachycephalosaurians (Zhao, 1983), but to date no description of that genus – assuming it is distinct from Young's genus – has been published.

Genus: *Echinodon* Owen, 1861
  = *Echinosaurus* Morris, 1976 [*sic*]
  = *Sauraechinodon* Falconer *vide* Owen, 1861 [*sic*]
  = *Sauraechmodon* Falconer, 1861
  = *Saurechinodon* Owen, 1861 [*sic*]
  E. becklesii Owen, 1861 (Type)
    = *Echinodon becclesii* Owen, 1861 [*sic*]
    = *Echinodon becklessii* Galton, 1978 [*sic*]

NOTE: Referred to as a possible thyreophoran by Weishampel & Witmer (1990) and as a possible heterodontosaurid by Sereno (1991). Referred to this family provisionally.

Genus: *Geranosaurus* Broom, 1911 [*nomen dubium*]
  G. atavus Broom, 1911 (Type)

Genus: *Heterodontosaurus* Crompton & Charig, 1962
  H. tucki Crompton & Charig, 1962 (Type)
    = *Lycorhinus tucki* (Crompton & Charig, 1962)

Genus: *Lycorhinus* Haughton, 1924
  = *Lanasaurus* Gow, 1975
  = *Lychorhinus* Hopson, 1975 [*sic*]
  = *Lycochinus* Galton, 1973 [*sic*]
  L. angustidens Haughton, 1924 (Type)
    = *Lanasaurus scalpridens* Gow, 1975
    = *Lycorhinus angusticeps* Gow, 1991 [*sic*]

Genus: *Revueltosaurus* Hunt, 1989 [*nomen dubium*]
  R. callenderi Hunt, 1989 (Type)

NOTE: The above genus was described from teeth that differ significantly in morphology from those of other ornithischians but most closely resemble those of heterodontosaurids. Referred to as Ornithischia indet. in Sereno, 1991; referred to this family provisionally.

Genus: [To be described from the Morrison Formation of the Fruita, Colorado; a small ornithischian possibly referable to *Echinodon*; Callison & Quimby, 1984; P. M. Galton, pers. comm.]

Parafamily: CHAOYOUNGOSAURIDAE [*nomen nudum; emendum ex* Chaoyoungosauroidea Zhao, 1983]

Census: Not taken

= Chaoyoungosauroidea Zhao, 1983 [*nomen nudum*]

Genus: *Chaoyoungosaurus* Zhao, 1983 [*nomen nudum*]
  = *Chaoyangosaurus* Dong, 1987 [*sic*]
  = *Chaoyoungosaurus* [Anonymous] 1981 [*nomen nudum*; transliterated from Japanese]
  C. liaosiensis Zhao, 1983 (Type)

NOTE: The name of the above genus was first published in Japanese in a dinosaur chart in the guidebook to the Chinese dinosaur exhibition in Japan in 1981; its spelling is a transliteration provided by M. Tanimoto (pers. comm.). It is said to be described in Zhao's 1983 monograph on Tibetan dinosaurs, but this work has thus far not been published. The family Chaoyoungosauridae is considered ancestral to the later pachycephalosaurs and the psittacosaurs, but because there is no description, it is referred to the order Pachycephalosauria provisionally. A description of *Chaoyoungosaurus* is in preparation (Dong Z., pers. comm.).

Zhao Xijin's name is now usually spelled Chao Shichin.

Genus: *Xuanhuasaurus* Zhao, 1986 [*nomen nudum*]
X. niei Zhao, 1986 (Type)
NOTE: Zhao (1986; partial translation by Xi G. provided by R. E. Molnar) notes that the above genus, published without description, is referable to the Chaoyoungosauridae.

Parafamily: HOMALOCEPHALIDAE (Dong, 1978) Perle, Maryanska & Osmólska, 1982

Census: 5 genera, 5 species

= Homalocephaleridae Dong, 1978
= Homalocephalosauridae Telles Antunes & Sigogneau-Russell, 1991 [*sic*]

Genus: *Goyocephale* Perle, Maryanska & Osmólska, 1982
G. lattimorei Perle, Maryanska & Osmólska, 1982 (Type)

Genus: *Homalocephale* Maryanska & Osmólska, 1974
= *Hamalocephale* Dong, 1978 [*sic*]
= *Homalecephale* Carroll, 1987 [*sic*]
= *Homoalcephale* Coombs, 1979 [*sic*]
= *Homocephale* Paul, 1987 [*sic*]
H. calathocercos Maryanska & Osmólska, 1974 (Type)
= *Homalocephale calathoceras* Morris, 1976 [*sic*]

Genus: *Micropachycephalosaurus* Dong, 1978
= *Micropachycephale* Dong, 1978 [*sic*]
M. hongtuyanensis Dong, 1978 (Type)

Genus: *Taveirosaurus* Telles Antunes & Sigogneau-Russell, 1991
T. costai Telles Antunes & Sigogneau-Russell, 1991 (Type)

Genus: *Wannanosaurus* Hou, 1977
= *Wannannosaurus* Dong, 1987 [*sic*]
= *Wannonosaurus* Dong, 1978 [*sic*]
W. yansiensis Hou, 1977 (Type)

Family: PACHYCEPHALOSAURIDAE C. M. Sternberg, 1945

Census: 9 genera, 11 species (1 doubtful)

= Domocephalinae Sereno, 1986
= Psalisauridae Lambe, 1918
= Tholocephalidae Sereno, 1986

Genus: *Gravitholus* Wall & Galton, 1979
G. albertae Wall & Galton, 1979 (Type)

Genus: *Majungatholus* Sues & Taquet, 1979
= *Majungotholus* Goodwin, 1990 [*sic*]
M. atopus Sues & Taquet, 1979 (Type)
= *Stegosaurus madagascariensis* Piveteau, 1926 [*nomen dubium*]

Genus: *Ornatotholus* Galton & Sues, 1983
= *Onatotholus* Lucas, 1991 [*sic*]
O. browni (Wall & Galton, 1979) (Type)
= *Stegoceras browni* Wall & Galton, 1979

Genus: *Pachycephalosaurus* Brown & Schlaikjer, 1943 [*nomen conservandum*]
= *Pachycephalosantus* Sanz, 1990 [*sic*]
= *Tylosteus* Leidy, 1872 [*nomen oblitum*]
P. wyomingensis (Gilmore, 1931) (Type, as a senior synonym of *P. grangeri*, the nominal type of the genus)
= *Troodon wyomingensis* Gilmore, 1931
= *Troödon wyomingensis* Gilmore, 1931*
= *Stegoceras wyomingense* (Gilmore, 1931)
= *Stegoceras wyomingensis* (Gilmore, 1931)*
= *Tylosteus ornatus* Leidy, 1872 [*nomen oblitum*]
= *Pachycephalosaurus grangeri* Brown & Schlaikjer, 1943
= *Pachycephalosaurus reinheimeri* Brown & Schlaikjer, 1943

Genus: *Prenocephale* Maryanska & Osmólska, 1974
P. prenes Maryanska & Osmólska, 1974 (Type)

Genus: *Stegoceras* Lambe, 1902
= *Stegoceros* Galton, 1975 [*sic*]
= *Toodon* Dong, 1979 [*sic*]
= *Troödon* Gilmore, 1924 *non* Leidy, 1856
S. validum Lambe, 1902 (Type)

= *Stegoceras validus* Lambe, 1902*
= *Troodon validus* (Lambe, 1902)
= *Troödon validus* (Lambe, 1902)*
= *Stegoceras breve* Lambe, 1918
= *Stegoceras brevis* Lambe, 1918*
= *Troodon sternbergi* Brown & Schlaikjer, 1943
= *Troödon sternbergi* Brown & Schlaikjer, 1943*
= *Stegoceras sternbergi* (Brown & Schlaikjer, 1943)
= *Stegoceras lambei* C. M. Sternberg, 1945
S. edmontonense (Brown & Schlaikjer, 1943)
= *Stegoceras edmontonensis* (Brown & Schlaikjer, 1943)*
= *Troodon edmontonensis* Brown & Schlaikjer, 1943
= *Troödon edmontonensis* Brown & Schlaikjer, 1943*

Genus: *Stygimoloch* Galton & Sues, 1983
= *Stenotholus* Giffin, Gabriel & Johnson, 1988
S. spinifer Galton & Sues, 1983 (Type)
= *Stenotholus kohlerorum* Giffin, Gabriel & Johnson, 1988
= *Stenotholus kohleri* Giffin, Gabriel & Johnson, 1988*

Genus: *Tylocephale* Maryanska & Osmólska, 1974
?*T. bexelli* (Bohlin, 1953) Olshevsky, 1978 [*nomen dubium*]
= *Troodon bexelli* Bohlin, 1953 [*nomen dubium*]
= *Troödon bexelli* Bohlin, 1953 [*nomen dubium*]*
= *Stegoceras bexelli* (Bohlin, 1953) [*nomen dubium*]
T. gilmorei Maryanska & Osmólska, 1974 (Type)

Genus: *Yaverlandia* Galton, 1971
= *Yarerlandia* Dong, 1978 [*sic*]
= *Yavelandia* Galton, 1975 [*sic*]
= *Yaverladia* Dong, 1979 [*sic*]
Y. bitholus Galton, 1971 (Type)

Genus: [To be described from northeastern Montana; a full-domed pachycephalosaur; Goodwin, 1990]

Order: Ceratopsia Marsh, 1890

Census: 3 families, 30 genera (4 doubtful), 56 species (9 doubtful)

Parafamily: PSITTACOSAURIDAE Osborn, 1923

Census: 1 genus, 5 species

= Protiguanodontinae Osborn, 1923
= Psittacosaurines Lavocat, 1955

Genus: *Psittacosaurus* Osborn, 1923
= *Prittacosaurus* Rozhdestvensky, 1974 [*sic*]
= *Proiguanodon* Dong, 1979 [*sic*]
= *Protiguanodon* Osborn, 1923
= *Psittacorus* Czerkas & Olson, 1987 [*sic*]
= *Pssitacosaurus* Santa Luca, 1980 [*sic*]
P. mongoliensis Osborn, 1923 (Type)
= *Protiguanodon mongoliensis* Osborn, 1923
= *Protiguanodon mongoliense* Osborn, 1923*
= *Psittacosaurus osborni* Young, 1931
= *Psittacosaurus tingi* Young, 1931
= *Psittacosaurus protiguanodonensis* Young, 1958
= *Psittacosaurus guyangensis* Cheng, 1982 (juvenile)
P. sinensis Young, 1958
P. youngi Chao, 1963
P. chaoyoungi Wang, 1983 [*nomen nudum*]

NOTE: This species has so far appeared only in faunal lists without description. It may prove to be *Chaoyoungosaurus* (D. A. Russell, pers. comm.).

P. xinjiangensis Sereno & Chao, 1988
= *Psittacosaurus xinjiangensis* Dong, 1987 [*nomen nudum*]
P. meileyingensis Sereno, Chao, Cheng & Rao, 1988

[New species to be described from the Lower Cretaceous of the eastern USSR; specimen discovered in the Moscow University collection but unlikely to be described in the near future; R. E. Molnar, pers. comm.]
[Possible new species to be described from the Cretaceous of Thailand; *cf.* *SVP Bulletin* #148, February, 1990: 57]
NOTE: Synonymy within this genus is organized according to Sereno, 1990

Genus: [To be described; a large, possibly aberrant psittacosaurid with a skull approximately 70 cm. long, presently stored in a USSR museum; P. C. Sereno, pers. comm.]

Parafamily: PROTOCERATOPSIDAE Granger & Gregory, 1923

Census: 9 genera, 10 species

= Asiaceratopsinae Nessov & Kaznyshkina, 1989
= Leptoceratopsinae Nopcsa, 1923
= Protoceratopidae Steel, 1970
= Protoceratopsinae Nessov & Kaznyshkina, 1989
= Stenopelixidae Kuhn, 1966
= Stenopelyxidae Nopcsa, 1917

Genus: *Asiaceratops* Nessov & Kaznyshkina, 1989
  A. sulcidens (Bohlin, 1953)
    = *Microceratops sulcidens* Bohlin, 1953
  A. salsopaludalis Nessov & Kaznyshkina, 1989 (Type)

Genus: *Bagaceratops* Maryanska & Osmólska, 1975
  B. rozhdestvenskyi Maryanska & Osmólska, 1975 (Type)

Genus: *Breviceratops* Kurzanov, 1990
  B. kozlowskii (Maryanska & Osmólska, 1975) Kurzanov, 1990 (Type)
    = *Protoceratops kozlowskii* Maryanska & Osmólska, 1975

Genus: *Leptoceratops* Brown, 1914
  = *Leptaceratops* Osmólska, 1986 [*sic*]
  L. gracilis Brown, 1914 (Type)

Genus: *Microceratops* Bohlin, 1953
  M. gobiensis Bohlin, 1953 (Type)

Genus: *Montanoceratops* C. M. Sternberg, 1951
  = *Montanaceratops* White, 1973 [*sic*]
  M. cerorhynchus (Brown & Schlaikjer, 1942) (Type)
    = *Leptoceratops cerorhynchus* Brown & Schlaikjer, 1942

Genus: *Notoceratops* Tapia, 1918
  N. bonarellii Tapia, 1918 (Type)
    = *Notoceratops bonarelli* Tapia, 1918*

Genus: *Protoceratops* Granger & Gregory, 1923
  = *Proceratops* Dong, 1979/Lull, 1906 [*sic*]
  P. andrewsi Granger & Gregory, 1923 (Type)
    = *Protoceratops andrewis* [Anonymous] 1990 [*sic*]

Genus: *Stenopelix* von Meyer, 1857
  = *Stenopelyx* Nopcsa, 1917 [*sic*]
  S. valdensis von Meyer, 1857 (Type)
  NOTE: This genus may belong in the Chaoyoungosauridae. It is classified as a "basal marginocephalian" by Dodson, 1990.

Family: CERATOPSIDAE Marsh, 1888

Census: 2 subfamilies, 16 genera (2 doubtful), 34 species (4 doubtful)

= Ceratopidae Lydekker, 1889
= Ceratopsoidae Hay, 1930

Parasubfamily: Eucentrosaurinae [*nomen novum ex* Centrosaurinae Lambe, 1915]

Census: 6 genera, 16 species (1 doubtful)

= Monocloniinae Nopcsa, 1928
= Monocloninae Nopcsa, 1923
= Pachyrhinosauridae C. M. Sternberg, 1950

Genus: *Avaceratops* Dodson, 1986
  = *Azaceratops* Stokes, 1988 [*sic*]
  A. lammersorum Dodson, 1986 (Type)
    = *Avaceratops lammersi* Dodson, 1986*

NOTE: The specific name of the type species is emended to the genitive plural ending, inasmuch as it honors the entire Lammers family.

Genus: *Brachyceratops* Gilmore, 1914
  B. montanensis Gilmore, 1914 (Type)
    = *Monoclonius montanensis* (Gilmore, 1914)

Genus: *Eucentrosaurus* Chure & McIntosh, 1989
  = *Centrosaurus* Lambe, 1904/Fitzinger, 1843
  = *Centrasaurus* L. S. Russell, 1966 [*sic*]
  ?*E. recurvicornis* (Cope, 1889) [*nomen dubium*]
    = *Monoclonius recurvicornis* Cope, 1889 [*nomen dubium*]
    = *Centrosaurus recurvicornis* (Cope, 1889) [*nomen dubium*]
    = *Centrosaurus recurvatus* Langston, 1975 [*sic*]
  E. apertus (Lambe, 1904) (Type)
    = *Centrosaurus apertus* Lambe, 1904
    = *Monoclonius apertus* (Lambe, 1904)
  E. flexus (Brown, 1914)
    = *Centrosaurus flexus* Brown, 1914
    = *Monoclonius flexus* (Brown, 1914)
    = *Monoclonius inflexus* Kuhn, 1936 [*sic*]
  E. nasicornus (Brown, 1917)
    = *Monoclonius nasicornus* Brown, 1917
    = *Centrosaurus nasicornus* (Brown, 1917)
  E. cutleri (Brown, 1917)
    = *Monoclonius cutleri* Brown, 1917
    = *Centrosaurus cutleri* (Brown, 1917)
  E. longirostris (C. M. Sternberg, 1940)
    = *Centrosaurus longirostris* C. M. Sternberg, 1940
    = *Monoclonius longirostris* (C. M. Sternberg, 1940)

NOTE: If *Styracosaurus* is found to be a synonym of the genus *Centrosaurus* (Dodson, 1990), then renaming the genus *Eucentrosaurus* would be superfluous; *Styracosaurus* would simply replace the preoccupied *Centrosaurus*. Also, it is possible that *Centrosaurus* Fitzinger, 1843 is a *nomen oblitum* under the "50-year rule," in which case *Centrosaurus* Lambe, 1904 would not be preoccupied after all. Until these questions are satisfactorily resolved, however, the new name suggested in Chure & McIntosh (1989) should be used for this genus. This is also reflected in the name change of this parasubfamily to Eucentrosaurinae from Centrosaurinae.

Genus: *Monoclonius* Cope, 1876
  = *Monoclonins* Kuhn, 1964 [*sic*]
  M. crassus Cope, 1876 (Type)
    = *Monoclonius sphenocerus* Cope, 1889 [*nomen dubium*]
    = *Styracosaurus sphenocerus* (Cope, 1889) [*nomen dubium*]
  M. fissus Cope, 1889
  M. dawsoni Lambe, 1902
    = *Brachyceratops dawsoni* (Lambe, 1902) Parks, 1925
  M. lowei C. M. Sternberg, 1940

NOTE: Work on ceratopsid bone beds in Alberta, Canada by S. Sampson and D. Tanke, reported at the 1990 SVP annual meeting, indicates that much if not all material referred to the genus *Monoclonius* represents juvenile, subadult, or sexually immature individuals of other centrosaurine ceratopsids.

Genus: *Pachyrhinosaurus* C. M. Sternberg, 1950
  P. canadensis C. M. Sternberg, 1950 (Type)
  [New species to be described from the Judith River Formation of Alberta, Canada by W. Langston, P. J. Currie, and D. Tanke]

Genus: *Styracosaurus* Lambe, 1913 (= *Eucentrosaurus* or *Monoclonius*?)
  = *Stylacosaurus* Charig & Horsfield, 1975 [*sic*]
  S. albertensis Lambe, 1913 (Type)
    = *Monoclonius albertensis* (Lambe, 1913)
  S. ovatus Gilmore, 1930
  S. parksi Brown & Schlaikjer, 1937

NOTE: The name *Styracosaurus borealis*, coined by Barnum Brown in the 1930s but never published, appears on file photographs of the type specimen of the above species at the American Museum of Natural History. Also see note for *Eucentrosaurus* above.

  S. makeli Czerkas & Czerkas, 1990 [*nomen nudum*]

NOTE: The above species name appears without formal description in a picture caption for an as-yet-undescribed species of *Styracosau-*

rus from the Two Medicine Formation of Montana. It is characterized by a single long epoccipital horn on each parietal and a nasal horn that overhangs the beak. The name may be spelled differently when the species is formally described.

Subfamily: Chasmosaurinae Lambe, 1915

Census: 10 genera (2 doubtful),
18 species (3 doubtful)

= Ceratopsinae Abel, 1919
= Eoceratopsinae Lambe, 1915

Genus: *Anchiceratops* Brown, 1914
A. ornatus Brown, 1914 (Type)
A. longirostris C. M. Sternberg, 1929

Paragenus: *Arrhinoceratops* Parks, 1925
A. brachyops Parks, 1925 (Type)

NOTE: Listed as a paragenus because it is almost certainly ancestral to the genus *Torosaurus*.

Paragenus: *Chasmosaurus* Lambe, 1914 (= *Ceratops*?)
= *Chasamosaurus* C. H. Sternberg, 1932 [*sic*]
= *Chasmatosaurus* Maryanska & Osmólska, 1979/Haughton, 1924 [*sic*]
= *Protorosaurus* Lambe, 1914/von Meyer, 1830
C. belli (Lambe, 1902) (Type)
= *Monoclonius belli* Lambe, 1902
= *Protorosaurus belli* (Lambe, 1902)
= *Chasamosaurus ceratops* C. H. Sternberg, 1932 [*sic*]
= *Chasmosaurus brevirostris* Lull, 1933 (juvenile)
?*C. kaiseni* Brown, 1933

NOTE: The above species may represent a new ceratopsid genus, though it may also be a "male" *Chasmosaurus belli* if sexual dimorphism can be proved within the genus.

C. russelli C. M. Sternberg, 1940
C. mariscalensis Lehman, 1989

NOTE: Listed as a paragenus because it is almost certainly ancestral to the genus *Pentaceratops*.

Genus: *Ceratops* Marsh, 1888/Rafinesque, 1815 [*nomen dubium*]
= *Proceratops* Lull, 1906
C. montanus Marsh, 1888 (Type)
= *Proceratops montanus* (Marsh, 1888)
= *Triceratops montanus* (Marsh, 1888) [*sic*; a typographical error in Ostrom & Wellnhofer, 1986; J. H. Ostrom, pers. comm.]

NOTE: Substitution of *Proceratops* for *Ceratops* by Lull, 1906 was unnecessary, as *Ceratops* Rafinesque, 1815 was by then a *nomen oblitum* (R. E. Molnar, pers. comm.).

Genus: *Diceratops* Hatcher *vide* Lull, 1905
D. hatcheri Lull, 1907 (Type)
= *Triceratops hatcheri* (Lull, 1907)

NOTE: Recent work on the systematics of the genus *Triceratops* by Catherine Forster (presented at the 1990 SVP annual meeting) indicates that *Diceratops* is distinct from *Triceratops* rather than a junior synonym as usually classified.

Genus: *Eoceratops* Lambe, 1915 (= juvenile *Chasmosaurus* or *Ceratops*?)
E. canadensis (Lambe, 1902) (Type)
= *Monoclonius canadensis* Lambe 1902
= *Ceratops canadensis* (Lambe, 1902)

Genus: *Pentaceratops* Osborn, 1923
P. sternbergii Osborn, 1923 (Type)
= *Chasmosaurus sternbergii* (Osborn, 1923)
P. fenestratus Wiman, 1930

Genus: *Torosaurus* Marsh, 1891
T. latus Marsh, 1891 (Type)
= *Torosaurus gladius* Marsh, 1891
T. utahensis (Gilmore, 1946) Lawson, 1976
= *Arrhinoceratops utahensis* Gilmore, 1946

Genus: *Triceratops* Marsh, 1889
= *Claorhynchus* Cope, 1892 [*nomen dubium*]
= *Polyonax* Cope, 1874 [*nomen dubium*]
= *Sterrholophus* Marsh, 1891
= *Tirceratops* Parks, 1925 [*sic*]
= *Tricerotops* Stokes, 1988 [*sic*]
?*T. alticornis* (Marsh, 1887) [*nomen dubium*]

= *Bison alticornis* Marsh, 1887 [*nomen dubium*]
= *Ceratops alticornis* (Marsh, 1887) [*nomen dubium*]
T. horridus (Marsh, 1889) (Type)
= *Ceratops horridus* Marsh, 1889
= *Polyonax mortuarius* Cope, 1874 [*nomen dubium*; juvenile]
= *Agathaumas mortuarius* (Cope, 1874) [*nomen dubium*; juvenile]
= *Triceratops mortuarius* (Cope, 1874) [*nomen dubium*; juvenile]
= *Triceratops flabellatus* Marsh, 1889
= *Sterrholophus flabellatus* (Marsh, 1889) Marsh, 1891
= *Triceratops galeus* Marsh, 1889 [*nomen dubium*]
= *Triceratops sulcatus* Marsh, 1890 [*nomen dubium*]
= *Triceratops prorsus* Marsh, 1890
= *Triceratops serratus* Marsh, 1890
= *Triceratops elatus* Marsh, 1891
= *Claorhynchus trihedrus* Cope, 1892 [*nomen dubium*]
= *Triceratops obtusus* Marsh, 1898
= *Triceratops calicornis* Marsh, 1898
= *Triceratops californis* Wolcott, 1900 [*sic*]
= *Triceratops brevicornus* Hatcher, 1905 (juvenile)
= *Triceratops ingens* Lull, 1915 [*nomen nudum*]
= *Triceratops maximus* Brown, 1933 [*nomen dubium*]
= *Triceratops albertensis* C. M. Sternberg, 1949
= *Triceratops brevirostris* Sloan, 1976 [*sic*]
?*T. eurycephalus* Schlaikjer, 1935

NOTE: Recent work on the systematics of *Triceratops* by Catherine Forster, reported at the 1990 SVP annual meeting, indicates that the above species of *Triceratops* is distinct from *T. horridus* and may even belong in a different genus. All the other species of *Triceratops* except *T. alticornus* remain junior synonyms of *T. horridus*, as shown in Ostrom & Wellnhofer, 1986.

Genus: *Ugrosaurus* Cobabe & Fastovsky, 1987 [*nomen dubium*; = *Triceratops*?]
U. olsoni Cobabe & Fastovsky, 1987 (Type)

Ceratopsidae *incertae sedis*

Census: 4 genera (2 doubtful), 7 species (5 doubtful)

= Agathaumidae Cope, 1889

Genus: *Agathaumas* Cope, 1872 [*nomen dubium*; = *Brachyceratops*?]
= *Agathaumus* Baur, 1891 *vide* Hay, 1901 [*sic*]
A. sylvestris Cope, 1872 (Type)
= *Triceratops sylvestris* (Cope, 1872) [*nomen dubium*]

Genus: *Arstanosaurus* Suslov *vide* Suslov & Shilin, 1982
A. akkurganensis Suslov & Shilin, 1982 (Type)

NOTE: The type specimen of this species is a maxilla referable to the Ceratopsidae (D. B. Weishampel, pers. comm.; Nessov & Kaznyshkina, 1989).

Genus: *Dysganus* Cope, 1876 [*nomen dubium*]
D. encaustus Cope, 1876 (Type)
D. bicarinatus Cope, 1876 [*nomen dubium*]
D. haydenianus Cope, 1876 [*nomen dubium*]
D. peiganus Cope, 1876 [*nomen dubium*]

NOTE: Coombs & Galton (1988) review the material (teeth) assigned to the species in this genus and conclude that although it is all ceratopsid, it cannot be defined below the family level. The genus and all included species are considered *nomina dubia*.

Genus: *Turanoceratops* Nessov & Kaznyshkina, 1989
T. tardabilis Nessov & Kaznyshkina, 1989 (Type)

Superorder: Ornithischia Seeley, 1888 (continued)

Order: Ornithopoda Marsh, 1871

Census: 6 families, 74 genera (17 doubtful), 115 species (35 doubtful)

Parafamily: HYPSILOPHODONTIDAE Dollo, 1882

Census: 17 genera (4 doubtful), 25 species (5 doubtful)

= Hypsilophodontinae Abel, 1919
= Laosauridae Marsh, 1879 [*nomen oblitum*]
= Laosaurinae Abel, 1919
= Thescelosauridae C. M. Sternberg, 1937

Genus: *Atlascopcosaurus* T. Rich & P. Rich, 1989
  = *Atlascoplosaurus* Haubold, 1990 [*sic*]
  A. loadsi T. Rich & P. Rich, 1989 (Type)

Genus: *Drinker* Bakker, Galton, Siegwarth & Filla, 1990
  D. nisti Bakker, Galton, Siegwarth & Filla, 1990 (Type)
  NOTE: The above genus, along with *Othnielia*, is excluded from the Hypsilophodontidae in the original description. Referred to this family provisionally.

Genus: *Fulgurotherium* von Huene, 1932 [*nomen dubium*]
  F. australe von Huene, 1932 (Type)

Genus: *Gongbusaurus* Dong, Zhou & Zhang, 1983
  = *Gubisaurus* Dong, Zhou & Zhang, 1983 [*sic*]
  G. shiyii Dong, Zhou & Zhang, 1983 (Type)
    = *Gongbusaurus shiyi* Dong, 1987 [*sic*]
  G. wucaiwanensis Dong, 1989
    = *Gongbusaurus wucaiwanensis* Dong, 1986 [*nomen nudum*]

Genus: *Hypsilophodon* Huxley, 1869
  H. foxii Huxley, 1869 (Type)
    = *Hypsilophodon foxi* (Huxley, 1869)
    = *Iguanodon foxi* (Huxley, 1869)
    = *Camptosaurus valdensis* Lydekker, 1889 [*nomen dubium* in Sues & Norman, 1990]
  H. wielandi Galton & Jensen, 1979 (not 1978) [*nomen dubium* in Sues & Norman, 1990]

Genus: *Laosaurus* Marsh, 1878 [*nomen dubium*]
  L. celer Marsh, 1878 (Type)

Genus: *Leaellynasaura* T. Rich & P. Rich, 1989
  = *Leaellynasaurus* Haubold, 1990 [*sic*]
  L. amicagraphica T. Rich & P. Rich, 1989 (Type)

Genus: *Othnielia* Galton, 1977
  = *Othneilia* Galton & H. P. Powell, 1980 [*sic*]
  O. rex (Marsh, 1877) (Type)
    = *Nanosaurus rex* Marsh, 1877
    = *Laosaurus rex* (Marsh, 1877)
    = *Laosaurus gracilis* Marsh, 1878
  O. consors (Marsh, 1894; = *O. rex*?)
    = *Laosaurus consors* Marsh, 1894
  NOTE: The above genus, along with *Drinker*, is excluded from the Hypsilophodontidae by

Bakker, Galton, Siegwarth & Filla, 1990. Referred to this family provisionally.

Genus: *Orodromeus* Horner & Weishampel, 1988
  O. makelai Horner & Weishampel, 1988 (Type)

Genus: *Parksosaurus* C. M. Sternberg, 1937
  = *Parkosaurus* Czerkas & Olson, 1987 [*sic*]
  P. warreni (Parks, 1926) (Type)
    = *Thescelosaurus warreni* Parks, 1926

NOTE: The above genus is referred to this family provisionally.

Genus: *Phyllodon* Thulborn, 1973 [*nomen dubium* in Sues & Norman, 1990]
  P. henkeli Thulborn, 1973 (Type)

Genus: *Rhabdodon* Matheron, 1869 [*nomen conservandum*]
  = *Machlodon* Glut, 1972 [*sic*]
  = *Mochlodon* Seeley, 1881
  = *Oligosaurus* Seeley, 1881 [*nomen dubium*]
  = *Onychosaurus* Nopcsa, 1902 [*nomen dubium*]
  = *Ornithomerus* Seeley, 1881 [*nomen dubium*]
  = *Rabdodon* Matheron, 1869 [*sic*]
  = *Rhabodon* Kuhn, 1964 [*sic*]
  R. priscus Matheron, 1869 (Type)
    = *Rhabdodon priscum* Matheron, 1869*
    = *Rabdodon priscum* Matheron, 1869 [*sic*]
    = *Iguanodon suessi* Bunzel, 1871
    = *Mochlodon suessi* (Bunzel, 1871)
    = *Rhabdodon suessi* (Bunzel, 1871)
    = *Oligosaurus adelus* Seeley, 1881 [*nomen dubium*]
    = *Ornithomerus gracilis* Seeley, 1881 [*nomen dubium*; juvenile?]
    = *Camptosaurus inkeyi* Nopcsa, 1899
    = *Mochlodon inkeyi* (Nopcsa, 1899)
    = *Rhabdodon inkeyi* (Nopcsa, 1899)
    = *Mochlodon robustus* Nopcsa, 1900 [*nomen dubium*]
    = *Mochlodon robustum* Nopcsa, 1900 [*nomen dubium*]*
    = *Rhabdodon robustus* (Nopcsa, 1900) [*nomen dubium*]
    = *Rhabdodon robustum* (Nopcsa, 1900) [*nomen dubium*]*
    = *Mochlodon suessi* var. *robustus* Nopcsa, 1901 [*nomen dubium*]
    = *Mochlodon suessi* var. *robustum* Nopcsa, 1901 [*nomen dubium*]*
    = *Onychosaurus hungaricus* Nopcsa, 1902 [*nomen dubium*]
  R. septimanicus Buffetaut & Le Loeuff, 1991

NOTE: ICZN Opinion #1483 suppresses the earlier genus *Rhabdodon* Fleischmann, 1831 as a *nomen oblitum* and conserves *Rhabdodon* Matheron, 1869 for the unpreoccupied name of this genus. The same publication also corrects the spelling of the type-specific name to *Rhabdodon priscus*.

Genus: *Tenontosaurus* Ostrom, 1970
  = *Tenantosaurus* Brown *vide* Chure & McIntosh, 1989
  T. tillettorum Ostrom, 1970 (Type)
    = *Tenontosaurus tilletti* Ostrom, 1970*
    = *Tenantosaurus kaiseni* Brown *vide* Chure & McIntosh, 1989

NOTE: The specific name of the type species is here emended to the genitive plural ending, inasmuch as it is in honor of the entire Tillett family (see Ostrom, 1970). The names *Eureodon kaiseni* and *Tenantosaurus kaiseni*, coined in the 1930s by Barnum Brown but never published, appear on American Museum of Natural History file photographs of the "camptosaurid" specimen (AMNH 3034) that is referred to *Tenontosaurus* in Ostrom, 1970.

  [New species to be described from the Comanchean of Texas; Langston, 1974]
  [New species to be described from Doss Ranch, Texas; may represent a new genus; discussed at the 1989 SVP Annual Meeting]

NOTE: This genus is classified outside the Hypsilophodontidae, Dryosauridae, and Camptosauridae by Sues & Norman (1990) and on further study will probably require its own family. Referred to the Hypsilophodontidae provisionally.

Genus: *Thescelosaurus* Gilmore, 1913
  T. neglectus Gilmore, 1913 (Type)
  ?*T. edmontonensis* Sternberg, 1940
  ?*T. garbanii* Morris, 1976

Genus: *Xiaosaurus* Dong & Tang, 1983 [*nomen dubium* in Weishampel & Witmer, 1990]
= *Xiaosaurus* Dong, 1983 [*nomen nudum*]
X. dashanpensis Dong & Tang, 1983 (Type)
= *Xiaosaurus dashanpenensis* Dong, 1983 [*nomen nudum*]

NOTE: Some references list this species as a synonym of *Yandusaurus multidens*, but Sereno (1991) considers it a *nomen dubium* and classifies the genus as Ornithischia *incertae sedis*.

Genus: *Yandusaurus* He, 1979
= *Honghesaurus* [Anonymous] 1981 [*sic*]
= *Hunhosaurus* Dong, Zhou & Zhang, 1983 [*sic*]
= *Yubasaurus* He, 1975? [*sic*]
Y. hongheensis He, 1979 (Type)
Y. multidens He & Cai, 1983

NOTE: The reference to *Yubasaurus* has not yet been seen. If the date given above is correct, the name may have priority over *Yandusaurus*.

Genus: *Zephyrosaurus* Sues, 1980
Z. schaffi Sues, 1980 (Type)

Genus: [To be described; may be *Orodromeus* or a new genus; J. R. Horner, pers. comm.]
[Type species to be redescribed]
= *Laosaurus minimus* Gilmore, 1924
= *Othnielia minima* (Gilmore, 1924)

Genus: [To be described from the Newark Formation; Olsen & Galton, 1977]

Genus: [To be described from the Newark Formation; Olsen & Galton, 1977]

Genus: [To be described from the Newark Formation; Olsen & Galton, 1977]

Genus: [To be described from the Hell Creek Formation; referred to as *Thescelosaurus* sp. in Morris, 1976; Sues, 1980]

Genus: [To be described from the Morrison Formation; based on remains originally referred to *Nanosaurus agilis*; P. M. Galton, pers. comm.]

Genus: [To be described from Proctor Lake, Texas; Winkler, Jacobs, *et al.*, 1988]

Genus: [To be described from James Ross Island, British Antarctica; based on partial skull, anterior vertebral column, pectoral girdle, and pelvis of an animal about 5 meters long]

Family: DRYOSAURIDAE
Milner & Norman, 1984

Census: 3 genera (1 doubtful), 5 species (1 doubtful)

= Dryosaurinae Cooper, 1985

Genus: *Dryosaurus* Marsh, 1894
= *Drysaurus* Galton, 1977 [*sic*]
= *Dypsalotosaurus* Galton, 1973 [*sic*]
= *Dysalatosaurus* Colbert, 1961 [*sic*]
= *Dysalotasaurus* Ostrom, 1970 [*sic*]
= *Dysalotosaurus* Virchow, 1919
D. altus (Marsh, 1878) (Type)
= *Laosaurus altus* Marsh, 1878
D. lettowvorbecki (Virchow, 1919)
= *Dysalotosaurus lettowvorbecki* Virchow, 1919
= *Dysalotosaurus lettow-vorbecki* Virchow, 1919*

Genus: *Kangnasaurus* Haughton, 1915 [*nomen dubium* in Sues & Norman, 1990]
K. coetzeei Haughton, 1915 (Type)

Genus: *Valdosaurus* Galton, 1977
V. canaliculatus (Galton, 1975) (Type)
= *Dryosaurus canaliculatus* Galton, 1975
V. nigeriensis Galton & Taquet, 1982

Family: CAMPTOSAURIDAE
Marsh, 1885

Census: 3 genera, 5 species

= Camptonotidae Marsh, 1881
= Camptosaurinae Abel, 1919

Genus: *Callovosaurus* Galton, 1980
C. leedsi (Lydekker, 1889) (Type)
= *Camptosaurus leedsi* Lydekker, 1889

Genus: *Camptosaurus* Marsh, 1885
- = *Brachyrophus* Cope, 1878 [*nomen dubium*]
- = *Brachyrhophus* Kuhn, 1965 [*sic*]
- = *Campotonodus* Romer, 1966 [*sic*]
- = *Camptonodus* Hoffmann, 1880 [*sic*]
- = *Camptonotus* Marsh, 1879/Uhler, 1864
- = *Camptonutus* Galton & Jensen, 1979 (not 1978) [*sic*]
- = *Cumnoria* Seeley, 1888
- = *Cumnovia* Carus, 1888 [*sic*]
- = *Cunmoria* Nopcsa, 1917 [*sic*]
- = *Symphyrophus* Cope, 1878 [*nomen dubium*]
- = *Symphyrosaurus* von Huene, 1908 [*sic*]
- *C. dispar* (Marsh, 1879) (Type)
  - = *Camptonotus dispar* Marsh, 1879
  - = *Cumnoria dispar* (Marsh, 1879)
  - = *Brachyrophus altarkansanus* Cope, 1878 [*nomen dubium*]
  - = *Symphyrophus musculosus* Cope, 1878 [*nomen dubium*]
  - = *Camptosaurus medius* Marsh, 1894
  - = *Camptosaurus nanus* Marsh, 1894
  - = *Camptosaurus browni* Gilmore, 1909
- *C. prestwichii* (Hulke, 1880)
  - = *Iguanodon prestwichii* Hulke, 1880
  - = *Cumnoria prestwichi* (Hulke, 1880)
- ?*C. depressus* Gilmore, 1909

Genus: *Muttaburrasaurus* Bartholomai & Molnar, 1981
- *M. langdoni* Bartholomai & Molnar, 1981 (Type)

NOTE: Generally classified as an iguanodontid, this genus may actually be a large camptosaurid (R. E. Molnar, pers. comm.). Referred to this family provisionally.

Genus: [To be described from the Lower Cretaceous of North America; bears a cranial crest]

Genus: [To be described from the Lower Cretaceous of North America]

Genus: [To be described from the Lower Cretaceous of North America]

Parafamily: IGUANODONTIDAE Cope, 1869

Census: 7 genera (3 doubtful), 21 species (9 doubtful)

= Iguanodontinae Abel, 1919
= Iguanodontoidae Hay, 1930
= Iguanodontoides Gervais, 1853
= Iguanodotidae Delair, 1959 [*sic*]
= Kalodontidae Nopcsa, 1901

Genus: *Anoplosaurus* Seeley, 1878 [*nomen dubium*]
- = *Anoplocephalus* Hennig, 1924 [*sic*]
- = *Eucercosaurus* Seeley, 1879 [*nomen dubium*]
- = *Eucerosaurus* Romer, 1966 [*sic*]
- = *Sygmosaurus* Sauvage, 1878 [*sic*]
- = *Syngonosaurus* Seeley, 1878 [*nomen dubium*]
- *A. macrocercus* (Seeley, 1869) [*nomen dubium*]
  - = *Acanthopholis macrocercus* Seeley, 1869 [*nomen dubium*; in part]
  - = *Syngonosaurus macrocercus* (Seeley, 1869) [*nomen dubium*]
  - = *Syngonosaurus macrourus* Hennig, 1924 [*sic*]
  - = *Anoplosaurus macromerus* Kuhn, 1936 [*sic*]
- *A. curtonotus* Seeley, 1878 (Type)
  - = *Anoplosaurus curtonodus* Coombs, 1971 [*sic*]
- *A. major* Seeley, 1878 [*nomen dubium*]
  - = *Acanthopholis stereocercus* Seeley, 1869 [*nomen dubium*; in part]
- *A. tanyspondylus* (Seeley, 1878) [*nomen dubium*]
  - = *Eucercosaurus tanyspondylus* Seeley, 1878 [*nomen dubium*]

Genus: *Craspedodon* Dollo, 1883 [*nomen dubium*]
- = *Craspedon* Galton, 1980 [*sic*]
- *C. lonzeensis* Dollo, 1883 (Type)

Genus: "Fukuisaurus" Lambert, 1990 [to be described from Japan; based on very scanty material]

Genus: *Gravisaurus* Chabli, 1988 [*nomen nudum*]
- = *Gravisaurus* Norman, 1989 [*nomen nudum*]
- *G. tenerensis* Chabli, 1988 (Type)
  - = *Gravisaurus tenerensis* Norman, 1989 [*nomen nudum*]

NOTE: This is the stout iguanodontid ("*iguanodontide trapu*") from Gadoufaoua (Taquet, 1975; Taquet, 1976). Coined by Fouad Chabli in her 1988 doctoral dissertation, the generic and specific names first appeared in print in the bibliography of *The Age of Dinosaurs: Short Courses in Paleontology* #2, edited by K. Padian and D. Chure, published in 1989 by the Paleontological Society. The bibliographic reference is from Norman's article in that volume.

Genus: *Iguanodon* Mantell, 1825
- = *Heterosaurus* Cornuel, 1850 [*nomen dubium*; in part]
- = *Hikanodon* Keferstein?, 1825? [*nomen oblitum*; reference not found]
- = *Iguanaodon* Galton & H. P. Powell, 1980 [*sic*]
- = *Iguanosaurus* [Anonymous] 1824 [*nomen oblitum*]
- = *Iguonodon* Galton & H. P. Powell, 1980 [*sic*]
- = *Iquanadon* Stokes, 1988 [*sic*]
- = *Iquanodon* A. Walker, 1964 [*sic*]
- = *Jguanodon* Kalandadze & Kurzanov, 1973 [*sic*]
- = *Sphenospondylus* Seeley, 1882 [*nomen dubium*]
- = *Therosaurus* Fitzinger, 1843
- = *Vectisaurus* Hulke, 1879 (juvenile)
- *I. anglicus* Holl, 1829 (Type)
  - = *Iguanodon anglicum* Holl, 1829*
  - = *Iguanodon mantelli* von Meyer, 1832
  - = *Therosaurus mantelli* (von Meyer, 1832)
  - = *Streptospondylus major* Owen, 1842 [*nomen dubium*]
  - = *Iguanodon major* (Owen, 1842) [*nomen dubium*]
  - = *Streptospondylus recentior* Owen, 1851 [*nomen dubium*]
  - = *Streptospondylus meyeri* Owen, 1854 [*nomen dubium*]
  - = *Streptospondylus grandis* Hulke, 1879 [*nomen dubium*]
- *I. hoggi* Owen, 1874
- ?*I. exogirarum* Fritsch, 1878 [*nomen dubium*]
  - = *Procerosaurus exogirarum* (Fritsch, 1878) Fritsch, 1905 [*nomen dubium*]
  - = *Iguanodon exogyrarum* Chure & McIntosh, 1989 [*sic*]
  - = *Procerosaurus exogyrarum* Chure & McIntosh, 1989 [*sic*]
- *I. bernissartensis* Boulenger *vide* van Beneden, 1881
  - = *Iguanodon seeleyi* Hulke, 1882

NOTE: This species will be redescribed as the type species of a new genus by G. Paul (pers. comm.).

- *I. dawsoni* Lydekker, 1888
- *I. fittoni* Lydekker, 1889
  - = *Iguanodon hollingtoniensis* Lydekker, 1889
- *I. atherfieldensis* Hooley, 1924
  - = *Cetiosaurus brachyurus* Owen, 1842 [*nomen dubium*]
  - = *Heterosaurus neocomiensis* Cornuel, 1850 [*nomen dubium*; in part]
  - = *Vectisaurus valdensis* Hulke, 1879 (juvenile)
  - = *Sphenospondylus gracilis* Lydekker, 1888 [*nomen dubium*]
  - = *Iguanodon gracilis* (Lydekker, 1888) [*nomen dubium*]
- *I. orientalis* Rozhdestvensky, 1952
- *I. ottingeri* Galton & Jensen, 1979 (not 1978) [*nomen dubium* in Norman & Weishampel, 1990]
- *I. lakotaensis* Weishampel & Bjork, 1989

Genus: *Loncosaurus* Ameghino, 1898 [*nomen dubium*]
- *L. argentinus* Ameghino, 1898 (Type)
  - = *Megalosaurus argentinus* (Ameghino, 1898) [*nomen dubium*]

NOTE: This species is not a theropod as often classified but an ornithopod (Molnar, 1980) apparently based on a femur. If it turns out that the type specimen is a tooth, however, then the genus will have to be classified as Theropoda *incertae sedis* (R. E. Molnar, pers. comm.). Referred to this family provisionally.

Genus: *Ouranosaurus* Taquet, 1976
= *Ouranosaurus* Taquet, 1972 [*nomen nudum*]
O. nigeriensis Taquet, 1976 (Type)
= *Ouranosaurus nigeriensis* Taquet, 1972 [*nomen nudum*]

Genus: *Probactrosaurus* Rozhdestvensky, 1966
P. gobiensis Rozhdestvensky, 1966 (Type)
P. alashanicus Rozhdestvensky, 1966

Genus: *Sanpasaurus* Young, 1946
S. yaoi Young, 1946 (Type)
?*S. imperfectus* (Young, 1946) [*nomen dubium*]
= Gen. indet. *imperfectus* Young, 1946 [*nomen dubium*]
= *Trachodon imperfectus* (Young, 1946) [*nomen dubium*]

NOTE: The above genus was originally described as an iguanodontid, but Rozhdestvensky, 1966 listed several non-ornithischian characters of the type species and ultimately concluded that *Sanpasaurus* was a juvenile sauropod. Chinese workers have generally not accepted this judgment.

Genus: [To be described]
= *Gadolosaurus* Saito, 1979 [*nomen nudum*; juvenile]

NOTE: The generic name *Gadolosaurus* was used to label a juvenile ornithopod skeleton on display by the Soviet Union in Japan in 1973–74 and was published (without specific name) in *Wonder of the World's Dinosaurs* by T. Saito in 1979. That specimen was eventually referred to *Arstanosaurus* (P. C. Sereno, pers. comm.; Ivakhnenko & Korabelnikov, 1987), but this assignment is probably incorrect (D. B. Norman, pers. comm.), and the *Gadolosaurus* specimen probably represents a new iguanodontid genus from central Asia. Although much hadrosaurid material from the Soviet Union has recently been referred to *Arstanosaurus*, the type specimen of *Arstanosaurus akkurganensis* is a ceratopsid maxilla (D. Weishampel, pers. comm.; Nessov & Kaznyshkina, 1989).

Genus: [To be described from central Asia, based on skull and skeletal material referred to *Iguanodon orientalis* by Kalandadze & Kurzanov, 1974; a large-nosed Mongolian iguanodontid; a photograph of the nearly complete skull was first published in the guidebook to the USSR paleontological exhibition in Japan in 1973–74; D. Norman, pers. comm.; M. K. Brett-Surman, pers. comm.; J. R. Horner, pers. comm.; M. Tanimoto, pers. comm.; Norman & Weishampel, 1990]

Genus: [To be described from the Early Cretaceous of western North America; an ornithopod with elongated neural spines discovered by J. A. Jensen; R. A. Long, pers. comm.; B. B. Britt, pers. comm.]

Genus: [To be described from central Asia; based on remains presently in the collection of the Paleontological Institute of the USSR Academy of Sciences; two or three genera may be present; D. Norman, pers. comm.]

Family: HADROSAURIDAE Cope, 1869

Census: 24 genera (7 doubtful),
40 species (14 doubtful)

= Claosauridae Marsh, 1890
= Hadrosaurinae Lambe, 1918
= Kritosaurines de Lapparent & Lavocat, 1955
= Ornithotarsidae Cope, 1871
= Prohadrosauridae von Huene, 1956
= Protrachodontidae Flower, 1928
= Protrachodontinae Abel, 1919
= Saurolophidae Nopcsa, 1917
= Saurolophinae Brown, 1914

Genus: *Amtosaurus* Kurzanov & Tumanova, 1978 [*nomen dubium*]
A. magnus Kurzanov & Tumanova, 1978 (Type)

NOTE: The this genus is probably a hadrosaurid, because the occipital condyle of the type specimen lacks a neck (K. Carpenter, pers. comm.; Coombs, 1990).

Genus: *Anatotitan* Brett-Surman *vide* Chapman & Brett-Surman, 1990
= *Anatotitan* Brett-Surman, 1988 (chironym)
= *Anatotitan* Norman, 1989 [*nomen nudum*]
A. longiceps (Marsh, 1890) n. comb.

= *Trachodon longiceps* Marsh, 1890
= *Anatosaurus longiceps* (Marsh, 1890) Lull & Wright, 1942
= *Hadrosaurus longiceps* (Marsh, 1890)
A. copei (Lull & Wright, 1942) (Type)
= *Anatosaurus copei* Lull & Wright, 1942
= *Edmontosaurus copei* (Lull & Wright, 1942)
= *Diclonius mirabilis* Cope, 1876 [*nomen dubium*; in part]

NOTE: The type specimen of *Anatotitan longiceps* is a long and slender right dentary lacking teeth (YPM 616; one of the longest hadrosaurid dentaries known) that satisfies Brett-Surman's (1988, 1990) diagnosis of the genus *Anatotitan*. As noted in Lull & Wright, 1942, however, YPM 616 differs enough from *Anatotitan copei* to warrant retaining *A. longiceps* as a distinct species, which is morphologically intermediate between the genera *Anatotitan* and *Edmontosaurus*. *Anatotitan* was originally described in Brett-Surman's (1988) doctoral dissertation.

Genus: *Aralosaurus* Rozhdestvensky, 1968
A. tuberiferus Rozhdestvensky, 1968 (Type)
= *Aralosaurus tuberifrons* Maryanska, 1977 [*sic*]

Genus: *Brachylophosaurus* C. M. Sternberg, 1953
= *Brachylosaurus* Czerkas & Czerkas, 1990 [*sic*]
B. canadensis C. M. Sternberg, 1953 (Type)
B. goodwini Horner, 1988

Genus: *Cionodon* Cope, 1874 [*nomen dubium*]
= *Cinodon* Cope, 1874 [*sic*]
C. arctatus Cope, 1874 (Type)
= *Thespesius arctatus* (Cope, 1874) [*nomen dubium*]
= *Trachodon arctatus* (Cope, 1874) [*nomen dubium*]
C. stenopsis Cope, 1875 [*nomen dubium*]
= *Thespesius stenopsis* (Cope, 1875) [*nomen dubium*]
= *Trachodon stenopsis* (Cope, 1875) [*nomen dubium*]

Genus: *Claosaurus* Marsh, 1890
C. agilis (Marsh, 1872) (Type)
= *Hadrosaurus agilis* Marsh, 1872
= *Trachodon agilis* (Marsh, 1872)

Genus: *Diclonius* Cope, 1876 [*nomen dubium*]
D. pentagonus Cope, 1876 (Type)
= *Thespesius pentagonus* (Cope, 1876) [*nomen dubium*]
= *Trachodon pentagonus* (Cope, 1876) [*nomen dubium*]
D. calamarius Cope, 1876 [*nomen dubium*]
= *Thespesius calamarius* (Cope, 1876) [*nomen dubium*]
= *Trachodon calamarius* (Cope, 1876) [*nomen dubium*]
D. perangulatus Cope, 1876 [*nomen dubium*]
= *Hadrosaurus perangulatus* (Cope, 1876) [*nomen dubium*]
= *Thespesius perangulatus* (Cope, 1876) [*nomen dubium*]
= *Trachodon perangulatus* (Cope, 1876) [*nomen dubium*]

Paragenus: *Edmontosaurus* Lambe, 1917
= *Amatosaurus* D. A. Russell, 1982 [*sic*]
= *Anatosaurus* Lull & Wright, 1942
= *Anotosaurus* Colbert, 1962 [*sic*]
= *Edmontasaurus* Stokes, 1988 [*sic*]
= *Edomontosaurus* Chapman & Brett-Surman, 1990 [*sic*]
E. annectens (Marsh, 1892)
= *Claosaurus annectens* Marsh, 1892
= *Anatosaurus annectens* (Marsh, 1892) Lull & Wright, 1942
= *Thespesius annectens* (Marsh, 1892)
= *Trachodon annectens* (Marsh, 1892)
= *Claosaurus annectans* Williston, 1898 [*sic*]
= *Thespesius edmontonensis* Gilmore, 1924
= *Thespesius edmontoni* Gilmore, 1924*
= *Anatosaurus edmontonensis* (Gilmore, 1924) Lull & Wright, 1942
= *Anatosaurus edmontoni* (Gilmore, 1924) Lull & Wright, 1942*
= *Edmontosaurus edmontonensis* (Gilmore, 1924)
= *Edmontosaurus edmontoni* (Gilmore, 1924)*
= *Trachodon edmontonensis* (Gilmore, 1924)
= *Trachodon edmontoni* (Gilmore, 1924)*
= *Thespesius edmonti* Parks, 1935 [*sic*]

= *Edmontosaurus minor* Parks, 1935 *vide* Lull & Wright, 1942 *non* (Marsh, 1870)

E. regalis Lambe, 1917 (Type)
= *Trachodon atavus* Cope, 1871 [*nomen oblitum*]
= *Agathaumas milo* Cope, 1874 [*nomen oblitum*]
= *Claosaurus affinis* Wieland, 1903 [*nomen dubium*]
= *Trachodon affinis* (Wieland, 1903) [*nomen dubium*]

E. saskatchewanensis (C. M. Sternberg, 1926)
= *Thespesius saskatchewanensis* C. M. Sternberg, 1926
= *Anatosaurus saskatchewanensis* (C. M. Sternberg, 1926) Lull & Wright, 1942
= *Trachodon saskatchewanensis* (C. M. Sternberg, 1926)

NOTE: This is a paragenus because it is almost certainly ancestral to the genus *Anatotitan*.

Genus: *Gilmoreosaurus* Brett-Surman, 1979
= *Gilmoreosautus* Hu & Cheng, 1988 [*sic*]

G. mongoliensis (Gilmore, 1933) (Type)
= *Mandschurosaurus mongoliensis* Gilmore, 1933
= *Gilmoreosautus mongliensis* Hu & Cheng, 1988 [*sic*]
= *Manschurosaurus mongoliensis* Hu & Cheng, 1988 [*sic*]
= *Manschurosaurus monoliensis* Hu & Cheng, 1988 [*sic*]

Genus: *Gryposaurus* Lambe, 1914
= *Gryposourus* Langston, 1965 [*sic*]
= *Gryptosaurus* Maryanska & Osmólska, 1979 [*sic*]

G. notabilis Lambe, 1914 (Type)
= *Hadrosaurus notabilis* (Lambe, 1914)
= *Kritosaurus notabilis* (Lambe, 1914)
= *Trachodon marginatus* Lambe, 1902 [*nomen dubium*; in part]
= *Kritosaurus marginatus* (Lambe, 1902) [*nomen dubium*]
= *Thespesius marginatus* (Lambe, 1902) [*nomen dubium*]
= *Pteropelyx marginata* (Lambe, 1902) [*nomen dubium*]
= *Pteropelyx marginatus* (Lambe, 1902) [*nomen dubium*]*

Genus: *Hadrosaurus* Leidy, 1858
= *Hadrasaurus* C. H. Sternberg, 1909 [*sic*]
= *Hodeosaurus* Wu, 1985 [*sic*]
= *Ornithosaurus* Riabinin, 1930 [*sic*]
= *Ornithotarsus* Cope, 1869

H. foulkii Leidy, 1858 (Type)
= *Trachodon foulkii* (Leidy, 1858)
= *Ornithotarsus immanis* Cope, 1869
= *Hadrosaurus foulkei* Cope, 1870 [*sic*]
= *Hadrosaurus cavatus* Cope, 1871 [*nomen nudum*]
= *Trachodon cavatus* (Cope, 1871) [*nomen nudum*]
= *Hadrosaurus faulkii* Langston, 1960 [*sic*]

H. minor Marsh, 1870
= *Edmontosaurus minor* (Marsh, 1870)
= *Trachodon minor* (Marsh, 1870)

?*H. breviceps* Marsh, 1889
= *Kritosaurus breviceps* (Marsh, 1889)
= *Trachodon breviceps* (Marsh, 1889)

NOTE: The above species either belongs in the genus *Prosaurolophus* or represents a new genus (J. R. Horner, pers. comm.).

Genus: "Hironosaurus" Hisa, 1988 [to be described from Japan, based on a ?caudal vertebra; in *Utan Scientific Magazine* #4: 25]

Genus: *Hypsibema* Cope, 1869 [*nomen dubium*]
= *Hypsibaema* von Huene, 1909 [*sic*]
= *Neosaurus* Gilmore *vide* Gilmore & Stewart, 1945/Nopcsa, 1923
= *Parrasaurus* White, 1973 [*sic*]
= *Parrosaurus* Gilmore, 1945 [*nomen dubium*]

H. crassicauda Cope, 1869 (Type)

H. missouriense (Gilmore & Stewart, 1945) Baird & Horner, 1979 [*nomen dubium*]
= *Neosaurus missouriensis* Gilmore *vide* Gilmore & Stewart, 1945 [*nomen dubium*]
= *Parrosaurus missouriensis* (Gilmore *vide* Gilmore & Stewart, 1945) Gilmore, 1945 [*nomen dubium*]

NOTE: The syntypes of *Hypsibema crassicauda* include theropod material as well as ornithopod material; the lectotype caudal vertebra designated by Baird & Horner, 1979, however, represents an indeterminate large hadrosaurid that by direct comparison is a senior synonym of *Parrosaurus*. Baird & Horner referred *Hypsibema* to the Sauropoda, but this assignment is strongly questioned by J. S. McIntosh (pers. comm.) and M. K. Brett-Surman (pers. comm.). *Hypsibema* is retained as an indeterminate hadrosaurid in most recent dinosaur taxonomies (*e.g.*, Weishampel & Horner, 1990).

Genus: *Kritosaurus* Brown, 1910
  = *Krikotosaurus* de Lapparent, 1978 [*sic*]
  = *Kristosaurus* Young, 1958 [*sic*]
  = *Kritosaurs* Nagao, 1936 [*sic*]
  K. navajovius Brown, 1910 (Type)
    = *Hadrosaurus navajovius* (Brown, 1910)
    = *Kritosaurus navajovous* Stokes, 1988 [*sic*]

Genus: *Lophorhothon* Langston, 1960 (juvenile *Prosaurolophus*?)
  = *Lophorothon* Horner, 1979 [*sic*]
  = *Lophoroton* Maryanska & Osmólska, 1979 [*sic*]
  = *Lorphorhothon* Glut, 1972 [*sic*]
  L. atopus Langston, 1960 (Type)

Genus: *Maiasaura* Horner & Makela, 1979
  = *Maiasauria* Stokes, 1988 [*sic*]
  = *Maiasaurus* Browne, 1980 [*sic*; *New York Times* News Service, February 14, 1980]
  M. peeblesorum Horner & Makela, 1979 (Type)

Genus: *Mandschurosaurus* Riabinin, 1930 [*nomen dubium*]
  = *Manchurisaurus* Dong, 1979 [*sic*]
  = *Manchurosaurus* Nagao, 1936 [*sic*]
  = *Mandchurosaurus* Young, 1958 [*sic*]
  = *Mandschurisaurus* Dong, 1979 [*sic*]
  = *Mandschurosaus* Young, 1958 [*sic*]
  = *Mandshurosaurus* Young, 1958 [*sic*]
  = *Manschurosaurus* Hu & Cheng, 1988 [*sic*]
  M. amurensis (Riabinin, 1925) (Type)
    = *Trachodon amurensis* Riabinin, 1925 [*nomen dubium*]
    = *Trachodon amurense* Riabinin, 1925 [*nomen dubium*]*
    = *Thespesius amurensis* (Riabinin, 1925) [*nomen dubium*]
    = *Manschurosaurus amurensis* Hu & Cheng, 1988 [*sic*]
    = *Tracodon amurense* Hu & Cheng, 1988 [*sic*]
    = *Mandschurosaurus amwensis* [Anonymous] 1990 [*sic*]
  ?*M. laosensis* Hoffet, 1943 [*nomen dubium*]

NOTE: Recently discovered more complete material of this species indicates it is probably an iguanodontid rather than a hadrosaurid (reported by Taquet in *SVP Bulletin* #152).
  ?*M. jiainensis* Luo, Zhang & Li, 1983 [*nomen nudum*]

Genus: *Microhadrosaurus* Dong, 1979 [*nomen dubium*]
  M. nanshiungensis Dong, 1979 (Type)

Genus: *Orthomerus* Seeley, 1883 [*nomen dubium*]
  O. dolloi Seeley, 1883 (Type)
    = *Telmatosaurus dolloi* (Seeley, 1883)
  ?*O. weberi* Riabinin, 1941 [*nomen dubium*]

Paragenus: *Prosaurolophus* Brown, 1916
  P. maximus Brown, 1916
    = *Saurolophus maximus* (Brown, 1916)
  [New species to be described from the Upper Two Medicine Formation of Montana]
  NOTE: This is a paragenus because it is almost certainly ancestral to the genus *Saurolophus*.

Genus: *Saurolophus* Brown, 1912
  = *Sauralophus* Matthew, 1912 [*sic*]
  S. osborni Brown, 1912 (Type)
  ?*S. kryschtofovici* Riabinin, 1930 [*nomen dubium*]
  S. angustirostris Rozhdestvensky, 1952

Genus: *Secernosaurus* Brett-Surman, 1979
  S. koerneri Brett-Surman, 1979 (Type)

Genus: *Shantungosaurus* Hu, 1973
  = *Shantungsaurus* Gee, 1989 [*sic*]
  S. giganteus Hu, 1973 (Type)

Genus: *Tanius* Wiman, 1929
  = *Tsintaosaurus* Young, 1958
  = *Tsintaosourus* Young, 1958 [*sic*]
  T. sinensis Wiman, 1929 (Type)
    = *Cionodon kysylkumensis* Riabinin, 1931 [*nomen dubium*]
    = *Cionodon kysylkumense* Riabinin, 1931 [*nomen dubium*]*
    = *Thespesius kysylkumensis* (Riabinin, 1931) [*nomen dubium*]
    = *Trachodon kysylkumense* (Riabinin, 1931) [*nomen dubium*]

= *Tsintaosaurus spinorhinus* Young, 1958
= *Tanius chingkankouensis* Young, 1958

NOTE: Taquet (1991) indicates that the tall nasal spike observed in the type specimen of *Tsintaosaurus spinorhinus* is an artifact of preservation, and that the genus *Tsintaosaurus* is actually a junior synonym of the flat-headed hadrosaurid *Tanius*. Cranial and postcranial lambeosaurid material incorrectly referred to *Tsintaosaurus* in the original description probably belongs to a new or different genus (M. K. Brett-Surman, pers. comm.; Weishampel & Horner, 1990). *Tanius chingkankouensis* is likely based on a subadult individual of *Tanius sinensis*, while *Tanius laiyangensis* is a lambeosaurid that may be a species of that undescribed genus whose material was mixed in with *Tsintaosaurus* (Weishampel & Horner, 1990).

Genus: *Telmatosaurus* Nopcsa, 1903 (= *Orthomerus*?)
  = *Hecatasaurus* Brown, 1910
  = *Hecatosaurus* White, 1973 [*sic*]
  = *Hectasaurus* Nagao, 1936 [*sic*]
  = *Limnosaurus* Nopcsa, 1899/Marsh, 1872
  T. transsylvanicus (Nopcsa, 1899) (Type)
    = *Limnosaurus transsylvanicus* Nopcsa, 1899
    = *Hecatasaurus transsylvanicus* (Nopcsa, 1899)
    = *Orthomerus transsylvanicus* (Nopcsa, 1899)

Genus: *Thespesius* Leidy, 1856 [*nomen dubium*]
  T. occidentalis Leidy, 1856 (Type)
    = *Hadrosaurus occidentalis* (Leidy, 1856) [*nomen dubium*]
    = *Trachodon occidentalis* (Leidy, 1856) [*nomen dubium*]

Genus: [To be described]
  [Type species to be redescribed]
    = *Kritosaurus incurvimanus* Parks, 1920
    = *Kritosaurs incruvimanus* Nagao, 1936 [*sic*]

Genus: [To be described]
  [Type species to be redescribed]
    = *Kritosaurus australis* Bonaparte, Franchi, J. Powell & Sepulveda 1984
    = *Kritosaurus australis* Bonaparte, 1984 [*nomen nudum*]

Genus: [To be described]
  [Type species to be redescribed]
    = *Iguanodon hilli* Newton, 1892
    = *Craspedodon hilli* (Newton, 1892)
    = *Limnosaurus hilli* (Newton, 1892)
    = *Orthomerus hilli* (Newton, 1892)

Genus: [To be described from Baishin-Tsav, Mongolia; Kurzanov, 1976]

Genus: [To be described from the Senonian of Chubut, Argentina; reported as Paleocene by Casamiquela, 1964; Bonaparte, 1980]

Genus: [To be described from the Late Cretaceous Yacoraite Formation of Argentina; Bonaparte, 1980]

Genus: [To be described from the Oldman Formation of Alberta, Canada; a solid-crested hadrosaurid; D. Tanke, D. McInnes & P. Currie, pers. comm.]

Genus: [To be described from the St. Mary River Formation of Montana; Horner, 1983]

Genus: [To be described from the Lower Two Medicine Formation of Montana; Weishampel & Horner, 1990]

Genus: [To be described, based on material referred to *Hadrosaurus minor* by Colbert, 1948; Weishampel & Horner, 1990]

Genus: [To be described, based on material referred to *Hadrosaurus notabilis* by Horner, 1979; Weishampel & Horner, 1990]

Family: LAMBEOSAURIDAE von Huene, 1948

Census: 10 genera (2 doubtful), 19 species (6 doubtful)

= Cheneosauridae von Huene, 1956
= Cheneosaurinae Lull & Wright, 1942
= Lambeosaurinae Parks, 1923
= Stephanosaurinae Lambe, 1920
= Trachodontidae Brown, 1914

Genus: *Bactrosaurus* Gilmore, 1933
  = *Batractosaurus* Halstead, 1975 [*sic*]
  B. johnsoni Gilmore, 1933 (Type)

?*B. prynadai* Riabinin, 1937 [*nomen dubium*]
= *Tanius prynadai* (Riabinin, 1937) [*nomen dubium*]

NOTE: The name *Paraiguanodon incolapaludis*, coined by Barnum Brown in the early 1930s, perhaps for a lecture series, appears on figures of the skeleton of *Bactrosaurus johnsoni* in the files of the American Museum of Natural History.

The type material of *Bactrosaurus prynadai* is largely indeterminate and may include specimens from other genera.

Genus: *Barsboldia* Maryanska & Osmólska, 1981
B. sicinskii Maryanska & Osmólska, 1981 (Type)

Paragenus: *Corythosaurus* Brown, 1914
C. casuarius Brown, 1914 (Type) (male)
= *Hypacrosaurus casuarius* (Brown, 1914)
= *Corythosaurus excavatus* Gilmore, 1923 (female)
= *Corythosaurus intermedius* Parks, 1923 (female)
= *Tetragonosaurus erectofrons* Parks, 1931 (juvenile)
= *Procheneosaurus erectofrons* (Parks, 1931) (juvenile)
= *Corythosaurus bicristatus* Parks, 1935 (female)
= *Corythosaurus brevicristatus* Parks, 1935 (juvenile male)
= *Tetragonosaurus cranibrevis* C. M. Sternberg, 1935 (juvenile)
= *Procheneosaurus cranibrevis* (C. M. Sternberg, 1935) (juvenile)

NOTE: The assignment of synonymous species to presumed growth stages and sexes in the above genus is according to Dodson, 1975.

This is a paragenus because it is almost certainly ancestral to the genera *Lambeosaurus* and *Hypacrosaurus*.

Genus: *Hypacrosaurus* Brown, 1913
= *Cheneosaurus* Lambe, 1917
= *Cheneousaurus* Nagao, 1936 [*sic*]
= *Hypacrosaurs* Nagao, 1936 [*sic*]
= *Hypocrosaurus* C. M. Sternberg, 1953 [*sic*]
H. altispinus Brown, 1913 (Type)
= *Cheneosaurus tolmanensis* Lambe, 1917 (juvenile)
[New species to be described; D. Weishampel, pers. comm.]

NOTE: The assignment of synonymous species to presumed growth stages and sexes in the above genus is according to Dodson, 1975.

Genus: *Jaxartosaurus* Riabinin, 1937
= *Taxartosaurus* Riabinin, 1939 [*sic*]
= *Yaxartosaurus* Young, 1958 [*sic*]
J. aralensis Riabinin, 1937 (Type)
= *Yaxartosaurus aralensis* (Riabinin, 1937)
= *Procheneosaurus convincens* Rozhdestvensky, 1968 (juvenile)
J. fuyunensis Wu, 1984 [*nomen dubium* in Weishampel & Horner, 1990]
= *Yaxartosaurus fuyunensis* Wu, 1984* [*nomen dubium*]

Genus: *Lambeosaurus* Parks, 1923
= *Didamodon* von Huene, 1956 [*sic*]
= *Didanodon* Osborn, 1902
= *Procheneosaurus* Matthew, 1920 [*nomen conservandum*]
= *Stephanosaurus* Lambe, 1914 [*nomen dubium*]
= *Tetragonasaurus* Nagao, 1936 [*sic*]
= *Tetragonosauros* Parks, 1931 [*sic*]
= *Tetragonosaurus* Parks, 1931
L. lambei Parks, 1923 (Type) (male)
= *Hypacrosaurus lambei* (Parks, 1923) (male)
= *Trachodon marginatus* Lambe, 1902 [*nomen dubium*; in part]
= *Stephanosaurus marginatus* (Lambe, 1902) [*nomen dubium*]
= *Hadrosaurus paucidens* Marsh, 1889 [*nomen dubium*]
= *Ceratops paucidens* (Marsh, 1889) [*nomen dubium*]
= *Lambeosaurus paucidens* (Marsh, 1889) [*nomen dubium*]
= *Didanodon* Osborn, 1902 (no specific name assigned)
= *Trachodon altidens* Lambe, 1902 [*nomen dubium*]
= *Didanodon altidens* (Lambe, 1902) [*nomen dubium*]
= *Procheneosaurus altidens* (Lambe, 1902) [*nomen dubium*]

= *Pteropelyx altidens* (Lambe, 1902) [*nomen dubium*]
= *Thespesius altidens* (Lambe, 1902) [*nomen dubium*]
= *Procheneosaurus* Matthew, 1920 (no specific name assigned) (juvenile)
= *Tetragonosaurus praeceps* Parks, 1931 (juvenile)
= *Procheneosaurus praeceps* (Parks, 1931) (juvenile)
= *Corythosaurus frontalis* Parks, 1935 (juvenile female)
= *Lambeosaurus clavinitialis* C. M. Sternberg, 1935 (female)
L. magnicristatus C. M. Sternberg, 1935 (male)
= *Lambeosaurus magnicristatum* C. M. Sternberg, 1935* (male)
?*L. laticaudus* Morris, 1981

NOTE: The assignment of synonymous species to presumed growth stages and sexes in the above genus is according to Dodson, 1975.

Genus: *Nipponosaurus* Nagao, 1936
N. sachalinensis Nagao, 1936 (Type)

NOTE: The above genus is a juvenile lambeosaurid. Adult Asian lambeosaurid genera should be examined for possible synonymy.

Genus: *Parasaurolophus* Parks, 1922
= *Parasaurolophis* Stokes, 1988 [*sic*]
= *Parasaurophus* Nagao, 1936 [*sic*]
= *Parosaurolophus* C. M. Sternberg, 1946 [*sic*]
P. walkeri Parks, 1922 (Type) (male)
P. tubicen Wiman, 1931 (male)
P. cyrtocristatus Ostrom, 1961 (female)
= *Parasaurolophus cyrotocristatus* Stokes, 1988 [*sic*]

NOTE: The assignment of species to presumed sexes in the above genus is according to Dodson, 1975.

Genus: *Pteropelyx* Cope, 1889 [*nomen dubium*]
P. grallipes Cope, 1889 (Type)
= *Thespesius grallipes* (Cope, 1889) [*nomen dubium*]
= *Trachodon grallipes* (Cope, 1889) [*nomen dubium*]

NOTE: The above genus is based on a partial skeleton that cannot be distinguished from *Hypacrosaurus*, *Corythosaurus*, or *Lambeosaurus* because it lacks a skull (M. K. Brett-Surman, pers. comm.).

Genus: *Trachodon* Leidy, 1856 [*nomen dubium*]
= *Tracodon* Morris, 1978 [*sic*]
T. mirabilis Leidy, 1856 (Type)
= *Hadrosaurus mirabilis* (Leidy, 1856) [*nomen dubium*]
= *Trachodon mirabile* Nopcsa, 1917 [*sic*; may have been confused with *Diclonius mirabilis* Cope, 1876]
?*T. cantabrigiensis* Lydekker, 1888 [*nomen dubium*]
= *Hadrosaurus cantabrigiensis* (Lydekker, 1888) [*nomen dubium*]
= *Telmatosaurus cantabrigiensis* (Lydekker, 1888) Olshevsky, 1978 [*nomen dubium*]
?*T. selwyni* Lambe, 1902 [*nomen dubium*]
= *Gryposaurus selwyni* (Lambe, 1902) [*nomen dubium*]
= *Pteropelyx selwyni* (Lambe, 1902) [*nomen dubium*]
= *Thespesius selwyni* (Lambe, 1902) [*nomen dubium*]

NOTE: This genus may be a senior synonym of either *Prosaurolophus* or *Corythosaurus* (J. R. Horner, pers. comm.). If the type teeth are shown to be birooted, then it may prove to be ceratopsian (M. K. Brett-Surman, pers. comm.).

Genus: [To be described; to contain lambeosaurid material incorrectly referred to *Tsintaosaurus spinorhinus*, now synonymized with *Tanius sinensis*; see note for *Tanius*]
[Type species to be redescribed]
= *Tanius laiyangensis* Zhen, 1976

Genus: [To be described from the far-eastern USSR by Kurzanov & Bolotsky; indicated in *SVP Bulletin* #149, June, 1990 (p. 46) as already described, but paper not yet seen]

Genus: [To be described from the Upper Two Medicine Formation of Montana; Weishampel & Horner, 1990]

Genus: [To be described from the Judith River Formation of Alberta, Canada; a large lambeosaurid with a crest resembling that of *Procheneosaurus*; P. Dodson, pers. comm.]

Ornithischia incertae sedis

Census: 3 doubtful genera, 4 doubtful species

Genus: *Rhadinosaurus* Seeley, 1881 [*nomen dubium*]

R. alcinus Seeley, 1881 (Type)

= *Struthiosaurus alcinus* (Seeley, 1881) [*nomen dubium*]

= *Rhadinosaurus alcimus* Coombs, 1971 [*sic*]

= *Struthiosaurus alcimus* Coombs, 1971 [*sic*]

NOTE: This genus has been classified as an ankylosaurian and as an ornithopod, but it might also be synonymous with *Doratodon*, a crocodilian. Until further work is published, it will be left as an ornithischian *incertae sedis*.

Genus: *Thecospondylus* Seeley, 1882 [*nomen dubium*]

T. horneri Seeley, 1882 (Type)

NOTE: Generally classified as a theropod, this genus may be ornithischian (R. E. Molnar, pers. comm.).

Genus: *Tichosteus* Cope, 1877 [*nomen dubium*]

= *Thichosteus* Kuhn, 1965 [*sic*]

T. lucasanus Cope, 1877 (Type)

?T. aequifacies Cope, 1877 [*nomen dubium*]

NOTE: Generally classified as a theropod, this genus is probably ornithischian (R. E. Molnar, pers. comm.).

Notes and New Taxa

Excluded Taxa

The following genera and species have at one time or another been classified as non-crocodilian archosaurs but are presently regarded as outside that domain.

Genus: *Aachenosaurus* Smets, 1888 [*nomen dubium*]
A. multidens Smets, 1888 (Type)
NOTE: Originally classified as a hadrosaurid, the type specimen was shown by Dollo, 1888 to be petrified wood.

Genus: *Aggiosaurus* Ambayrac, 1913
A. nicaeensis Ambayrac, 1913 (Type)
= *Megalosaurus nicaeensis* (Ambayrac, 1913)
NOTE: The above genus was originally classified as a large theropod but is now considered a marine crocodilian (Buffetaut, 1982).

Genus: *Aidachar* Nessov, 1981
A. paludalis Nessov, 1981 (Type)
NOTE: Initially described as a pterosaur and later given its own family **Aidacharidae** Nessov, 1982, the above genus is now classified as an ichthyodectid fish (Nessov, 1982).

Genus: *Albisaurus* Fritsch, 1905 [*nomen dubium*]
A. scutifer Fritsch, 1905 (Type)
= *Iguanodon albinus* Fritsch, 1893 [*nomen dubium*]
NOTE: Originally classified as an iguanodontid, the type specimen is indeterminate and probably non-dinosaurian (J. S. McIntosh, pers. comm.).

Genus: *Anisodontosaurus* Welles, 1947
= *Anisodonsaurus* Romer, 1966 [*sic*]
A. greeri Welles, 1947 (Type)
NOTE: The above genus is frequently classified as a thecodontian *incertae sedis* but is probably a trilophosaurid (Charig & Reig, 1970).

Genus: *Arctosaurus* Adams, 1875 [*nomen dubium*]
A. osborni Adams, 1875 (Type)
NOTE: Sometimes considered to be a primitive saurischian dinosaur, the above genus may be a trilophosaurid (D. Baird, in Russell, 1984). The shape of the vertebral centrum of *Arctosaurus*, however, is unlike that of typical trilophosaurids (R. E. Molnar, pers. comm.).

Genus: *Bathygnathus* Leidy, 1854
B. borealis Leidy, 1854 (Type)
NOTE: The above genus has occasionally been classified as archosaurian, but it is most likely a sphenacodontid.

Genus: *Belonochasma* Broili, 1939
B. aenigmaticum Broili, 1939 (Type)
NOTE: Originally classified as a pterosaur (and even given its own family, **Belonochasmatidae** Young, 1964), the type specimen is now known to comprise part of an amiid fish (Mayr, 1973).

Genus: *Brasileosaurus* von Huene, 1931
B. pachecoi von Huene, 1931 (Type)
NOTE: The above genus has occasionally been classified as a thecodontian, but it is now considered to be a notosuchid crocodilian.

Genus: *Chienkosaurus* Young, 1942
= *Chienleosaurus* Colbert, 1961 [*sic*]
C. ceratosauroides Young, 1942 (Type)
NOTE: The above genus, frequently classified as a megalosaurid or ceratosaurid theropod, is based on four teeth, three of which are referable to the crocodilian *Hsisosuchus* and

the fourth to the theropod *Szechuanosaurus* (Dong Z., pers. comm.).

Genus: *Chigutisaurus* Rusconi, 1947
= *Icanosaurus* Rusconi, 1951
C. tunuyanensis Rusconi, 1947 (Type)
= *Icanosaurus rectifrons* Rusconi, 1951
= *Chigutisaurus tununyanensis* Reig, 1961 [*sic*]

NOTE: The postcranial skeleton of an erythrosuchid thecodontian was originally referred to this genus, which is based on a brachyopid amphibian skull, by Rusconi (1951) – an error corrected by Shishkin (1961). Tatarinov, (1961) referred the genus to *Erythrosuchus*, and then Reig (1961) independently erected the genus *Cuyosuchus* for the postcranial skeleton. Romer (1966) incorrectly synonymized *Icanosaurus* with *Cuyosuchus* – it is actually a synonym of the amphibian *Chigutisaurus*, as pointed out by Charig & Reig (1970) – and at the same time synonymized *Chigutisaurus* and *Icanosaurus* with the amphibian genus *Pelorocephalus* Cabrera, 1944. Shishkin (1987), however, has pointed out differences between *Chigutisaurus* and *Pelorocephalus* and considers them to be distinct amphibian genera.

Cetiosaurus rigauxi Sauvage, 1874

NOTE: The above species is indeterminate and almost certainly not a sauropod (J. S. McIntosh, pers. comm.).

Genus: *Colonosaurus* Marsh, 1872
C. mudgei Marsh, 1872 (Type)

NOTE: The above genus has occasionally been classified as a small theropod dinosaur, but the type specimen is actually a portion of the type specimen of the bird *Ichthyornis dispar* (Feduccia, 1980).

Ctenosauriscus rugosus (von Huene, 1902)
= *Ctenosaurus rugosus* von Huene, 1902

NOTE: The above species is referable to the dissorophid amphibian genus *Platyhystrix* (D. Baird, pers. comm.).

Genus: *Doratodon* Seeley, 1881
= *Diratodon* von Huene, 1909 [*sic*]
D. carcharidens (Bunzel, 1871) (Type)
= *Crocodilus carcharidens* Bunzel, 1871

NOTE: Occasionally classified as a theropod, the above genus is actually a mesosuchian crocodilian.

Genus: *Elachistosuchus* Janensch, 1949
E. huenei Janensch, 1949 (Type)

NOTE: The above genus, originally classified as a pseudosuchian thecodontian, was reclassified as a rhynchosaur by Walker, 1966. It was given its own family **Elachistosuchidae** in von Huene, 1956.

Genus: *Elopteryx* Andrews, 1913
E. nopcsai Andrews, 1913 (Type)

NOTE: The above genus, occasionally referred to as a possible synonym of *Heptasteornis andrewsi* in Paul, 1988, is possibly a pelecaniform bird (Grigorescu & Kessler, 1980).

Genus: *Ephoenosaurus* [Anonymous] 1839 [*nomen nudum*]
E. solodurensis [Anonymous] 1839 (Type)
= *Ephoenosaurus gracilis* [Anonymous] 1839

NOTE: The above possibly dinosaurian genus and two included species appeared in the *Allgemeine Schweizer Zeitschrift*, Volume 11, p. 344. R. Wild (pers. comm.) speculates that the "bone fragment of unusual size," found by a Dr. Hugi, in the newspaper account may have become the type specimen of the crocodilian *Machimosaurus*, which Hugi discovered.

Genus: *Eupodosaurus* Boulenger, 1891
E. longobardicus Boulenger, 1891 (Type)

NOTE: Originally classified as a stegosaur, the above genus was synonymized with the nothosaurid genus *Lariosaurus* by von Huene, 1914.

Genus: *Gobipteryx* Elzanowski, 1974
G. minuta Elzanowski, 1974 (Type)

NOTE: Originally described as avian, the above genus has been referred on occasion to the Theropoda. It is presently considered to be the only known gobipterygiform bird (see, *e.g.*, Carroll, 1987).

Genus: *Gwyneddosaurus* Bock, 1945 [*nomen dubium*]
G. erici Bock, 1945 (Type)

NOTE: Originally classified as a small theropod, the above genus was subsequently classified as an askeptosaurid prolacertilian by von Huene, 1956. Olsen & Flynn, 1989, however, have determined that the type specimen is a mixture of *Tanytrachelos* (a tanystropheid) remains and coelacanth scrap.

Hadrosaurus tripos Cope, 1869
  = *Trachodon tripos* (Cope, 1869)
  NOTE: The above species is based on the partial skeleton of a Pliocene whale (Baird & Horner, 1979).

Genus: *Heleosaurus* Broom, 1907
  H. scholtzi Broom, 1907 (Type)
  NOTE: Generally considered to be an eosuchian, this genus is classified as Thecodontia *incertae sedis* by Carroll (1988), who considers it a possible early archosaur.

Genus: *Laornis* Marsh, 1870
  L. edvardsianus Marsh, 1870 (Type)
  NOTE: Originally described as avian, the above genus has on occasion been referred to the Pterosauria, but a recent restudy by S. Olson indicates it is a charadriiform bird.

Genus: *Macelognathus* Marsh, 1884
  = *Macellognathus* von Huene, 1956 [*sic*]
  = *Marcellognathus* Romer, 1966 [*sic*]
  M. vagans Marsh, 1884 (Type)
  NOTE: Originally classified in its own reptilian order and considered on occasion to be a small dinosaur, the above genus is now placed in its own crocodilian family (Ostrom, 1961).

Megalosaurus mersensis de Lapparent, 1955
  NOTE: This species of *Megalosaurus* is based on three teeth and 23 vertebrae that are now thought to belong to a teleosaurid crocodilian (Chabli, 1985).

Megalosaurus schnaitheimii Bunzel, 1871
  NOTE: This species is probably a metriorhynchid crocodilian (R. E. Molnar, pers. comm.).

Palaeosauriscus sternbergii (Fitzinger, 1843) [*nomen nudum*]
  = *Palaeosaurus sternbergii* Fitzinger, 1843 [*nomen nudum*]
  NOTE: The above species may belong to the crocodilian genus *Palaeosaurus* Geoffroy Saint-Hilaire, 1833 and not the thecodontian genus *Palaeosauriscus* Kuhn, 1959, but because it is a *nomen nudum*, this question cannot be decided. It has also been suggested in the literature that it is a captorhinomorph (R. E. Molnar, pers. comm.).

Genus: *Pneumatoarthrus* Cope, 1870
  = *Pneumatarthrus* Cope, 1872 [*sic*]
  P. peloreus Cope, 1870 (Type)
  NOTE: Baird, 1978, conclusively demonstrated that the above genus, originally described as dinosaurian but subsequently referred, on occasion, to the Chelonia, is actually a protostegid turtle and could well be a senior synonym of the genus *Archelon*.

Genus: *Procerosaurus* von Huene, 1902
  P. cruralis von Huene, 1902 (Type)
  NOTE: The above genus, sometimes classified as ornithischian, is based on a femur of the prolacertilian *Tanystropheus conspicuus* (von Huene, 1910; see Wild, 1973).

Genus: *Rhabdopelix* von Huene, 1921 [*nomen dubium*]
  R. longispinis (Cope, 1869) (Type)
    = *Pterodactylus longispinis* Cope, 1869 [*nomen dubium*]
  NOTE: The type specimen of the above genus, now lost, is composite, but the most diagnostic portions appear to be referable to *Icarosaurus siefkeri*, a species of gliding lacertilian (Colbert, 1966; D. Baird, pers. comm.). Olsen & Flynn, 1989, regard some of the remains of the type specimen as referable to the tanystropheid *Tanytrachelos*.

Genus: *Stenaulorhynchus* Haughton, 1932
  S. stockleyi Haughton, 1932 (Type)
  NOTE: Referred to the Thecodontia in its own family **Stenaulorhynchidae** Kuhn, 1933, the above genus is presently considered to be a rhynchosaur.

Genus: *Stereosaurus* Seeley, 1869 [*nomen dubium*]
  S. platyomus Seeley, 1869 (Type)
  S. cratynotus Seeley, 1869 [*nomen dubium*]
  S. stenomus Seeley, 1869 [*nomen dubium*]
  NOTE: The above genus and its three species have been mentioned as possible dinosaurs

(Olshevsky, 1978), but they are probably plesiosaurian (J. S. McIntosh, pers. comm.).

Genus: *Succinodon* von Huene, 1941
S. putzeri von Huene, 1941 (Type)
NOTE: Said to be based on sauropod teeth, this genus is now thought to consist of filled borings of bivalve molluscs of the genus *Kuphus* (Pozaryska & Pugaczewska, 1981).

Genus: *Sultanuvaisia* Nessov, 1981
S. antiqua Nessov, 1981 (Type)
NOTE: Initially classified as a pterosaur and later placed in the family Aidacharidae Nessov, 1982, the above genus is now classified as an ichthyodectid fish (Nessov, 1982).

Genus: *Tanystropheus* von Meyer, 1855
= *Tanistropheus* Alberti, 1864 [*sic*]
= *Tanystrophaeus* Cope, 1888 [*sic*]
= *Tanystrophyaeus* von Huene, 1914 [*sic*]
= *Tranystropheus* Wild, 1980 [*sic*]
T. conspicuus von Meyer, 1855 (Type)
and others...
NOTE: The above genus, containing much material previously classified as archosaurian, is actually prolacertilian. For a list of species and synonymies within this genus, see Wild, 1973.

Genus: *Tapinosaurus* Lennier, 1887 [*nomen nudum*]
No type species named
NOTE: The name of this genus, in a caption to a figure of fragmentary but large remains from the Kimmeridgian of Normandy, is probably a misspelling of *Tapinocephalus*, a therapsid. Classified as Sauropoda *incertae sedis* in Steel, 1970, the figured remains, as well as other specimens referred to this genus by Rabeck (1923), are probably plesiosaurian (R. E. Molnar, pers. comm.; Buffetaut, Cuny & Le Loeuff, 1991).

Thecodontosaurus latespinatus von Huene, 1908
= *Thecodontosaurus latespinatus* von Huene, 1905 [*nomen nudum*]
NOTE: The above species is a junior synonym of the prolacertilian *Tanystropheus conspicuus* (Wild, 1973).

Thecodontosaurus primus von Huene, 1908
= *Thecodontosaurus primus* von Huene, 1905 [*nomen nudum*]
NOTE: The above species is a junior synonym of the prolacertilian *Tanystropheus antiquus* (Wild, 1973).

Genus: *Tribelesodon* Bassani, 1886
T. longobardicus Bassani, 1886 (Type)
NOTE: Thought to be a Triassic pterosaur by Zittel, 1890 and others, the above genus is referable to the prolacertilian genus *Tanystropheus* (Wild, 1973).

Genus: *Unicerosaurus* Armstrong, 1987 [*nomen nudum*]
No type species designated
NOTE: The above genus is mentioned in an article (J. R. Armstrong, 1987: *Creation/Evolution Newsletter* 7(5): p. 21) debunking an exhibition in a creationist "museum" (a trailer, called the Creation Evidences Museum, operated by the Rev. Dr. Carl Baugh). The name appears on the label of an exhibited fossil bone said to be a dinosaur horn that could "be folded back like a jack knife blade." Armstrong speculates that the specimen is actually a fin spine of a huge fish, such as *Portheus*.

Genus: *Wyleyia* Harrison & C. A. Walker, 1973 [*nomen dubium*]
W. valdensis Harrison & C. A. Walker, 1973 (Type)
NOTE: Originally classified as avian, this genus has been considered to be a small theropod (Brodkorb, 1978; Olshevsky, 1979; Feduccia, 1980). It may now be classified as an enantiornithid bird (R. E. Molnar, pers. comm.), although it is still listed as an indeterminate theropod in Norman, 1990.

Genus: *Yezosaurus* Obata & Muramoto, 1977 [*nomen nudum*]
Y. mikasaensis Obata & Muramoto, 1977 (Type)
NOTE: Appearing without description in a short article on theropod dinosaurs, the specimen identified by the above generic and specific names is apparently mosasaurian (D. Chure, pers. comm.).

References

THE FOLLOWING REFERENCES pertain solely to the introductory textual sections. To provide references for *each* individual taxon in the archosaur list would more than double this book's size (and production costs) but would just duplicate information readily available elsewhere. In most cases, specifying author and year of a taxon manageably restricts the time required to locate the reference in standard bibliographies. For dinosaurs, I strongly recommend Chure & McIntosh's monumental dinosaur bibliography (1989) and the enormous bibliographic section of the landmark volume *The Dinosauria* (Weishampel, Dodson & Osmólska, eds., 1990). For pterosaurs, the footnote references in the superlative semipopular study by Wellnhofer (1991) provide an excellent entry into the literature. References to the remaining archosaurs may be found in the bibliography sections of Charig, Krebs, Sues & Westphal, 1976 and Benton, ed., 1988. Of course, references to some of the taxa in the table can be found among the works listed here.

In the rush of preparing the first printing of this work in time for the 1991 SVP annual meeting, it was impossible for me to ensure that all textual citations were included below. My apologies to authors whose works may thus have been inadvertently omitted; any necessary corrections will appear in subsequent printings.

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