

Saurischian Monophyly and the Origin of Birds

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And if the whole hind quarters from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified, and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us from referring them to the Dinosauria.

T. H. Huxley 1870a

INTRODUCTION

The origin of birds has long been of interest to evolutionary biologists. Darwin and his colleagues were well aware of the problem presented by the "embarrassing gap" between birds and other amniotes (Desmond 1984). Indeed, because birds appear so different from other tetrapods, it could be argued that next to the question of the origin of man, that of the origin of birds was one of the most serious impediments to a general acceptance of Darwin's concept of the transmutation of species. The precise relationships of birds remain controversial, although the hypothesis that birds are archosaurs is now widely accepted. One of the goals of this report is to show that this controversy has much less to do with the evidence than it does with philosophical issues regarding interpretations of the evidence. I believe that the simplest and most interesting interpretation of the limited evidence available to T. H. Huxley and his contemporaries was that birds are part of Dinosauria. One would have hoped that work subsequent to Huxley's would have been directed towards determining the precise position of birds within dinosaurs. However, for reasons that will be discussed below, this was not to be the case. In fact, Huxley's views on bird origins were largely abandoned for much of the twentieth century, and the phylogenetic relationships of birds remain a persistent controversy.

Among current hypotheses for the relationships of birds among amniotes, only three have been supported by shared apomorphies and thus can be considered legitimate hypotheses in a phylogenetic context. Simply stated, these hypotheses are: 1) birds are the sister-group of mammals; 2) birds are the sister-group of crocodiles; and 3) birds are dinosaurs. The last two hypotheses agree that birds are archosaurs. The third could be divided into competing subhypotheses regarding the precise position of birds within Dinosauria, but this need not concern us. The first two hypotheses will be briefly reviewed below, along with a summary of the history of the third alternative, the principal focus of this paper.

Early workers suggested hypotheses, such as that birds were derived from early pterosaurs (Owen 1875; Seeley 1881), or from "lizards"¹ (Vogt 1879, 1880), or from "thecondonts" (Broom 1913). These and other hypotheses of their kind are ill-advised

because they violate a basic tenet of evolutionary theory; as Michael Ghiselin put it (pers. comm.), "only species speciate, genera do not generate." Leaving aside the objection to the idea that higher taxa can act as ancestors in the usual sense, these hypotheses suffer for other reasons.

The pterosaur-bird hypothesis never received much attention, and the bird-"lizard" proposition deservedly received even less in that it was based entirely on plesiomorphic resemblances (such as sharing a long tail). In light of current knowledge, many apomorphies shared by birds and pterosaurs are most parsimoniously interpreted as convergences, which explains why the similarities between birds and pterosaurs are seldom either detailed or general to both taxa. However, the analysis below reveals some evidence that could be interpreted as supporting a somewhat modified version of Owen and Seeley's hypothesis: namely, that pterosaurs might be most closely related to theropods as a whole and thus to the subgroup of theropods including birds. Martin (1983a:111) cited *Scleromochlus* as sharing "a remarkably high percentage of the features suggested to relate birds to coelurosaur." Martin evidently was unaware that Huene (1914a, 1948, 1956) thought that *Scleromochlus* might be related to pterosaurs. A more explicit restatement of Huene's hypothesis, including additional corroborating evidence, may be found in Gauthier (1984) and Padian (1984).

The Thecodont-Bird Hypothesis

One of the oldest and most popular hypotheses for the origin of birds has been that they evolved from "pseudosuchians" (hereinafter referred to as the "thecondont" ancestry hypothesis). "Pseudosuchians" comprise a basal group within the basal group of archosaurs, the "thecondonts," from which all other archosaurs, including birds, are supposed to have evolved. This hypothesis has been the chief rival of the dinosaur hypothesis for much of the twentieth century. The "thecondont" ancestry hypothesis was proposed by workers who were impressed with two main objections to the dinosaur hypothesis: 1) "dinosaurs" were either morphologically too specialized or stratigraphically too late to have given rise to birds; 2) convergence could explain equally well the similarities shared by "dinosaurs" and birds.

The first objection is not without merit, but it addresses only part of the issue. It emphasizes the dearth of evidence for direct filial relations of birds among dinosaurs, but it ignores the abundant evidence supporting common ancestry. (Just because one's cousins are not one's ancestors does not mean that one is not related to them.)

The second objection to the dinosaur hypothesis is more sub-

¹ The use of quotation marks around a group name means that in this context that group is paraphyletic. Paraphyletic groups include an ancestor and some (but not all) of its descendants (e.g., "mammals" without humans, or "lizards" without snakes, which are more closely related to some "lizards" than other "lizards" are). Monophyletic groups include an ancestor and all of its descendants, and these are the only kinds of groups that are considered legitimate for phylogenetic analysis.

tle than the first but is equally misguided. It is possible that birds and "dinosaurs" are convergent on one another because of their bipedal habits, but this is not the same as having evidence to support such a claim. Simply invoking the possibility of convergence is not enough (e.g., Charig 1976a, b). Both homology and homoplasy are deductive concepts contingent upon accepting one of several phylogenetic hypotheses (Rieppel 1980); the apomorphies supporting the preferred hypothesis are considered synapomorphies and those supporting alternatives are considered nonhomologous (e.g., convergent). Thus, without an alternative hypothesis of relationship, it is not possible to recognize convergence. Moreover, one must accept a shared apomorphy as a potential synapomorphy; to assume otherwise at the outset simply makes the convergence argument invulnerable to test.

For example, one is able to reject the proposition that two taxa possessing an apomorphic, mesotarsal ankle joint shared a more recent common ancestor within Archosauria; one need only observe that a newly discovered sister-taxon of either one of these mesotarsal archosaurs displays the ancestral condition (assuming no reversals). Indeed, both the convergence and homology propositions would agree on the significance of finding a member of the ingroup with the ancestral condition (i.e., convergence). However, if one simply asserts that the mesotarsal condition arose convergently, this proposition would be immune to new data; that is to say, no matter how many times newly discovered members of the ingroup were found to possess mesotarsal joints, one could still say that the crucial fossil (i.e., the unknown common ancestor) with the ancestral condition has yet to be found. There is only one simple and informative explanation for the mesotarsal joints of the birdlike archosaurs, and that is homology. There is, however, no limit to how complex an alternative explanation might be; taken to its logical extreme, it might as well be argued that all 9,000 species of birds acquired their mesotarsal ankles convergently.

By the early twentieth century an apparent alternative, the hypothesis of "thecodont" origins, became fashionable, and accepting this thesis required accepting the convergence argument. The two objections listed above may have set the stage for acceptance of the "thecodont" origins hypothesis, but broad acceptance of this idea arose with the description of one of the earliest and most generalized archosaurs, *Euparkeria capensis*. Broom (1913) and Heilmann (1926) then had an archosaur that was so ancient and primitive that it enabled them to derive birds directly from such a stage in archosaur evolution without having to pass through dinosaurs.

If in fact birds were so related, then one would expect to find evidence that all dinosaurs shared a more recent common ancestor with one another than any of them did with birds. Heilmann (1926) may have recognized this necessity, because he noted that the dinosaurs then known lacked clavicles. This suggested that birds, which have clavicles, were plesiomorphic compared to dinosaurs in this respect, and must have diverged from other, more primitive archosaurs that retained clavicles. The single piece of evidence supporting the "thecodont" origins hypothesis was refuted in 1936 when clavicles were found in nonavian dinosaurs (see Part IV, character 58).

More importantly, the great weight of evidence marshalled by Heilmann (1926) provides clear evidence that birds are theropod dinosaurs. That is to say, even if Heilmann were correct in concluding that nonavian dinosaurs lacked clavicles, the weight

of his evidence still favored the thesis that birds are dinosaurs. Heilmann ultimately rejected the evidence favoring the dinosaur hypothesis and concluded instead that birds diverged from other archosaurs prior to the origin of dinosaurs. Heilmann's decision appears to have been predicated on a strict interpretation of Dollo's law of the irreversibility of evolution. Granted, one would not expect a hummingbird to evolve back into *Archaeopteryx*, especially by exactly reversing the historical sequence leading from the latter to the former, but one stretches the point by concluding that if clavicles were lost then they could never be regained.

The inadequacies of the "thecodont" ancestry hypothesis are most clearly seen in its claim that birds arose from an unknown member of "Thecodontia." From a phylogenetic perspective, "Thecodontia" and Archosauria are diagnosed by the same synapomorphies. Thus, these taxa are redundant, and when one says that birds evolved from "thecodonts" one is simply reiterating that birds are part of Archosauria. To say that birds are archosaurs would be true regardless of whether or not they were most closely related to crocodiles, pterosaurs, ornithischians, or any other monophyletic group within archosaurs. Thus, the "thecodont" ancestry hypothesis cannot be considered a legitimate alternative to the mammal-bird, crocodile-bird, or dinosaur hypotheses. Moreover, the "thecodont" ancestry hypothesis is a red herring that has served to deflect interest in and examination of the legitimate hypotheses of bird origins.

For example, as recently as 1980, Tarsitano and Hecht argued that birds were derived from "advanced thecodonts" that lacked dermal armor and had a birdlike ankle joint. In fact, these and other attributes apply to *Lagosuchus*, pterosaurs, and all dinosaurs, including birds (see Appendix A). Tarsitano and Hecht's (1980:176, fig. 9) cladogram correctly depicted birds as part of this group, but it also made other claims that were unsupported by evidence. For example, their "Theropoda" and other "Saurischia" were shown to be most closely related within this group, with *Lagosuchus* as their sister-group, and birds as the sister-taxon of the *Lagosuchus*-"saurischian" group. With the exception of birds, however, they failed to diagnose these taxa and thus support their conclusions. A more accurate depiction of their results would have been a cladogram with an unresolved multichotomy from the level at which the characters "mesotarsus" and "unarmored" arose. This would have established that "thecodonts" are a paraphyletic group, and that birds are part of the unarmored, mesotarsal group of archosaurs. One is still left with the possibility that birds are more closely related to some members of this group than they are to others. Rather than address this issue, however, Tarsitano and Hecht (1980:177) opted instead to "await better thecodont material and studies." In so doing, they provided an example of how the use of paraphyletic groups as ancestors can deflect interest from evidence relevant to hypotheses of common ancestry.

In conclusion, because the "thecodont" ancestry hypothesis is at best redundant and at worst a red herring, I recommend that it be ignored by future workers; discovering phylogenetic relationships among the birdlike archosaurs is difficult enough without the further obfuscation afforded by relying on paraphyletic groups as ancestors.

The Mammal-Bird Hypothesis

According to Desmond (1975, 1979, 1984), Owen (1841) used Lamarck's three criteria of nervous, respiratory, and vascular

organization to argue that dinosaurs, like birds and mammals, ascended to the physiological heights on Nature's ladder. Owen could hardly have been driven to such a conclusion by the scant remains of the three dinosaurs then known. Indeed, Desmond argued that by raising these huge saurians to ordinal status, Owen could argue that the "reptilian type" had long ago reached its apex, and that it had subsequently "degenerated into a sorry swarm of lizards" (Desmond 1984:119). Thus, Owen's Dinosauria depended less on evidence than on his abhorrence of Progressivism; his ulterior motive in recognizing the taxon was "to add one more nail to the transmutationist coffin" (Desmond 1979:233).

Owen's hypothesis received little attention in the post-Darwinian era, but it has been revived recently by Gardiner (1982). I will not here offer an extensive criticism of Gardiner's work, which dealt with tetrapod phylogeny in general and not just with the relationships of birds. Rather, I will confine myself to more general criticisms and let the evidence discussed below speak to Gardiner's (1982:227) claim that the "detailed correspondence between mammals and birds far outweighs" synapomorphy schemes supporting alternative hypotheses.

Gardiner intended to discover the relationships of "various living tetrapod groups . . . to one another" (1982:208) through "consistent patterns of derived characters" (1982:228). His actual effort was somewhat less ambitious, however, for he reviewed only that evidence consistent with the conclusions of some pre-Darwinian comparative anatomists. Moreover, he appears to have overlooked much of the evidence pertinent to tetrapod classification gathered by comparative biologists in the post-Darwinian era. Leaving aside these oversights, and certain misinterpretations of the evidence, Gardiner must be applauded for summarizing the apomorphies shared by mammals and birds that are absent in other extant amniotes; his hypothesis at least marshalled evidence in an explicitly phylogenetic context, unlike the case of the "thecodont" ancestry hypotheses.

In view of Gardiner's sedulous pursuit of apomorphies shared by mammals and birds, it is curious that he uncovered only four shared apomorphies—the form of the heart, aortic arches, occipital condyle, and pattern of temporal fenestration—that might contradict his hypothesized close relationship between mammals and birds. As Gardiner's sources for this evidence reveal, however, his search for contrary evidence came to a virtual halt at the beginning of the twentieth century. Moreover, Gardiner claimed that he was unable to find a single unique feature shared by dinosaurs and birds (1982:222). In view of the evidence presented below, which summarizes only part of the relevant information already in the literature, it is difficult to comprehend his failure in this endeavor. Perhaps the problem resides in Gardiner's use of the term "unique"? But this cannot be the case because if one accepts the mammal-bird hypothesis, then endothermy is unique, but if one accepts an alternative, such as the crocodile-bird hypothesis, then endothermy is not unique. Thus, the term "unique" as used by Gardiner reflects a conclusion, rather than an observation, and it cannot be a complete explanation of his oversight.

Perhaps Gardiner, like Owen, pursued the question of avian relationships with an ulterior motive. By virtually ignoring evidence determinable in both fossil and Recent taxa, and by stressing instead only part of the evidence determinable exclusively in extant forms, Gardiner may have revealed his intent: he was considerably less interested in reviewing all the evidence than

in chastizing post-Darwinian paleontology for what he viewed as its excessive influence on our views of tetrapod phylogeny. If Gardiner had been more faithful to his avowed goals as a comparative biologist, he would have made a more complete survey of the literature upon which the evidentiary basis of the traditional view rests. The evidence supporting the traditional view that birds are archosaurian diapsids is reason enough to understand why comparative biologists have long held that, although birds and mammals are "warm in the palm of the hand," their immediate common ancestor among amniotes was not.

The Crocodile-Bird Hypothesis

Few have doubted that birds and crocodiles are one another's nearest relatives among extant amniotes. But Walker (1972, 1974, 1977) went further by claiming that birds and crocodiles were most closely related even within archosaurs. Walker (pers. comm.) subsequently rejected this hypothesis in favor of the theropod dinosaur hypothesis, but the crocodile-bird hypothesis has received further attention from Whetstone and Martin (1979, 1981), Martin, Stewart, and Whetstone (1980), and Martin (1983a). Martin (1983a) listed thirty characters that had been used to support the crocodile-bird hypothesis, but he accepted Tarsitano and Hecht's (1980) argument that nearly half of them are plesiomorphic resemblances. Among the characters that he did not reject owing to obvious plesiomorphy are the following.

- 1) Bipartite quadrate articulation, with apomorphic attachments anteriorly with the prootic and laterosphenoid and posteriorly with the prootic (in that the quadrate cotylus lies at the anterior base of the parocciput);
- 2) Fenestra pseudorotundum carrying the perilymphatic duct;
- 3) Foramen aereum in mandible;
- 4) Periotic pneumatic cavities in dorsal, central, and rostral positions;
- 5) Two pneumatic cavities surrounding the cerebral carotid arteries;
- 6) Pneumatic quadrate;
- 7) Unserrated teeth;
- 8) Tooth crowns short, bluntly conical, and with triangular profile;
- 9) Constriction between crowns and roots of teeth;
- 10) Expanded bony root covered with cementum and connected to jaw by periodontal ligaments;
- 11) Oval or round resorption pit;
- 12) Replacement tooth tilts labially and its main development takes place within the pulp cavity of its predecessor;
- 13) Teeth implanted in open groove at least in young individuals; and
- 14) Lingual walls and septa of major tooth-bearing bones formed by extensions of dense bone.

With the possible exception of a foramen aereum, at least some of the pneumatic sinuses in the skull, and characters 10, 13, and 14 among those related to tooth-form and implantation, these characters do not appear to have been present in Archosauria ancestrally. I have observed a foramen aereum in the carnosaur theropods *Tyrannosaurus* and *Albertosaurus* in a form essentially identical to that of extant birds (and unlike that of crocodylians). Other archosaurs are reported to have a crocodilelike foramen aereum. For example, Wellnhofer (1985) has

reported it in pterosaurs and J. Clark (pers. comm.) has observed this structure in the archaic archosaur *Euparkeria*. Thus, the distribution of this character among archosaurs indicates that it may be the ancestral condition. However, L. Witmer (pers. comm.) notes that this foramen is absent in *Deinonychus*. Further examination of other archosaurs must be undertaken to determine the level of synapomorphy, and subsequent history, of this character.

Martin (1983a) noted that the fenestra pseudorotundum in birds and crocodiles can be distinguished on developmental novelties from analogous structures that evolved independently in mammals on the one hand and squamates on the other (see Gauthier, Estes, and de Queiroz, in prep.). Identification of a fenestra pseudorotundum in fossils is complicated by the absence of soft anatomical and developmental evidence, and one is left only with such evidence as can be inferred from the bony cranium and endocasts. Unfortunately, there are few well prepared braincases preserved in a way that could provide an unambiguous conclusion regarding its presence or absence among archosaurs. According to Walker (1972, 1974, 1977, pers. comm.), fenestra pseudorotunda are absent in the extinct relatives of crocodylomorphs, the aetosaurs and parasuchians, so this fenestra appears to be absent in Archosauria ancestrally. However, Raath and Walker (pers. comm.) identified a fenestra pseudorotundum in the theropod *Syntarsus*. I have observed a small fenestra in the same part of the ear region that might be the fenestra pseudorotundum in another member of the *Syntarsus* clade, *Dilophosaurus* (see Ceratosauria below). This structure also appears to be present in one carnosaur, *Acrocanthosaurus*, although it is said to be absent in the carnosaur *Tyrannosaurus* (Whetstone and Martin 1979, 1981). However, L. Witmer (pers. comm.) also examined *Tyrannosaurus* and concluded that the fenestra pseudorotundum was present. Witmer and Martin (pers. comm.) used different criteria for recognition of this character, so further study will be necessary to resolve this issue. Fenestra pseudorotunda are also reported in troodontid, ornithomimid, and caenagnathid theropods (e.g., Barsbold 1983; Currie 1986a, b), all of which appear to be closer to birds than are either *Syntarsus-Dilophosaurus* or carnosaur (see Coelurosauria below). Whetstone and Martin (1981) questioned these identifications, and not without reason, for it is difficult to distinguish this fenestra from others connected to the more (e.g., caenagnathid) or less (e.g., ornithomimid) extensive periotic pneumatic cavities in the crania of these theropods. Whetstone and Martin (1979, 1981) were unable to identify a fenestra pseudorotundum in an ankylosaur ornithischian or in hadrosaurian ornithopod ornithischians. However, Sues (1980) and Galton (1983) claimed that it was present at least in ornithopods ancestrally. Thus, there appears to be some question regarding the level(s) at which this synapomorphy arose within Archosauria. Finally, characters 1, 2, 4, 5, 9, and 13 do not appear to support an exclusive relationship between crocodiles and birds within Archosauria, because Currie (1986a, b) has recorded their presence in the theropod *Troodon* (= *Stenonychosaurus*).

Martin (1983a) noted that no one has argued that the ancestry of birds lies within crocodiles, only that they both share an "unknown common ancestor." Martin (1983a:111) argued that the crocodylomorph *Sphenosuchus* is not "as similar to birds as is the Crocodilia"; the common ancestor of birds and croc-

odiles, as so proposed, must lie within Crocodylomorpha. Unfortunately, this relationship has not been made explicit; birds have yet to be placed within a cladogram depicting their precise relationship among crocodylomorphs. Such an analysis must eventually be undertaken by the proponents of the crocodile-bird hypothesis in order to make their hypothesis more amenable to test. For example, in a preliminary phylogenetic analysis of crocodiles and their extinct relatives, Crocodylomorpha was diagnosed by 13 synapomorphies (Gauthier 1984). Of these, only 7 are present in birds, indicating that if birds are crocodylomorphs, the former diverged from within the latter after the acquisition of the first seven shared apomorphies but before the remaining 6 crocodylomorph characters appeared. Moreover, the 14 additional characters diagnostic of true crocodiles within Crocodylomorpha must have evolved later still. This raises questions regarding Martin's interpretations of the level of synapomorphy of several characters, among them being the characters in tooth form and implantation cited above. That is to say, the tooth form unique to crocodiles appeared within crocodylomorphs only after the evolution of an anterodorsally inclined quadratojugal that extends to the skull roof, a partial secondary palate formed by the maxillae, loss of the ventral process of the squamosal, loss of clavicles, ventromedial elongation of the coracoid, and development of a characteristic wrist joint involving an elongate and columnar radiale and ulnare. However, some crocodylomorphs, such as *Terrestriuchus* (Crush 1984), possess all six of the characters listed above in addition to those shared by birds and other crocodylomorphs, indicating that it is closer to true crocodiles than are birds. The problem emerges in the presence of sharply pointed, serrated teeth in *Terrestriuchus* that appear to be implanted and replaced as in Archosauria ancestrally. If, as these data suggest, *Terrestriuchus* and true crocodiles are closer to one another than either is to birds, then the dental apomorphies shared by birds and part of Crocodylomorpha must have been acquired convergently. This class of problems faces several of the supposed bird-crocodile characters listed above. In order to recognize and come to grips with such cases of character discordance, however, one requires a more precisely stated hypothesis than that birds and crocodiles share "some unknown common ancestor" (Martin 1983a:111), because this would be true in any case under the traditional view that birds are archosaurs.

The Dinosaur Hypothesis

Huxley's dinosaur hypothesis found its roots in Haeckel (1866), who considered birds to be basically "reptilian," and in earlier work of his own (Huxley 1864, 1867) in which he concluded that birds were derivatives of "sauropsid reptiles." Huxley was joined in supporting a "dinosaurian" origin of birds by other comparative anatomists including Cope (1867), Schmidt (1874), Marsh (1877), Gegenbaur (1878), Williston (1879), W. K. Parker (1864), T. J. Parker (1882), Baur (1883, 1884, 1885, 1886), and Darwin (1872). Indeed, Huxley's proposed "dinosaurian affinities" of birds gained broad acceptance during the latter quarter of the nineteenth century, even among the ranks of those who were "at best indifferent to Darwin" (Desmond 1984: 132).

In Huxley's 1869 address before the Geological Society, he described the "ornithic peculiarities" of Dinosauria as opening

up “a very interesting field of inquiry” that inspired him to devote “all my disposable leisure during the winter of 1867–8” to discovering characters shared by “dinosaurs” and birds that are not also shared by “lizards” and crocodiles. During this time Huxley also set out to examine critically “the material in the British Museum in order to ascertain how far the peculiarities of *Megalosaurus* were common to the Dinosauria in general.” Huxley (1868, 1870*a, b*) cited 35 characters as “evidence of the affinity between dinosaurian reptiles and birds.” Of these the following 17 characters survive critical examination in light of our current knowledge.

- 1) The skeleton is hollow and lightly constructed.
- 2) The cervical vertebrae are elongate.
- 3) There are more than two sacral vertebrae.
- 4) The scapula is elongate and narrow.
- 5) The coracoid is short and rounded.
- 6) The ilium is prolonged anteroposteriorly.
- 7) The acetabulum is roofed above by a supracetabular buttress of the ilium.
- 8) The bony contribution of the ilium to the acetabulum is more or less replaced by membrane.
- 9) The ischium and pubis are much elongated.
- 10) The femur has a strong anterior trochanter.
- 11) The femur has a crest on the ventral face of the outer condyle that passes between the tibia and the fibula.
- 12) The proximal end of the tibia is produced anteriorly into a strong crest, which is bent outwardly, or towards the fibular side.
- 13) There is a crest on the lateral side of the proximal end of the tibia for attachment of the fibula.
- 14) The tibia has a fossa distally for the reception of the ascending process of the astragalus.
- 15) The fibula is gracile compared to the tibia, and its distal end is much smaller than the proximal.
- 16) The astragalus is compressed, its articulation with the tibia is concave proximally and it has a convex, pulleylike distal surface, and the disparity in size between the tibia and fibula is also reflected in the astragalus being much larger than the calcaneum.
- 17) An “ascending process” (the intermedium) more or less tightly connects the astragalus and tibia.

Only some of these characters can now be considered to have arisen in the immediate common ancestor of Dinosauria (see Appendix A). Nevertheless, all of them appeared within the subgroup of archosaurs containing birds and thus they speak against the crocodile-bird hypothesis. At first glance, the explanatory powers of the crocodile-bird versus dinosaur hypotheses do not appear to differ greatly in that the former is supported by 14 shared apomorphies and the latter by 17. One must bear in mind, however, that the dinosaur hypothesis was formulated over a century ago with a fraction of the evidence currently available (see Appendix A). Although the crocodile-bird hypothesis is based on current knowledge, there would have been no reason to accept it over the dinosaur hypothesis as it stood in 1870, and there is even less reason to do so now. Huxley (1870*b*) mistakenly claimed that the absence of clavicles was diagnostic of Dinosauria, but this did not deter him from hypothesizing a bird-“dinosaur” affinity. I doubt that he considered the matter in this way, but he was correct in his judgement

to the extent that it would have been simpler to accept the reappearance of clavicles in birds than to accept convergence as an explanation for each of the seventeen characters listed above.

In the discussion following Huxley’s presentation before the Geological Society in 1869, Seeley remarked that he “thought it possible that the peculiar structure of the hinder limbs of the Dinosauria was due to the functions they performed rather than to any actual affinity with birds” (Huxley 1870*a*:31). With this simple declaration arose the issue that was to become the bane of Huxley’s hypothesis. Seeley suggested convergence as an alternative explanation for the apomorphies shared by “dinosaurs” and birds without proposing the requisite alternative hypothesis of relationship.

The assertion of convergence was to be heard time and again in the ensuing years (e.g., Mudge 1879; Dollo 1882, 1883; Dames 1884; Parker 1887; Furbringer 1888; Osborn 1900). What made matters worse was the rise of the “thecodont” ancestry hypothesis in the early part of the twentieth century (e.g., Broom 1913; Heilmann 1926); this hypothesis appeared to dignify the otherwise bald assertion of convergence. The error was compounded even further when the convergence argument was applied not only to bird origins but to the question of dinosaur monophyly as well. Pandora’s box had been opened; if an erect, bipedal posture and gait arose convergently in dinosaurs and birds, then what was to forbid multiple evolutions of such adaptively significant characters? The demise of the dinosaur-bird hypothesis went hand in hand with the demise of dinosaur monophyly; if one accepted the nonparsimonious reasoning behind the hypothesis that birds were “derived independently” from “thecodonts,” then why not accept the even less parsimonious hypothesis that each of the remaining dinosaurian groups were “derived independently” from “thecodonts” as well? I see nothing that would forbid the multiple evolution of “dinosaurian” characters, but what evidence indicated that this did in fact take place? Although a few researchers advocated the dinosaur hypothesis (e.g., Boas 1930), the “unknown ancestor,” coupled with the convergence argument, enthralled most systematists (e.g., Simpson 1946; de Beer 1954; Romer 1966).

There was renewed interest in the origin of birds in the 1970’s, beginning with the publications of Galton (1970), Walker (1972), and Ostrom (1973). Galton (1970) stressed one of the characters initially employed by Huxley (1870*a, b*)—a reversed pubis—to suggest that birds were “derived” from ornithischian dinosaurs. Upon introduction to Ostrom’s (1973) evidence, Galton rejected the ornithischian hypothesis (e.g., Bakker and Galton 1974). Martin (1983*a*) suggested that the presence of a predeontary bone in *Hesperornithes* and its inferred presence in *Ichthyornis* may be further evidence of an ornithischian-bird relationship. The absence of a predeontary bone in *Archaeopteryx* and all other birds speaks against Martin’s conclusion; even if ornithischians were the sister-group of birds, it would still be simpler to accept a predeontary bone as diagnostic of a taxon including only *Ichthyornis* and *Hesperornithes*.

Just as *Euparkeria* spurred interest in the “thecodont” ancestry hypothesis, Ostrom’s finds of a new and strikingly birdlike theropod, *Deinonychus antirrhopus* (Ostrom 1969*a, b*, 1974*b*, 1976*b*), revitalized the dinosaur hypothesis. Ostrom’s (1973, 1974*a*, 1975*a, b*, 1976*a*) hypothesized “coelurosaurian” ancestry of birds could be viewed as an extension of Huxley’s pro-

posals, since the theropod *Megalosaurus* figured prominently in Huxley's arguments. The two hypotheses differed, however, in that Huxley looked at "dinosaurs" in general as "intermediate" between "reptiles" and birds, while Ostrom sought the ancestry of birds among "coelurosaur theropods" alone and skirted the question of dinosaur monophyly.

Early workers found favorable comparisons between birds and "coelurosaurs," and these comparisons were ably reviewed by Heilmann (1926). Although Heilmann has been considered the champion of the "thecodont" hypothesis, his closing comment (1926:185) upon finishing his comparisons between birds and "coelurosaurs" was: "We have therefore reasons to hope that in a group of reptiles closely akin to the Coelurosaurs we shall be able to find an animal wholly without the shortcomings here indicated for a bird ancestor."

After Heilmann (1926), a few authors advocated a special bird-"coelurosaur" connection (e.g., Lowe 1935, 1944a, b; Holmgren 1955). As Ostrom (1976a) noted, however, their ideas received little attention because they saddled themselves with burdens—most notably avian polyphyly—that inspired others to reject their ideas out of hand (e.g., Simpson 1946; de Beer 1954). Ostrom's resurrection of the "coelurosaur" hypothesis met with wider acceptance (e.g., Bakker and Galton 1974; Thulborn 1975, 1984; Thulborn and Hamley 1982), although his hypothesis was not without critics (e.g., Walker 1977; Tarsitano and Hecht 1980; Martin 1983a). Many of the criticisms were centered on the interpretation of certain anatomical details in imperfectly preserved fossils. Perhaps more troubling was the continued reliance on the part of Ostrom's critics on the "thecodont" hypothesis and its henchman, convergence.

Ostrom considered birds to have "evolved from coelurosaurs." However, in a phylogenetic perspective Ostrom's use of "coelurosaur" is no more informative than the name Theropoda, because both names are diagnosable by the same synapomorphies (see Introduction to the Basic Taxa, below). Thus, the "coelurosaur" hypothesis was no more precisely stated than was the crocodile-bird hypothesis, in that it merely claimed that birds and "theropods" shared an unknown common ancestor. In failing to let his hypothesis accurately reflect the structure of his evidence, Ostrom opened himself to a variety of criticisms, most of which were only misinterpretations invited by the obfuscation of paraphyly. It is inappropriate to consider each of these criticisms at this time, and the reader is referred to the character discussions below for examples of the problems stemming from treating paraphyletic and monophyletic taxa as if they possessed the same properties (i.e., a unique history involving origin, diversification, extinction, etc.).

Another result of Ostrom's vague conclusions regarding the relationships of birds to other theropods was that some workers mistakenly concluded that birds and theropods might be sister-groups (e.g., Tarsitano and Hecht 1980; Thulborn and Hamley 1982). The imprecision in Ostrom's proposition was rectified by Padian (1982), who extracted the relevant evidence from Ostrom's works and arrayed it in an explicitly phylogenetic context. Padian's provisional reanalysis demonstrated that birds are more closely related to some "coelurosaurs" than they are to others; the conclusion that birds and theropods are sister-groups could not be extracted from Ostrom's evidence. On the contrary, birds are deeply imbedded within Theropoda, just as

humans are deeply imbedded within the phylogenetic nexus of Mammalia.

Bakker and Galton (1974) integrated the hypotheses of Ostrom and Huxley and resurrected the concept of dinosaur monophyly. Their method of analysis was somewhat more rigorous than the Simpsonian "evolutionary systematics" of Ostrom, although they were also hampered by such paraphyletic taxa as "thecodonts" and "prosauropods." The essence of Bakker and Galton's (1974) argument was as follows.

- 1) Dinosaurs (including birds) shared apomorphies not also shared by "thecodonts" and were therefore monophyletic.
- 2) "Prosauropods" were a primitive grade of dinosaurs that bridged the gap between ornithischian and "saurischian" dinosaurs.
- 3) All dinosaurs, like modern birds, were active endotherms; the behavioral and physiological apomorphies shared by dinosaurs are important; Dinosauria should therefore be accorded Class status.

Bakker and Galton's paper inspired considerable controversy (e.g., Thulborn 1975; Charig 1976b). The most telling criticisms were directed to the second and third points. To be sure, the link between Bakker and Galton's evidence and the conclusion of endothermy was a bit tenuous. The question of categorical rank of Dinosauria is trivial; current methods of establishing taxonomic rank rely entirely upon the authority of a systematist's subjective notion of what constitutes an ideal Class, Order, etc., and such Platonic and typological notions are anachronistic at best. Charig's (1976b) criticisms of Bakker and Galton's second point were for the most part trenchant and insightful. However, although some of Thulborn's (1975) and Charig's (1976b) criticisms of the evidence supporting dinosaur monophyly were factually accurate, for the most part they did not bear on the question of dinosaur monophyly.

Most criticisms of the resurrected Dinosauria hypothesis fell into one of three classes: 1) saurischians and ornithischians are too different to be monophyletic, 2) some of the alleged dinosaur characters were in fact present in some "thecodonts," and 3) the rest of the characters are functionally related and they could have been acquired convergently. The first class of criticisms is beside the point. One may be different from one's siblings, yet still share the same parents; the differences between bats and whales do not preclude their being mammals any more than the differences between the postdentary bones of *Ophiacodon* and *Homo* indicate nonhomology. Criticisms in the second class only indicate that some "thecodonts" are closer to dinosaurs (including birds) than are others; thus, "Thecodontia" is paraphyletic. Such evidence may not support dinosaur monophyly, but it does not speak against it either. The third class of criticisms leveled at Bakker and Galton's evidence for dinosaur monophyly is exemplified by a quote from Charig (1976b:79): "Most of these dinosaurian character-states were obviously adaptations to the fully improved ('fully erect') posture and gait of the dinosaurs . . . which could easily have evolved several times over, in slightly different ways, in response to similar functional requirements."

We have now come full circle; the exchanges between Huxley and Seeley, and between Bakker and Galton on the one hand and Charig and Thulborn on the other, demonstrate that the

dinosaur controversy has not altered on this issue in over a century. This controversy has nothing to do with evidence, although it must be admitted that until Hennig 1966, it was not widely understood that ancestry, rather than overall similarity or dissimilarity, must be the basis of phylogenetic classification. Consequently, there is little to be gained from taking the position that the problems will be solved by finding more fossils. There are, after all, many more fossils now available than there were in Huxley's time, and they still have not forestalled the old objections. The implications are clear: if our understanding of bird origins is to progress, we ought to rid ourselves of typological thought, namely, paraphyletic "Thecodontia"; reserve hypotheses of convergence for cases of character discordance, without which there is nothing for the concept of convergence to explain; and remember that although the world has no obligation either to be simple or informative, our hypotheses had better be both (Beatty and Fink 1979). By following these precepts, issues in archosaur phylogeny can be brought into sharper focus.

Knowledge of theropod anatomy has increased vastly since Buckland described *Megalosaurus* in 1824. Unfortunately, this knowledge has not been translated into a deeper understanding of theropod phylogenetic relationships. This circumstance reflects, in part, that Theropoda has yet to be diagnosed on the basis of synapomorphies. Indeed, most workers have been content to define "theropods" as "primitive dinosaurs" or "carnivorous saurischians"; which is to say that theropods are those saurischians that are not sauropodomorphs, and saurischians are those dinosaurs that are not ornithischians. In order to bring these taxa into the phylogenetic system, and thereby address the question of the phylogenetic relationships of birds, it will first be necessary to determine which, if any, phylogenetic entities within Dinosauria might be parts of Saurischia and Theropoda.

MATERIALS AND METHODS

For the most part, the specimens examined are listed in the Introduction to the Basic Taxa. However, the materials constituting the core of the analysis were *Segisaurus*, *Dilophosaurus*, casts of the skull of *Ceratosaurus*, and several undescribed specimens in the collections of the University of California Museum of Paleontology (UCMP); *Coelophysis* in the collections of the Museum of Northern Arizona (MNA), UCMP, and American Museum of Natural History (AMNH); *Procompsognathus* in the collections of the Staatliches Museum für Naturkunde, Stuttgart (SMNS); *Compsognathus* in the collections of the Bayerische Staatssammlung für Palaontologie und historische Geologie, Munich (BSP); and the comparative osteological collections of extant birds housed in the UCMP, the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), the California Academy of Sciences (CAS), and the University of Michigan Museum of Zoology (UMMZ). These data were supplemented by photographs and notes on virtually every taxon referred to nonavian theropods compiled by Samuel Welles and Robert Long. Information on character ontogenies was derived from the literature and from cleared and double-stained series of *Alligator*, *Gallus*, and *Podiceps occidentalis* (UMMZ), in addition to late embryos and juveniles of a few passerines (CAS and pers. coll.), and the hindlimbs of three tinamou embryos

(MVZ). These data were supplemented by that derived from skeletons of a hatchling *Pterocnemia* (MVZ) and a juvenile *Apteryx* (UMMZ).

For the purposes of this work, ontogenies will be divided into four stages: embryos, juveniles, subadults, and fully adult/mature individuals. Embryos refer to prehatching individuals; juveniles include stages from hatchlings to nearly full-grown specimens (i.e., subadults); subadults are those individuals that are near to maximum size as is indicated by some, but not all, of the developmental events marking the cessation of growth (i.e., senility). As used here, the term "fully adult" makes no reference to sexual maturity, which may or may not be coincident with this stage in skeletal ontogeny. Individuals that have reached the terminal stage of ontogeny are referred to variously as fully adult, fully mature, or as having attained maximum adult size. Subadults may also be near or at maximum adult size, but they do not display the full suite of developmental events in the skeleton that mark the cessation of growth. The cessation of growth in theropods may be recognized by the following events in the skeleton: fusion between the axial intercentrum and atlantal centrum, and fusion of this compound structure to the axial centrum; fusion of neural arches to centra; fusion of the vertebral components of the sacrum; full ossification of distal tarsal II; and, at least in nonavian theropods aside from ratites, fusion of the scapula and coracoid. Some of these events may precede others; however, any specimen in which all of them are present is here considered to have attained maximum adult size. By this definition, there are few nonavian theropod fossils that have achieved maximum adult size (e.g., the type specimens of *Syntarsus rhodesiensis* and *Ceratosaurus nasicornis*). There are also few specimens that could be considered juveniles, and even these few represent approximately half-grown individuals (e.g., the type specimen of *Compsognathus longipes* and, contrary to Howgate's 1984 view, the Eichstätt specimen of *Archaeopteryx lithographica*).

The methods employed here are essentially those of Gauthier et al. (in prep.). Following the procedure of Maddison et al. (1984), at least two outgroups were employed to identify 84 apomorphic characters distributed among 2 or more of the 17 basic taxa (18 including outgroup) that were the subjects of this analysis (see Introduction to the Basic Taxa, Fig. 7, and Appendix B). These data were then analyzed with Swofford's Phylogenetic Analysis Using Parsimony (PAUP) program installed in the University of Michigan's Terminal System. The analysis was two-part; the first run included only the comparatively well known taxa whose interrelationships were the principal foci of this analysis (viz., Ornithischia, Sauropodomorpha, Ceratosauria, Carnosauria, Ornithomimidae, Deinonychosauria, and birds), and the second run included all taxa, including those for which we have relatively little information owing to incomplete preservation. The first run yielded a single cladogram depicting the most parsimonious interpretation of the phylogeny of the seven well-known dinosaur taxa (Fig. 8). This cladogram requires 94 evolutionary events to account for the distribution of 84 apomorphies among the seven taxa, thus yielding a consistency index of 89%; that is to say, the single tree so obtained represents a highly corroborated hypothesis of relationship. However, the second run, which included both the better known and less well known theropods, resulted in numerous, equally

parsimonious trees. Nevertheless, the sister-group relationship among the seven well-known taxa were consistent across all possible trees. The multiple trees obtained in the second run resulted from the missing data in the 10 less well known taxa. For example, let us say that Coelurosauria includes only three taxa: deinonychosaurs, birds, and *Hulsanpes perlei*. Only three of the 84 characters under review were determinable for *Hulsanpes*, and although these data indicate that it is a coelurosaur, they are moot on the point of its precise affinities within this taxon. The PAUP analysis is so constructed that it considers all possible positions that *Hulsanpes* could have among coelurosaurs (viz., it could be the sister-group of birds, deinonychosaurs, or a deinonychosaur-bird group) and thus yields three equally parsimonious cladograms for these three taxa. Of course, none of these cladograms is actually supported by any evidence observable in *Hulsanpes*. Thus, when one considers the added possibilities allowed by the very incomplete remains of the 10 less well known taxa, the source of the numerous possible trees becomes apparent. However, two critical points must be borne in mind: first, the relationships among the seven taxa for which there is more complete information remained unchanged, and second, the overwhelming majority of possible trees were in fact uninformative. Consequently, they were collapsed into a single consensus tree incorporating multichotomies stemming from the levels supported by observable characters (Fig. 9). The consensus tree required 99 evolutionary events to account for the distribution of 84 apomorphies among the 17 basic taxa, thus yielding a consistency index of 85%.

Following Gauthier et al. (in prep.), the classification used in this work was constructed according to the following five conventions.

1) Only monophyletic taxa including an ancestor and all of its descendants are recognized, and in no case will a demonstrably paraphyletic taxon be considered in this analysis. Ancestry, rather than overall similarity, must be the basis for a phylogenetic system. The single exception to this convention is the metataxon.

2) A new category, the metataxon, is employed for taxa for which there is no positive evidence for or against recency of common ancestry. Following the suggestion of M. Donoghue, metataxa are provisionally allowed in the classification and their uncertain status is denoted by an asterisk following the name. For example, as will be argued below, the monophyly or paraphyly of the five fossil skeletons and a single feather impression referred to the earliest bird, *Archaeopteryx lithographica**, has yet to be firmly established, and it is therefore accorded metataxon status.

3) Certain widely used names are standardized by restricting them to taxa whose monophyly among extant amniotes is firmly established. Accordingly, Archosauria is standardized by limiting this taxon to all the descendants of the most recent common ancestor of extant birds and crocodiles. And Aves is likewise restricted to all the descendants of the most recent common ancestor of Ratitae, Tinami, and Neognathae.

4) Although the spelling of current taxonomic names is retained, no formal categorical ranks are recognized and hierarchical relationships within taxa are expressed instead by branching diagrams. Categorical ranks such as Class, Order, Family, and Genus, will not be recognized in this work.

5) Except to preserve binomials, no redundant names will be

recognized. Thus, although *Archaeopteryx lithographica** is retained, redundant taxa conveying nothing further about phylogenetic relationships, such as Archaeopterygidae, Archaeopterygiformes, or Saururæ will be ignored.

INTRODUCTION TO THE BASIC TAXA

This section defines and diagnoses the theropod taxa that are the subjects of the present analysis (For diagnoses and definitions of the other basic taxa, Sauropodomorpha and Ornithischia, and the outgroup taxa, see Appendix A). These diagnoses are not definitive; the basic taxa are assumed to be monophyletic, and the characters are listed merely to show that there is at least some basis for the assumption of monophyly in each case.

Several workers have described the conventional groupings of "Carnosauria" for large theropods and "Coelurosauria" for small theropods as inadequate in view of the observed variation among Theropoda (e.g., Colbert and Russell 1969; Ostrom 1969b). Accordingly, modern classifications emphasize less inclusive taxa, typically ranked as "families," and these units will, for the most part, serve as the basic taxa of this analysis. In a phylogenetic context, "Coelurosauria" and "Theropoda" are redundant in that they have traditionally been diagnosed by the same synapomorphies. Huene (1914b) originally defined "Coelurosauria" on the basis of plesiomorphic resemblances, such as their small size and long necks. In other words, they are theropods that are not carnososaurs. However, because Huene based the concept on "coelurids," some of which have synapomorphies of a particular subgroup of Theropoda that includes birds, Coelurosauria will be retained in a modified form (see below).

A principal goal of this work is an examination of the phylogenetic relationships within Theropoda, with particular attention to the relationships among the better known theropods here included in Ceratosauria (n. comb.), Carnosauria (n. comb.), Ornithomimidae (n. comb.), Deinonychosauria, and birds. For the sake of completeness, the distribution of the characters discussed will also be noted in less well known taxa such as *Procompsognathus triasicus**, *Liliensternus liliensterni**, *Ornitholestes hermanni**, *Coehurus fragilis**, *Compsognathus longipes*, *Microvenator celer**, *Saurornitholestes langstoni**, *Hulsanpes perlei*, Elmisauridae*, and Caenagnathidae. As the use of the asterisk indicates, several of these taxa have not been adequately diagnosed; they may indeed be different from other theropods, but until they are diagnosed on the basis of characters relevant to the question of monophyly (i.e., synapomorphies), their status as phylogenetic entities must remain suspect. The position of these generally poorly known taxa are not so critical to the goals of this analysis, and the reader is referred to the literature for more information (Marsh 1881a; Osborn 1903, 1917; Ostrom 1970, 1978, 1981; Sues 1978; Osmolska 1981, 1982; Barsbold 1983; Welles 1984).

The more inclusive basic taxa may be newly recognized, or they may differ in diagnosis and content from concepts employed by other researchers. Some of the synapomorphies I consider diagnostic of the basic taxa could only have been recognized as such after the completion of the analysis; they are added now for the sake of completeness and in no case would the monophyly of any of the basic taxa depend on such determinations.

Elmisauridae* Osmolska, 1981

TEMPORAL RANGE.—late Cretaceous.

INCLUDED TAXA.—*Chirostenotes pregraelis**, *Macrophalangia canadensis**, and *Elmisaurus rarus**.

DIAGNOSIS.—Based on personal observation of *Macrophalangia** and *Chirostenotes**, and on published descriptions of these taxa in Gilmore (1924), Sternberg (1932), and Osmolska (1981). These taxa are represented by scant and often noncomplementary remains. Indeed, none of the referred taxa have been adequately diagnosed, and they are so poorly known that Osmolska (1981) suggested that they might be synonymous. According to Currie (pers. comm.), however, *Elmisaurus** and *Chirostenotes** are sympatric in Alberta in the late Cretaceous. Currie and Russell are in the process of describing a partial skeleton, including hands and feet, of *Chirostenotes**. Preliminary results indicate that *Chirostenotes** and *Macrophalangia** might be based on the same species. This conclusion is tentative because there appear to be two "morphs," and it is not yet clear if these morphs result from sexual or taxonomic differences. To further complicate matters, each of the apomorphies shared by elmisaurids* is either matched in some other theropods, or it could be considered part of a transformation series that is taken to extreme in some group of theropods (e.g., proportions of manal digit I approach those of ornithomimids). More evidence will be necessary to address these issues, but for the present Osmolska's Elmisauridae* will be accepted as a metataxon. Following is a list of apomorphies shared by elmisaurids*; as suggested above, these apomorphies may or may not prove to be synapomorphies.

Metacarpal I elongate and slender; relatively elongate first and second phalanges of manal digit III; metatarsus elongate and narrow; metatarsal III pinched between metatarsals II and IV, the latter two contacting one another proximally in front of III (similar modifications of the hands and tarsus are present in ornithomimids, troodontids, and ornithurine birds).

Caenagnathidae Sternberg, 1940

TEMPORAL RANGE.—late Cretaceous.

INCLUDED TAXA.—*Caenagnathus collinsi*, *C. sternbergi*, and *Oviraptor philoceratops*.

DIAGNOSIS.—No one doubts the monophyly of these peculiarly specialized theropods (Osborn 1924b; Osmolska 1976; Barsbold 1983). Caenagnathids were once thought to be related to ornithomimids because both share edentulous, beaklike snouts, but more recent work suggests otherwise (Barsbold 1983, and see below). Caenagnathids have highly modified skulls, and there is very little information regarding their postcranial skeletons. Several new specimens have been discovered, but they have yet to be completely described and illustrated (Osmolska 1976; Barsbold 1983). Barsbold is currently engaged in a revision of this taxon based on new material including as many as three species of *Oviraptor*, and an adequate diagnosis of this taxon must await his findings.

Currie (pers. comm.) has informed me that *Caenagnathus* (known only from cranial material) and *Chirostenotes** (known only from postcranial material) might represent the same species. Moreover, Wilson and Currie (pers. comm.) have suggested that *Microvenator** might be a caenagnathid. These hypotheses are only tentative, but they are included because Currie and Wil-

son's observations indicate that *Microvenator**, elmisaurids*, and caenagnathids might be monophyletic; such possibilities should always be borne in mind when dealing with metataxa.

Ceratosauria Marsh, 1884b (n. comb.)

TEMPORAL RANGE.—late Triassic to late Jurassic.

INCLUDED TAXA.—*Ceratosaurus nasicornis*, *Syntarsus rhodestensis*, *Coelophysus bauri*, *Segisaurus halli**, *Sarcosaurus woodi**, *Dilophosaurus wetherelli* (including UCMP 37302, 37303, and 77270), and some undescribed forms represented by UCMP 129618 (referred to *Coelophysus* by Padian, in press), UCMP 128659, and MNA V. 2623 (referred to *Syntarsus* by T. Rowe, pers. comm.).

DIAGNOSIS.—The initial basis for recognition of the monophyly of this taxon stemmed from Welles's (1984) observation that one specimen referred to *Dilophosaurus* (UCMP 77270) possessed a uniquely modified trochanteric shelf (=modified anterior trochanter: see photograph of *Sarcosaurus woodi** in Charig 1976b). T. Rowe later observed this apomorphy in *Segisaurus**, and we have since observed this and other shared apomorphies in all taxa here included in Ceratosauria.

The presence of the trochanteric shelf in only some ceratosaur specimens is perplexing. However, Colbert, Rowe, and Raath (pers. comm.) have separately observed the presence of two femoral types among the large series of *Coelophysus* and *Syntarsus*, a robust form in which the trochanteric shelf is developed in the form characteristic of ceratosaur, and a gracile form in which the trochanteric shelf is less modified and more like that seen in dinosaurs ancestrally. Dimorphism in femoral form, along with other differences in proportions, have been attributed to sexual dimorphism.

Although it has appeared elsewhere in theropods, another synapomorphy of Ceratosauria is the fusion between distal tarsals 2 and 3 and their respective metatarsals (T. Rowe, pers. comm.; Raath 1969). Rowe (pers. comm.) has discovered additional synapomorphies of Ceratosauria, including the shape and prominence of the supracetabular shelf, a fibular groove on the proximal end of the lateral side of the fibula (e.g., Gilmore 1920, fig. 65C), and a prominent groove on the ventrolateral side of the fibular condyle of the femur. Rowe (pers. comm.) also noted that, with the possible exception of *Segisaurus**, all ceratosaur have a narrower pubis than is seen in other theropods aside from birds. Because *Coelophysus* is one of the earliest theropods, its narrow pubis was thought to be diagnostic of Theropoda. However, this apomorphy is diagnostic of most, if not all, ceratosaur, and a relatively broader pubis appears to be the ancestral condition for Theropoda (e.g., *Allosaurus*, Madsen 1976).

A more complete discussion of the evidence supporting monophyly of Ceratosauria will be presented elsewhere (Rowe, in prep.).

Carnosauria Huene, 1920 (n. comb.)

TEMPORAL RANGE.—late Jurassic to late Cretaceous.

INCLUDED TAXA.—*Allosaurus fragilis*, *Acrocanthosaurus atokensis*, *Indosaurus matlevi*, *Alectrosaurus olsem*, *Dryptosaurus aqualungus*, *Albertosaurus sarcophagus*, *A. libratus*, *A. lancensis*, *Athoramus remotus*, *Daspletosaurus torosus*, *Indosuchus raptorius*, *Tarbosaurus bataar*, and *Tyrannosaurus rex*.

DIAGNOSIS.—Based primarily upon the series of *Allosaurus fragilis* as described by Madsen (1976) and *Albertosaurus libratus* as described by Lambe (1917) and Russell (1970). These data were supplemented by personal examination of *Allosaurus*,

Albertosaurus, and *Tyrannosaurus*, and the descriptions of carnosaurs published in Marsh (1896), Osborn (1905, 1906, 1912, 1917), Gilmore (1920), Matthew and Brown (1922), Janensch (1925), Sternberg (1932), Stovall and Langston (1950), Rozhdestvensky (1958, 1965), Walker (1964), Colbert and Russell (1969), Ostrom (1969a), Steel (1970), Galton and Jensen (1979), and Barsbold (1983).

The medium- to large-sized theropods such as *Megalosaurus** and *Eustreptospondylus** possess some carnosaurlike attributes. These taxa are examples of a pervasive problem in theropod phylogeny, namely, the "megalosaur" problem. *Megalosaurus** was the first dinosaur described, but it is represented by limited material with no diagnostic features distinguishing it from other large theropods. As the name implies, "megalosaurs" are larger theropods, and several of their apomorphies are probably size-related in that they are also seen in large ornithischians and sauropodomorphs (e.g., femur longer than tibia). In view of profound character discordance, it is more parsimonious to accept these shared apomorphies as examples of convergence between "megalosaurs" and large ornithischians or sauropodomorphs. When considering the "megalosaurs" and Carnosauria, however, the problem of distinguishing homology from convergence is more difficult. Carnosauria shares many apomorphies with a portion of Theropoda that includes extant birds, and these can hardly be considered size related (see below). The problem with "megalosaurs" is that they either do not have these apomorphies, or the appropriate portions of their skeletons are unknown. S. P. Welles is currently involved in a revision of the "megalosaurs," and until he has revised the alpha taxonomy of this confusing group of fossils, there is little point in considering them further.

Several carnosaur apomorphies listed below are also present in other medium to large theropods such as *Dilophosaurus* and *Ceratosaurus*. Among the size-related apomorphies are opisthocoelous cervicals, the greater length of the femur relative to the tibia, a robust skeleton, and enlarged neural spines and transverse processes in the trunk vertebrae. These attributes are seen in all large saurischians. Nevertheless, the taxa here included in Carnosauria possess corroborating synapomorphies in addition to those related to their size, and other large theropods, such as *Ceratosaurus* and *Dilophosaurus*, do not.

Carnosauria is distinguished from other Theropoda considered in this analysis in that it possesses the following synapomorphies: orbit dorsoventrally elongate and roughly keyhole-shaped (Fig. 1G, H); supraorbital crests in fully mature individuals (Fig. 1G, H); frontals and parietals narrow and very short; reduction of mandibular fenestra (Fig. 1G, H); further reduction of dentary overlap onto postdentary bones and mandibular symphysis (indicating improved intramandibular joint, Romer 1956); pronounced development of bony shelf below mandibular condyle on lateral surface of surangular, presumably associated with insertion of enlarged pterygoideus musculature (Fig. 1G, H); ilium expanded anterodorsally (Fig. 5D); strongly opisthocoelous cervical and anterior trunk vertebrae (convergent in penguins); digits II and III reduced in hand, especially the latter, which is shorter than digit I (Fig. 4L; analogous condition in ornithurine birds, but resulting from loss of phalanges); very robust postcranial skeleton with stout, relatively thick-walled long bones, shortened and stoutly constructed trunk and

cervical vertebrae (especially in tyrannosaurids), and large neural spines and transverse processes throughout vertebral column.

Tyrannosauridae, including *Albertosaurus*, *Tarbosaurus*, and *Tyrannosaurus*, are further derived within this assemblage in that they have the following synapomorphies: lacrimal excludes frontal from orbit (Currie, in press a, b); enlarged surangular fenestra and pterygoideus shelf (Fig. 1H); ventral process of squamosal nearly horizontally oriented (Fig. 1H); postorbital and jugal massive and anteriorly directed postorbital reentrant into orbit (Fig. 1H); tooth row fails to reach posterior to antorbital fenestra (Fig. 1H); forelimb less than one-quarter of hindlimb length; wrist bones very reduced (convergent in ornithomimids); third manual digit reduced to no more than metacarpal splint; ascending process very broad, extends dorsally for nearly one-third height of astragalus + tibia (convergent in coelurosaurs); calcaneum very reduced; and proximal end of metatarsal III strongly constricted between metatarsals II and IV (convergent in ornithomimids, elmsaurids*, and *Hulsanpes*).

Ornithomimidae Marsh, 1890

(n. comb.: includes Deinocheiridae of Osmolska and Roniewicz, 1970)

TEMPORAL RANGE.—late Jurassic to late Cretaceous.

INCLUDED TAXA.—*Elaphrosaurus bambergi*, *Archaeornithomimus asiaticus*, *Ornithomimus edmonticus*, *O. velox*, *O. sedens*, *Struthiomimus altus*, *Dromicimimus brevitertius*, *D. samueli*, *Gallimimus bullatus*, *Ingema yanshuni*, *Garrimimus brevipes*, and *Deinocheirus mirificus*.

DIAGNOSIS.—Based primarily upon *Gallimimus bullatus* as described by Osmolska et al. (1972) and data derived from Russell (1972). Additional evidence derived from personal observation of *Struthiomimus* and descriptions in Marsh (1890, 1896), Osborn (1917), Parks (1928, 1933), Gilmore (1920, 1933), Janensch (1925, 1929), Sternberg (1932, 1933, 1934), Ostrom (1969a, b, 1970, 1974a, 1976b), and Barsbold (1983). The diagnosis below is based on Upper Cretaceous ornithomimids, although more complete knowledge of Lower Cretaceous and Upper Jurassic taxa may alter it.

Cornified beak as indicated by form of unworn margins of edentulous, beaklike jaws (Fig. 1I; convergent in Caenagnathidae and modern birds); premaxilla enlarged and beaklike, broadly contacting nasal to exclude maxilla from external naris (Fig. 1I); secondary palate formed by premaxillae and maxillae; reduced jugal and ventrally elongate postorbital; reduced lower temporal fenestra; quadrate strongly inclined so that distal end lies far forward of proximal end; bulbous parasphenoid (also in Troodontidae, and to a lesser extent in birds); metacarpal I elongate and all digits of subequal length (Fig. 4M); carpus very reduced with poorly defined articular facets on individual carpals; terminal unguals less trenchant and recurved, with reduced basal tubera (suggesting loss of raptorial function for the hand); humerus lightly constructed and deltopectoral crest reduced; ischium ventrodistally recurved (Fig. 5E); metatarsus narrow, and elongate compared to tibia length; metatarsal III strongly pinched between metatarsal II and IV, barely contacting distal tarsals (analogous modifications of the metatarsus arose convergently in tyrannosaurid carnosaurids, elmsaurids*, ornithurine birds, and troodontids); pedal digits short and stout.

Deinonychosauria Colbert and Russell, 1969

TEMPORAL RANGE.—early to late Cretaceous.

INCLUDED TAXA.—Troodontidae and Dromaeosauridae.

DIAGNOSIS.—Modifications of the foot in general, and the second pedal digit in particular, indicate a raptorial function for the pes in Deinonychosauria (Colbert and Russell 1969; Ostrom 1969*a, b*). According to these authors, the subequal lengths of pedal digits III and IV, together with modification of the raptorial pedal digit II, indicate functional didactyly during locomotion. The ungual on pedal digit II bears a large, compressed, trenchant, strongly recurved, scimitarlike claw. The second phalanx is shortened and subequal to the first phalanx in length. Moreover, the second phalanx has a prominent heel posteroventrally, and its anterior and posterior articular surfaces allow increased digital excursion. Troodontids may not be the sister-group of dromaeosaurs (see Section V). This point is not clear, however, and following previous authors, this taxon is accepted on the basis of the shared apomorphic resemblances in their feet.

It is interesting to note that Osmolska (1982) argued that the form of the metatarso-phalangeal joint indicated that the second pedal digit functioned differently in troodontids (=saurornithoidids) and dromaeosaurs. This observation alone cannot be taken to indicate nonhomology, because the morphology of one could be a transformation of that seen in the other, or both could be transformations of some more general condition shared by their common ancestor. Troodontids vary in the degree to which the second pedal digit is modified (Russell, pers. comm.). For example, *Troodon* has a more specialized raptorial second pedal digit and is more like dromaeosaurs in this respect. However, the second pedal digit is less modified in other troodontids (Osmolska 1982; Barsbold 1977). The possible effects of age, size, and sex on the degree of development of these characters has yet to be determined. Information on the possible influence of these factors might be gained from extant cariamids, *Chunga* and *Cariama*, that have analogously modified second pedal digits; examination of the biological roles of their feet may also provide some insight into the function of the second pedal digit in Deinonychosauria. (Although the information was received too late to include in this analysis, Currie has informed me that there is some evidence for a possible troodontid-ornithomimid group; in light of this it would have been more appropriate to consider three separate basic taxa—1 *Dromaeosaurus*, 2 *Deinonychus-Velociraptor*, and 3 Troodontidae—rather than one, viz., Deinonychosauria.)

Troodontidae Gilmore, 1924
(=Saurornithoididae Barsbold, 1974)

TEMPORAL RANGE.—late Cretaceous.

INCLUDED TAXA.—*Saurornithoides mongoliensis*, *S. junior*, and *Troodon formosus* (= *Stenonychosaurus inequalis* and *Pectinodon bakkeri* following Currie (in press *b*)).

DIAGNOSIS.—Based upon personal observation of casts of *Stenonychosaurus inequalis* and descriptions and comparisons of both this taxon and *Saurornithoides* in Osborn (1924*b*), Sternberg (1932), Colbert and Russell (1969), Russell (1969), Barsbold (1974, 1977, 1979, 1983), Sues (1978), Osmolska (1981,

1982), Russell and Seguin (1982), Currie (in press *a, b*), and Wilson and Currie (in press).

Barsbold (1974) separated *S. junior* from *S. mongoliensis* because the former is 1.3 times larger, has a few more teeth, and the specimens derive from different stratigraphic formations. More specimens may indeed reveal that they are different taxa. However, the differences between these specimens could reflect size and age; current evidence cannot exclude the possibility that *S. junior* is merely an adult of the smaller *S. mongoliensis* (Currie, in press *a, b* notes a similar size range for *Troodon*). Accordingly, these taxa will be considered synonymous in the following analysis.

Anteromedially inclined orbits, suggesting broadly overlapping visual fields; deep depression in braincase in region of middle ear cavity (see Currie, in press *a*); bulbous parasphenoidal rostrum (also present in ornithomimids and in a less modified form in some birds); small, closely spaced teeth with enlarged (also seen in some dromaeosaurs), distally hooked denticles on posterior margin, anterior denticles reduced or absent at least in the lower jaw; deep, narrow Meckelian fossa of dentary; additional caudal vertebrae incorporated into sacrum (six sacral vertebrae); rodlike metatarsus with proximally attenuate metatarsal III wedged between slender metatarsal II and robust metatarsal IV; metatarsals II and IV in contact anteriorly in front of proximal end of metatarsal III (also in elmisaurids* and ornithomimids); and tongue-like distal articular surface of metatarsal III.

Dromaeosauridae Matthew and Brown, 1922

TEMPORAL RANGE.—early to late Cretaceous.

INCLUDED TAXA.—*Dromaeosaurus albertensis*, *Deinonychus antirrhopus*, *Velociraptor mongoliensis*, and *Adasaurus mongoliensis*.

DIAGNOSIS.—Based primarily upon *Deinonychus* as described by Ostrom (1969*a, b*, 1974*b*, 1976*b*). Supplementary data derived from descriptions in Matthew and Brown (1922), Osborn (1924*b*), Colbert and Russell (1969), Barsbold (1976, 1977, 1979, 1983), Sues (1977, 1978), Bonaparte and Powell (1980), and casts of the plastotype of *Deinonychus*. Sues (1978) included *Saurornitholestes** in Dromaeosauridae, but he did so on the basis of plesiomorphic resemblances; until the evidence supporting this placement is made explicit, this taxon will be considered separately.

Prezygapophyses and haemal arches exceed length of caudal vertebrae (Fig. 2*G*); short metatarsus compared to femur length; peculiar ginglymoid structure of the distal ends of metatarsals II and III; deeply grooved distal ginglymus of metatarsal II.

Avialae (n. txn.)(L.: *avis*, bird; *alae*, wings)

TEMPORAL RANGE.—late Jurassic to Recent.

INCLUDED TAXA.—*Archaeopteryx lithographica** plus ornithurine birds.

DIAGNOSIS.—Based primarily upon *Archaeopteryx lithographica** as described by Heilmann (1926), de Beer (1954), Ostrom (1972, 1973, 1974*a, b*, 1975*a, b*, 1976*a*), Wellnhofer (1974), Tarsitano and Hecht (1980), Martin (1983*a, b*), Whetstone (1983) and upon personal observation of the Eichstätt specimen and casts of the London and Berlin specimens.

This new taxon, Avialae, is named so as not to violate the

classificatory conventions of this work, in which widely used names like Aves are restricted to living taxa in order to maximize stability and phylogenetic informativeness. Because of feathers and the presumed ability to fly, *Archaeopteryx** has always been considered a bird. This informal usage has been maintained above, and use of the informal term "bird" for this taxon will be continued in the following discussion. In a formal sense, however, "birds" and Aves will not be synonymous. The "winged theropods" included in Avialae possess the following synapomorphies distinguishing them from other Theropoda.

Premaxillae elongate, narrow, and more pointed anteriorly, with longer nasal processes; maxillary process of premaxilla reduced so that maxilla participates broadly in external naris (also in troodontids; Currie, in press *a*); enlarged brain/basicranium (temporal musculature fails to extend origin onto frontal bones); double-condyled quadrate displaced from distal position on opisthotic to more anteromedial position in contact with prootic (Currie, pers. comm. and Walker, pers. comm., disagree with Whetstone's interpretation of the quadrate; Currie notes the anterior displacement of the quadrate in troodontids, and Walker does not consider the quadrate to be double-condyled in *Archaeopteryx**); maxillary and dentary teeth reduced in size and number (or lost), with unserrated crowns and enlarged roots that completely enclose replacement teeth within them (see Howgate 1984, for an alternative view); robust furcula for hypertrophied flight musculature (Olson and Feduccia 1979); scapula with more or less prominent acromion process for ligamentous connection to clavicle (see Martin 1983*b*, for alternative view); length/breadth ratio of scapula at midlength exceeds nine (not in penguins) and scapula tapers distally; acrocoracoid tuberosity larger than in other coelurosaurs; coracoid enlarged and inflected posteromedially more so than in other coelurosaurs; very long forelimbs and hands (e.g., in *Archaeopteryx** forelimb is 120–140% of hindlimb length, and more than twice as long as distance between glenoid and acetabulum), with forearm more than 87% of humerus length and metacarpal II approaching or exceeding one-half of humerus length; ischium compressed and dorsoventrally deep; compared to other theropods, tibia, fibula, and metatarsals relatively more elongate with respect to femur, regardless of body size (metatarsals short in penguins and some other birds, J. Cracraft, pers. comm.); fibula attenuate distally, and may not extend to end of tibia; proximal tarsals fused to tibia-fibula and to one another in adults; distal tarsals and metatarsals fused at least distally in fully adult individuals (convergent in some ceratosaurs, elmsaurids*, and *Hulsanpes*); first pedal digit elongate and reversed (may be reversed in some extant birds, R. Storer, pers. comm.), metatarsal I attached on distal quarter of metatarsal II; tail reduced to no more than 23 free caudal vertebrae; feathers cover limbs and tail, feathers on lateral margins of tail and posterior margins of arms enlarged, curved, and asymmetrically vaned, indicating aerodynamic function (e.g., Feduccia and Tordoff 1979).

It is not certain that feathers are confined only to avialans among coelurosaurs. *Compsognathus* apparently lacks them (Ostrom 1978), so feathers appear to have been absent in coelurosaurs ancestrally. However, *Compsognathus* is the only non-avian theropod that is preserved in an environment of deposition conducive to the preservation of feather impressions. Thus, future finds may demonstrate that feathers arose prior to the origin of birds.

As the use of the asterisk indicates, *Archaeopteryx lithographica** is here considered to possess no apomorphies that would not be expected in the common ancestor of all birds. Thus, the specimens referred to this taxon are placed here because of their geographic and stratigraphic occurrence and overall similarity. These specimens probably represent a single species, but such opinions should always be distinguished from those based on appropriate evidence. Notwithstanding the interesting possibilities suggested by Martin (1983*b*) and Howgate (1984), there is no unambiguous evidence indicating either parphyly or monophyly, and these specimens will be referred to collectively as the metataxon *Archaeopteryx lithographica**. Because of its generalized morphology and stratigraphic position, the specimens of *Archaeopteryx** could be parts of an ancestral population that gave rise to all later birds. Hypotheses of ancestral status can only be weakly supported in that they are based on negative evidence. Nevertheless, there is no unequivocal evidence supporting the alternative hypothesis, that *Archaeopteryx** is monophyletic and thus not an ancestral bird.

Whetstone (1983) and Martin (1983*a*) suggested that, compared to other birds, the squamosal is either reduced or absent in *Archaeopteryx**. This interpretation is open to doubt in view of the preservation of the specimens with cranial material; each of the specimens was preserved such that upon separating the slabs, the skulls fractured between the main body of the skull and the lightly constructed elements surrounding the orbit and temporal fenestra. These authors contended that the squamosal was absent because there is no evidence for its sutural connection to the skull. This contention loses much of its force because these sutural surfaces are also absent in theropods in which the squamosal is known to be present (e.g., *Syntarsus*; M. A. Raath, pers. comm.). Under such circumstances, it is difficult to distinguish between absence and nonpreservation. If further finds corroborate the Whetstone-Martin hypothesis, then *Archaeopteryx** must be removed from metataxon status and its hypothesized ancestral position must be rejected.

In keeping with one of the goals of this work, namely to provide a relevant series of outgroups for phylogenetic analyses among the major groups of extant birds, two more taxa within Avialae will be defined and diagnosed below. They are not basic taxa in this analysis, but it is necessary to consider Ornithurae and Aves at this point because the concepts represented by these names as used in this study may differ from those employed by others.

Ornithurae is defined here in keeping with its original intent as a taxon encompassing all extant birds, as well as all other birds that are closer phylogenetically to extant birds than is *Archaeopteryx**. Having been supplanted by Neornithes (Gadow 1893), Ornithurae (Haeckel 1866) is seldom used in current ornithological literature; the obscurity of the name has saved it from the diversity of meanings that possible alternative names have developed, and Ornithurae is thus an appropriate name for this taxon. As here defined, however, Ornithurae is a more inclusive taxon containing Aves, which reverses the traditional hierarchical relationship between these taxa. The terms Neornithes and Carinatae are avoided because their ambiguous and, at times, contradictory meanings in avian systematics have laden them with too much historical baggage to be useful in this work.

Ornithurae is recognized by a host of flight-related modifi-

cations in the skeleton that distinguish it from other theropods, including *Archaeopteryx**. The modifications indicate that the immediate common ancestor of Ornithurae possessed not only an inherited ability to fly, but the capacity for sustained flight approaching that seen in extant birds. It also appears that the immediate common ancestor of ornithurine birds had already overcome the energetically most demanding aspect of flight in modern birds—to become airborne from a standing start.

About 60 species of birds have been described from sediments of Cretaceous age, but most of these species are too poorly known to contribute much to our understanding of avian phylogeny (Elzanowski 1983; Thulborn 1984). To simplify the following discussion, only *Ichthyornis* and Hesperornithes will be considered. Moreover, because of character discordance, and ambiguities in character interpretations stemming from the specialized hesperornith morphology, it is not clear whether Hesperornithes or *Ichthyornis* is more closely related to extant birds. The evidence presented below indicates that neither taxon belongs within any subgroup of extant birds. Indeed, there is some evidence, such as the detailed form of the intramandibular joint and the possible presence of a "predeontary" bone in both taxa, indicating that *Ichthyornis* and Hesperornithes collectively constitute a sister-taxon of extant birds (Martin 1983a). It is beyond the scope of this work to address these questions, and Ornithurae will be diagnosed by synapomorphies that can be found in any two of the following three taxa, Hesperornithes, *Ichthyornis*, and extant birds. This approach assumes that the flightless, foot-propelled divers of Hesperornithes were derived from an ancestor possessing the full suite of characters diagnostic of Ornithurae. This may not be the case, but at least Hesperornithes do not retain an unmodified ancestral condition. For example, as diagnosed below, Ornithurae possess a keeled sternum; Hesperornithes do not possess a keel, but the morphology of its sternum is certainly derived with respect to the condition present in other dinosaurs.

Ornithurae Haeckel, 1866

TEMPORAL RANGE.—Lower Cretaceous (at least Albian Stage) to Recent.

INCLUDED TAXA.—Extant birds and all other taxa, such as *Ichthyornis* and Hesperornithes, that are closer to extant birds than is *Archaeopteryx**.

DIAGNOSIS.—This taxon is based on evidence derived from Marsh (1880), Martin and Tate (1976), Elzanowski (1977, 1981), Martin and Bonner (1977), Martin and Stewart (1977), McDowell (1978), Whetstone and Martin (1979, 1981), Martin (1980, 1983a, b, 1984), Martin et al. (1980), Whetstone (1983), and Thulborn (1984).

Body of premaxillae fused, edentulous, and beaklike; nasal process of premaxilla extends over nasal to closely approach frontal; facial process of maxilla reduced and naris enlarged (resulting in loss of maxillary fenestra); descending process of nasal contacts premaxilla to exclude maxilla from narial margin; maxilla with prominent medial phalange in palate (=maxillopalatine); ectopterygoid absent; palatine and pterygoid narrow and articulating near level of braincase (contra McDowell's 1978 interpretation of palatine as anterior pterygoid; pers. comm. L. Witmer and K. Warheit); peg and socket articulation between jugal and lateral cotylus of quadrate; extensive mesethmoid ossification appears early in ontogeny and is exposed on skull roof between nasals in late embryos/neonates (this character is re-

tained into adult stages in Hesperornithes [Martin, pers. comm.] and Ratitae [Pycraft 1900]); neck includes more than 9 vertebrae (convergent in Ornithomimidae, which have 10 cervicals—ornithurine birds have at least 13 cervicals ancestrally); anterior cervicals with moderately developed heterocoely (see below); prominent hypapophyses in posterior cervical and anterior trunk vertebrae; loss of hyposphene-hypantra intervertebral articulations; sacrum includes more than 5 vertebrae (convergent in troodontids, which have 6—ornithurine birds have at least 10); free portion of tail reduced to fewer than 16 vertebrae; absence of caudal zygapophyses; presence of pygostyle including variable number of coossified vertebrae (secondarily lost in some Hesperornithes and Tinami, and in most Ratitae); ossified uncinata processes (reversed in Anhimidae and megapods; R. Storer, pers. comm.); ossified (rather than calcified) ventral ribs attached to sternum (the last two characters may apply to a more inclusive taxon in that Ostrom [1969b] and Paul [1984b] identified ossified ventral ribs and uncinata processes in dromaeosaurs); absence of gastralia; enlarged and posteriorly displaced sternum, chondrogenic cells of which proliferate and migrate to form keel; appearance of new sternal ossification center, the lophosteon, arising in region of sternal keel; shoulder joint set posteriorly and dorsal to center of gravity; hollow scapula and coracoid articulate via scapular peg and coracoid socket below level of coracoid portion of glenoid (reversed in some flightless birds, such as Hesperornithes and Ratitae), and scapula and coracoid fail to fuse in adults (reversed in Ratitae); scapula long (exceeds length of 7 trunk vertebrae), narrow (length/breadth ratio at midlength exceeds 12), tapering distally, and scapula lies near to and parallel with vertebral column and closely approaches ilium posteriorly (these characters are reversed in flightless birds); coracoid long, slender, tapered at midlength, broad distally and in or near contact on midline, and articulate in prominent grooves along anterior edges of sternum, with prominent acromion process for articulation of clavicle (=triosseal canal; some aspects of coracoid form may reverse in flightless birds, such as Hesperornithes and Ratitae); prominent, conical, internal tuberosity on humerus separated from head by capital groove; ulna approximately twice as thick as radius and with nobs along posterior margin for flight feather attachment; ulna with semilunate articular surface distally (reversed in some flightless birds such as Hesperornithes and Ratitae); characteristic carpometacarpus in adults formed from coossification of some distal carpals and metacarpals, with metacarpals I, II, and III fused proximally, and II and III fused distally, second phalanx of digit II broad and flat, absence of two phalanges on digit III, clawed unguals usually absent in adults (various flightless birds have lost other manal elements, e.g., digit II is the only finger remaining in *Apteryx* and *Casuarinus*; present interpretation contradicts digital homology proposed by Hinchliffe and Hecht 1984); pelvis fused in adults; prominent antitrochanter above acetabulum; preacetabular portions of ilia elongate, closely appressed on midline, and in contact with at least some sacral neural spines, but postacetabular portions widely separated (reversed in some ornithurines such as Hesperornithes, Ratitae, Gaviidae); absence of bipartite distal moities of ischium (see Fig. 5H, I); pubes and ischia widely separated on midline; pubis shortened, without expanded foot distally, and with prepubic process proximally (not in *Ichthyornis*); femur with deep rotular groove anterodistally and prominent fibular condyle; tibia with

cnemial epiphysis; tibia with prominent tendinal groove anterodistally; fibula short, not in contact with proximal tarsals; proximal tarsals, including ascending process, fused to one another and to tibia early in postnatal ontogeny; distal tarsals form metatarsal cap with intercondylar prominence (reduced or lost in Ratitae), and this cap fuses to metatarsals early in postnatal ontogeny; proximal end of metatarsal III posterior to and more or less compressed by metatarsals II and IV (as in troodontids, ornithomimids, tyrannosaurids, and elmsaurids*); coossification among metatarsals begins distally (rather than proximally); small foramina between proximal ends of metatarsals (not perforating metatarsus in Hesperornithes); loss of raptorial modifications of pedal digit II (see below); loss of pedal digit V in adult (convergent in some ornithomimids and perhaps caenagnathids).

Aves Linne, 1758

TEMPORAL RANGE.—Late Cretaceous to Recent.

INCLUDED TAXA.—Aves is here restricted to the taxon encompassing all descendants of the most recent common ancestor of Ratitae, Tinami, and Neognathae, as these taxa are diagnosed in Gauthier et al. (in prep.).

DIAGNOSIS.—Based on data derived from Huxley (1867), Pycraft (1900), de Beer (1956), Bock (1963), Feduccia (1980), Cra-craft (1981), Elzanowski (1981), Martin (1983*b*, 1984), and Thulborn (1984), and references cited therein. Aves is diagnosed within ornithurine birds by the possession of the following synapomorphies: loss of teeth on maxilla and dentary, well-developed bill; parietals confined to posteriormost portion of skull roof; loss of coronoid bone; presence of bony mandibular symphysis; presence of tricondylar articulation between quadrate and mandible; narrow, fingerlike odontoid process of axis; saddle-shaped intervertebral articulations fully developed and extend into posterior trunk vertebrae (convergent within Hesperornithes); free portion of tail composed of fewer than nine vertebrae (some *Larus* and penguins display varying degrees of fusion of the first caudal, but the nine caudals so obtained are considered reversals); large, dorsally oriented, plowshare-shaped pygostyle that forms a single element in adults (pygostyle absent in some tinamous and neognaths, and in most ratites); fused uncinat processes (reversed in loons, grebes, penguins, and *Apteryx*, and occasionally unfused in other ratites); glenoid surface not perpendicular to external surface of scapula; single prominent articular surface of humerus separated from external tuberosity; pneumatic skeleton, including fossa and foramen in humerus (reversed in some diving birds; S. Hope, pers. comm.); ulnar crest not in plane of long axis of humeral head; presence of lateral extension of internal tuberosity of humerus (=crus laterale tuberculi medialis); deltopectoral crest of humerus with palmar deflection, and apex not distally placed, so distal profile does not curve abruptly to shaft at a steep angle; ilium further lengthened anteriorly so that it overlaps bases of at least one set of ribs; process on proximal portion of ischium contacts pubis; pubis thin; tibia with ossified supratendinal bridge in adult (reversed in some ratites and owls); hypotarsus forms as outgrowth of distal tarsal cap; small foramina pierce tarsometatarsus proximally; fully enclosed foramen between distal ends of metatarsals III and IV for passage of *M. extensor brevis* digiti IV (this foramen is incompletely enclosed in *Ichthyornis*, and the degree of enclosure may be variable in some ratites).

Numerous characters from less preservable portions of the anatomy, together with ethologic, physiologic, genetic, and immunological data attesting to the distinctiveness of Aves within extant Amniota could be cited at this point. However, because no one has ever mistakenly placed an extant bird in any other extant amniote group aside from Aves, there is little to be gained from belaboring the issue.

PHYLOGENETIC ANALYSIS

I. Phylogenetic Relationships within Dinosauria

In order to address the question of the phylogenetic relationships among the basic taxa, it is first necessary to develop a more inclusive hypothesis that would provide a relevant series of outgroups. Based on evidence presented in Appendix A, Dinosauria is considered monophyletic. Moreover, Herrerasauridae* is considered the sister-group(s) of all other dinosaurs, and Pterosauria-*Lagosuchus*, Ornithosuchidae, *Euparkeria**, and Pseudosuchia represent successively more remote outgroups of Dinosauria.

In view of the ample evidence supporting the hypotheses that Theropoda (see below), Ornithischia, and Sauropodomorpha (including "prosauropods") are each monophyletic (see Appendix A), none of these taxa could have "given rise" to the others. Accordingly, Bakker and Galton's (1974) suggestion that some dinosaurs evolved from "prosauropods" must be rejected (see Charig 1976*b*, for criticisms; see Bonaparte 1976, and Cooper 1981*a*, for more recent restatements of the "prosauropod" origins hypothesis). Instead, "prosauropods" are considered paraphyletic because some are closer to sauropods than others (Appendix A). Given the monophyly of Theropoda, Sauropodomorpha, and Ornithischia, there are only three phylogenetic relationships possible among these taxa: 1) Ornithischia could be the sister-group of Theropoda; 2) Ornithischia could be the sister-group of Sauropodomorpha; or 3) Sauropodomorpha could be the sister-group of Theropoda. The evidence supporting each of these alternatives will be considered below.

Hypothesis I: Two apomorphies are shared by Theropoda and Ornithischia that are not also present in Sauropodomorpha ancestrally. Ancestral Dinosauria possessed three sacral vertebrae, ancestral Sauropodomorpha retained this condition although subgroups within this taxon have as many as six sacral vertebrae (Appendix A). In contrast, Theropoda and Ornithischia have more than three sacrals; at least five are present in Theropoda ancestrally, and the lowest number reported in Ornithischia is the four in the "juvenile" *Scelidosaurus* (given the sexual dimorphism in ornithischian sacral number, the count should be four to five for ornithischians ancestrally; see Galton 1974, 1982).

Reduction of the fifth pedal digit to a metatarsal spur is another apomorphic condition that is shared by Ornithischia and Theropoda, because the fifth digit retains a single phalanx in Sauropodomorpha ancestrally.

Hypothesis II: Cooper (1981*a*:819–829) reviewed the "prosauropod" characters of ornithischians. Except for the structure of the iliac prong and cheek teeth, the characters he discussed are uniformly ancestral conditions at this level of analysis (i.e., they apply to the immediate common ancestor of Dinosauria). Bakker and Galton (1974) suggested that the elongate anterior process of the ilium (=iliac prong) present in two sauropodo-

morphs, *Anchisaurus* and *Ammosaurus*, indicated a more recent common ancestry between Sauropodomorpha and Ornithischia, in that the iliac prong in the latter group is relatively longer than in other archosaurs. Cooper (1981a, fig. 39) noted that the iliac prong may lengthen during ontogeny in *Massospondylus*, but not to the degree seen in either *Anchisaurus* or *Ammosaurus* (see Galton and Cluver 1976). Because the anterior iliac process is comparatively short in all other Sauropodomorpha, including the morphologically generalized members of this group such as *Thecodontosaurus**, this synapomorphy is diagnostic of *Anchisaurus* and *Ammosaurus* alone among Sauropodomorpha. Cooper (1981a) considered *Anchisaurus* to be a juvenile *Ammosaurus*. However, neither taxon displays the characteristic skeletal fusions indicating cessation of growth, so Cooper's hypothesis cannot yet be evaluated. Moreover, Galton (pers. comm.) doubts Cooper's ontogenetic argument because these taxa differ not only in size but in the morphology of the ischium, pubis, pes, and third sacral rib. In any case, this apomorphy cannot be considered evidence supporting sauropodomorph-ornithischian monophyly.

Closely packed, leaf-shaped cheek teeth are apomorphic for archosaurs. Analogous tooth-forms reflect herbivorous habits in extant lepidosaurs. Relatively widely spaced, sharply pointed teeth with finely serrated margins are the ancestral condition for archosaurs (Romer 1956). In sauropodomorphs and ornithischians ancestrally, however, the cheek teeth differ in that the compressed crowns are distinctly set off from the root, the teeth are more closely spaced, and there are fewer and larger serrations on the margins of the crowns than in archosaurs ancestrally. The cheek teeth differ in the two groups: in sauropodomorphs the crowns are elongate, and the serrations are finer and more numerous than in ornithischians; but in ornithischians the crowns are nearly as wide as tall, and the serrations are fewer and larger than in sauropodomorphs. Charig (1967b) argued that these differences preclude derivation of one tooth-form from the other, and that it was equally likely that both were derived from the more general condition retained by theropods ancestrally. In the absence of pertinent developmental information, Charig's first assertion is not testable. One must admit that the second assertion is possible, but fewer assumptions are involved in accepting that the apomorphic aspects of tooth-form shared by Ornithischia and Sauropodomorpha constitute a potential synapomorphy.

Hypothesis III: Hypotheses of theropod-ornithischian monophyly or ornithischian-sauropodomorph monophyly are each supported by only one or two potential synapomorphies. Thus, there is little basis for preferring one of these alternatives over the other. However, neither hypothesis fares well against the final alternative, the taxon composed of sauropodomorphs and theropods, the Saurischia.

Because Sauropodomorpha and Theropoda are likely to be plesiomorphic with respect to synapomorphies diagnostic of Ornithischia, we have from Seeley (1887, 1888) to the present day considered "saurischians" to be "primitive dinosaurs" (hence Galton's 1977 description of *Herrerasaurus** as a "primitive saurischian," even though it was described as being "primitive" compared to all other dinosaurs). In light of evidence presented below, it will be apparent that "saurischians" are not the paraphyletic "stem-group" of other dinosaurs. Indeed the lineage of dinosaurs of which extant birds are a part, the Saurischia, is the monophyletic sister-taxon of Ornithischia within Dinosauria.

Saurischia

(n. comb.=Saurischia Seeley, 1887, plus Aves Linne, 1758)

TEMPORAL RANGE.—late Triassic to Recent.

INCLUDED TAXA.—Sauropodomorpha and Theropoda (including birds).

DIAGNOSIS.—Saurischia is here defined to include birds and all dinosaurs that are closer to birds than they are to Ornithischia. In the ensuing analysis, Herrerasauridae*, Pterosauria-Lagosuchus, Ornithosuchidae, *Euparkeria**, and Pseudosuchia will be used as successively more remote outgroups. Saurischia possesses the following synapomorphies distinguishing it within Dinosauria.

1) Contact between maxillary process of premaxilla and nasal reduced or absent. The maxillary process of the premaxilla is broadly in contact with the nasal at the posterodorsal end of the lateral margin of the external naris in archosaurs ancestrally (Benton 1983; Gauthier 1984). This condition is also ancestral for dinosaurs because it is retained by all Pseudosuchia except some aetosaurs (Sawin 1947), and it is retained by *Euparkeria** (Fig. 1A), Ornithosuchidae (Fig. 1B), and Herrerasauridae* (D. Brinkman, pers. comm.). Compared to the ancestral condition, Ornithischia is further derived in the pronounced posterior extension of the premaxilla (Fig. 1C, D), which may completely separate the maxilla from the nasal in some ornithischians (Romer 1956). Raurisuchia is also diagnosed among Pseudosuchia by a long, but very thin, maxillary process of the premaxilla, and it is thus convergent on Ornithischia in this regard (Gauthier 1984). In contrast to the ancestral condition in Dinosauria, the maxillary process of the premaxilla is reduced and its contact with the nasal is either narrow or absent in Sauropodomorpha (Fig. 1E, F), Ceratosauria (Welles 1984), Carnosauria (Fig. 1G, H), *Compsognathus* (Ostrom 1978), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Deinonychosauria (Fig. 1J, K), and birds (Fig. 1L). Ornithomimidae (Fig. 1I) is an exception among Saurischia, in that it displays a prominent maxillary process of the premaxilla. In the context of the evidence presented below, however, ornithomimids are considered to have reversed this character. In all birds except *Archaeopteryx**, the maxilla is also excluded from the external naris. This is not the ancestral condition, however, in that exclusion is effected by an elongate descending process of the nasal, rather than an ascending process of the premaxilla (Marsh 1880; Gingerich 1976). Pterosauria also has a reduced maxillary process (Wellnhofer 1978), and in this detail of premaxillary form pterosaurs are considered convergent with Saurischia.

2) Temporal musculature extends onto frontal. The temporal musculature originates on the dorsolateral surface of the parietal in saurians ancestrally (Gauthier 1984). During postnatal ontogeny, the temporal musculature hypertrophies and its area of origin extends medially onto the parietal table (Gauthier et al., in press). This condition is retained by Pseudosuchia (Gauthier 1984), *Euparkeria** (Ewer 1965), Ornithosuchidae (Walker 1964), Pterosauria (Wellnhofer 1978), and Ornithischia (Galton 1974), so it appears to be ancestral for Dinosauria as well. In contrast, the temporal musculature extends onto the posterodorsal surface of the frontal bone in Sauropodomorpha (e.g., Huene 1906, 1908, 1932), *Procompsognathus** (Fraas 1913), Ceratosauria (T. Rowe, pers. comm.; Gilmore 1920), Carnosauria (Madsen 1976), *Saurornitholestes** (Sues 1978), Caenagnathidae (Barsbold 1983), Ornithomimidae (Osmolska et al. 1972), and Deinonychosauria (Colbert and Russell 1969). This character has not been reported

in any bird. In view of the evidence presented below, however, it is simpler to accept that the failure of the temporal musculature to reach the frontal results from expansion of the braincase in birds, rather than retention of an ancestral condition.

3) Posterior cervicals elongate. Except among the long-necked protorosaurs, the neck constitutes approximately 33% of the total length of the presacral vertebral column in nonarchosaur Archosauromorpha (Gauthier 1984). There are relatively few complete and articulated vertebral columns known for basal dinosaurian taxa, and comparisons may be complicated by differing numbers of cervical, trunk, and sacral vertebrae, but the available evidence suggests that the neck constituted approximately 40% of the presacral vertebral column in the common ancestor of Saurischia. For example, dividing the combined lengths of vertebrae 2–9 by the combined lengths of vertebrae 2–23 reveals that the neck constitutes 33–34% of the total length in crocodiles (pers. obs.), 34% in *Heterodontosaurus* (Santa Luca 1980), and 33% in *Hypsilophodon** (Galton 1974). In contrast, vertebrae 2–9 constitute 40% of the total length of 2–23 in *Coelophysis* (pers. obs.), 38% in *Compsognathus* (Ostrom 1978), 41%–43% in *Archaeopteryx** (Wellnhofer 1974), and 41% in *Gallimimus* (Osmolska et al. 1972). As has been noted by Galton (1976) and Galton and Cluver (1976), the neck is at least 41% in Sauropodomorpha, not only because of the length of the individual cervicals, but because at least one additional vertebra has been added to the cervical series (see Appendix A). The elongation of the neck appears to have been accomplished by lengthening of the posterior cervicals in Saurischia. Leaving aside the length of the axis, it is evident that vertebrae 3, 4, and 5 are the longest elements in the neck in Pseudosuchia (pers. obs.), *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte 1975a), *Lagosuchus** (Bonaparte 1975b), and Pterosauria ancestrally (the neck becomes long within Pterosauria but the neck is short in *Scleromochlus**, the sister-taxon of all other pterosaurs [Gauthier 1984]). This condition is ancestral for Dinosauria in that cervicals 3–5 are also longest in Herrerasauridae* (Galton 1977) and Ornithischia (Galton 1974, 1975, 1978; Santa Luca 1980; Colbert 1981). In contrast, the longest (postaxial) cervicals in saurischians are 6–9. For example, vertebrae 6 and 12 are subequal in length in crocodiles (pers. obs.) and such ornithischians as *Heterodontosaurus* (Santa Luca 1980) and *Hypsilophodon** (Galton 1974). In contrast, cervical 6 is 22% longer than cervical 12 in *Dilophosaurus* (Welles 1984), 37% in *Coelophysis* (pers. obs.), 35% in *Compsognathus* (Ostrom 1978), 62% in *Gallimimus* (Osmolska et al. 1972), and 45% in *Archaeopteryx** (Wellnhofer 1974). Sauropodomorphs also share the apomorphic proportional difference between the lengths of vertebral centra 6 and 12 (e.g., Galton and Cluver 1976). Although our knowledge is less than complete, it appears that elongation of the cervicals posterior to cervical 5 accounts for the neck forming more than 33% of the length of the presacral vertebral column in Sauropodomorpha and Theropoda aside from taxa with large leads and consequently short necks, such as *Tyrannosaurus* (Charig et al. 1965).

4) Axial postzygapophyses set lateral to prezygapophyses. In anterior view, the pre- and post-zygapophyses are approximately equidistant from the midline of the axial centrum in Pseudosuchia (pers. obs.), *Euparkeria** (Ewer 1965), *Lagosuchus** (Bonaparte 1975b), and Pterosauria ancestrally (Welln-

hofer 1975). This condition appears to be ancestral for Dinosauria in that it is retained in Ornithischia (e.g., Ostrom and McIntosh 1966; Ostrom 1970). In contrast, the prezygapophyses lie closer to the midline so that the postzygapophyses are entirely lateral to the prezygapophyses in anterior view in Sauropodomorpha (Fig. 3D), Ceratosauria (Fig. 3E), Carnosauria (Madsen 1976), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 3F), and Avialae (Fig. 3G).

5) Epiphysis present on anterior cervical postzygapophyses. Epiphyses (=processus dorsalis of Boas 1929, or anapophysis of Zusi and Storer 1969) on the anterior cervical vertebrae are absent in Pseudosuchia (pers. obs.), *Euparkeria* (Ewer 1965), Ornithosuchidae (Bonaparte 1975a), and *Lagosuchus* (Bonaparte 1975b), although they may be present at the base of the neck in fully adult archosaurs such as *Alligator* (pers. obs.). Epiphyses are also absent in Pterosauria ancestrally although they are present in Pteranodontidae (Wellnhofer 1978). The anterior cervicals lack epiphyses in Dinosauria ancestrally because these processes are absent in Herrerasauridae* (Galton 1977) and Ornithischia (e.g., Santa Luca 1980). In contrast to the ancestral condition in Dinosauria, epiphyses are present in Sauropodomorpha (Fig. 3D; and see Hatcher 1901, 1903; Huene 1908), Ceratosauria (Fig. 3E; and see Welles 1984), Carnosauria (Osborn 1917), *Compsognathus* (pers. obs.), *Coelurus** (Marsh 1881a, 1884a), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 3F), and birds (Fig. 3G). Epiphyses are present on at least the second through the fourth cervicals, with those on the axis being the most prominent; less prominent epiphyses may be present throughout the cervical series in large theropods (e.g., *Allosaurus*; Madsen 1976). Epiphyses extend caudally and somewhat laterally from the dorsal surfaces of the cervical postzygapophyses; they are largest anteriorly and diminish in size posteriorly. In birds they are associated with the insertions and origins of a variety of dorsal cervical muscles, such as the M. spleni colli, M. spinalis cervicis, M. ascendentes cervicis, and M. intercostales. Some muscles insert directly onto the epiphyses, and others indirectly through insertion on an aponeurosis extending back from the epiphysis (Zusi and Storer 1969). The crocodylian homologues of these muscles have yet to be determined.

6) Hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae. Accessory intervertebral articulations are absent in all Pseudosuchia except some Rauisuchia (Charig 1976b; Bonaparte 1981) and Aetosauria (M. Parrish, pers. comm.); such articulations are also absent in *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte, pers. comm.), *Lagosuchus** (Bonaparte 1975b), Pterosauria (Wellnhofer 1978), Herrerasauridae* (Galton 1977), and Ornithischia (Steel 1969). Thus, accessory intervertebral articulations are absent in Dinosauria ancestrally. As noted most recently by Steel (1970) and Bakker and Galton (1974), Theropoda and Sauropodomorpha alone among dinosaurs possess hyposphene-hypantra accessory intervertebral articulations in the trunk region. Hyposphene-hypantra articulations are present in Sauropodomorpha (e.g., Cooper 1981a), *Liliensternus** (Huene 1934), Ceratosauria (Welles 1984), Carnosauria (Madsen 1976), *Coelurus** (Marsh 1884a), *Microvenator** (Ostrom 1970), Ornithomimidae (Osmolska et al. 1972), and Deinonychosauria (Ostrom 1969b). The vertebrae of *Archaeopteryx** are not exposed appropriately

to determine if hyposphene-hypantra accessory intervertebral articulations are present, but other birds do not possess hyposphene-hypantra. The vertebrae of birds are highly modified, however, and in the context of all the evidence it is simpler to accept that their intervertebral articulations are further modifications of the saurischian condition, not the retention of an ancestral intervertebral articulation.

7) Manus more than 45% of length of humerus plus radius. The longest digit in the manus (plus its metacarpal) is 28% of the length of the humerus plus radius in the early crocodile *Protosuchus* (Colbert and Mook 1951); this length is proportionately longer in extant crocodiles displaying negative allometry in limb length (e.g., 37% in *Crocodylus porosus* and *Caiman sclerops*, pers. obs.). These size relationships appear to be ancestral for dinosaurs because in ornithischians such as *Scutellosaurus** (38%; Colbert 1981), *Lesothosaurus* (26–29%; estimates based on Galton 1978), and *Hypsilophodon* (34%; Galton 1974), the longest manal digit and its metacarpal is no more than 38% of the length of the humerus plus radius. The single exception appears to be *Heterodontosaurus*, in which the manus is 56% of the length of the humerus plus radius. This attribute is considered diagnostic of this taxon among Ornithischia (Santa Luca 1980). In contrast, the longest digit and its metacarpal is at least 45% of the length of the humerus plus radius in Saurischia ancestrally. For example, the manus is 45% to 47% of the length of the humerus plus radius in *Thecodontosaurus**, 60% in *Efraasia** (estimates based on Huene 1914c and Galton 1973a), 47% in *Syntarsus* (Raath 1969) and *Coelophysis* (Osborn 1969b), 77% in *Allosaurus*, 75% in *Deinonychus*, and 58% in *Ornithomimus* (Ostrom 1969b).

8) Manus markedly asymmetrical. In archosaurs ancestrally, the inner digits of the manus are stouter than are the outer digits, and the third digit is the longest digit in the manus (Fig. 4G). The asymmetry of the manus becomes more pronounced within ornithosuchian archosaurs and yields a further reduction of the outer two digits of the manus in dinosaurs ancestrally (Fig. 4H–O). Pterosaurs are exceptional among Archosauria: the enormously enlarged fourth digit supporting the wing membrane can hardly be considered the ancestral condition for archosaurs, and the hand is not modified this way in *Scleromochlus* (Huene 1914a). Nevertheless, the pterosaur's third digit is the longest of the digits remaining unmodified. Ornithischia retains the ancestral condition: digit three is longest (Fig. 4H). In contrast to the ancestral condition in dinosaurs, however, the inner two digits (two and three) of the manus are further enlarged, so that the second, rather than the third, is now the longest digit in the hand in Sauropodomorpha (Fig. 4I, J), Ceratosauria (Fig. 4K), Carnosauria (Fig. 4L), *Ornitholestes** (Osborn 1917), Elmsauridae* (Osmolska 1981), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 4M), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O). Asymmetrically developed hands are characteristic of Archosauria, and this modification becomes more pronounced within Ornithosuchia, culminating in the markedly asymmetrical hands of birds. To be complete, a process-related theory of limb development must account for this peculiarity; likewise, one must be cautious in developing a general theory of hand morphogenesis based largely or exclusively on the hands of extant birds.

9) Bases of metacarpals IV and V lie on palmar surfaces of

manal digits three and four respectively. The ancestral condition in Sauria (=extant diapsids; Gauthier 1984) is that the bases of the medial metacarpals overlap the bases of the lateral metacarpals. This condition is retained by Pseudosuchia (Fig. 4G), *Euparkeria** (Ewer 1965), Ornithosuchidae (Walker 1964), Pterosauria (Wellnhofer 1978), and Ornithischia (Fig. 4H). Unlike other archosaurs, however, the base of metacarpal IV, and to a greater extent that of V, lie more on the palmar surface of the hand in Sauropodomorpha (e.g., Janensch 1922; Cooper 1981a:740, fig. 37, 38). The base of the fourth digit of early theropods such as Ceratosauria also lies on the palmar surface of the base of the third digit (e.g., Welles 1984:153, fig. 37; I thank T. Rowe for pointing out that the sauropodomorph condition also applies to theropods). The fifth manal digit is absent from the ontogeny of extant Theropoda; however, Colbert's unpublished drawing of an intact hand of *Coelophysis* reveals a nubbin of bone lying on the palmar surface of the base of metacarpal IV. Because this piece of bone lies in the same position as the fifth digit in sauropodomorphs, Colbert's interpretation of this element as a remnant of the fifth digit is probably correct. In more derived Theropoda the fourth manal digit is lost, although it is retained in embryos of extant birds, and a small remnant of this digit has been observed on the palmar surface of the hand in *Ornitholestes** (Osborn 1917; see Part III, character 45 for further discussion).

10) Saurischian pollex. In Archosauria ancestrally, metacarpal I is only a little shorter than II, phalanx I of the first digit is shorter than metacarpal I, and the claw-bearing ungual is neither very large nor sharply pointed (Gauthier 1984). This condition is retained in Pseudosuchia (Fig. 4G). Aside from the offset head of metacarpal I and a relatively larger and more sharply pointed ungual, the first digit and its metacarpal in Ornithosuchidae (Bonaparte 1975a) and Ornithischia (Fig. 4H) is as in archosaurs ancestrally. Manal digit one, the pollex, of Theropoda and Sauropodomorpha differs from that of other Archosauria in several ways. First, the pollex is more robust and bears a larger ungual phalanx (Fig. 4I–O); this character is extreme within Sauropodomorpha (Fig. 4I, J). Second, metacarpal I is only half or less the length of metacarpal II, and the distal condyles are more markedly asymmetrical (Fig. 4I, K; see Welles 1984). Third, the first phalanx is much longer than metacarpal I; the first phalanx equals or exceeds the length of any other phalanx in the hand (Fig. 4I–O). Galton (1971), Bakker and Galton (1974), and Baird (1980) discussed the grasping ability of dinosaur hands, and commented on the range of motion possible in the saurischian pollex, noting that the articular surfaces allow a fairly precise reconstruction of the range of possible movements. Galton (1971) described how the articular surfaces within the saurischian pollex force the claw to diverge and point inward during extension and to converge with the second and third digits and point downwards during flexion; at maximum extension the claw points inward to a greater degree in Sauropodomorpha than in Theropoda. As *Massospondylus* indicates (Fig. 4J), the manus was modified to play a greater role in support and locomotion early in sauropodomorph history; the entire hand became broader, shorter, and more robust, and the first phalanx and metacarpal were likewise shortened. Aside from the large claw, scarcely any evidence of the grasping hand of saurischians remains in the elephantine hands of Sauropoda (e.g., Janensch 1922). Although

the first digit is seldom used for grasping in ornithurine birds, its functional independence has been conserved. Indeed, the dinosaurian modifications of the first digit toward the alula, appears to have been essential to the development of powered flight in birds (Bellairs and Jenkin 1960).

Saurischian monophyly is supported by shared apomorphies in construction of the snout, pattern of hypertrophy of the temporal musculature, elongation of the cervical region, modification of the axial zygapophyses, presence of epiphyses in the anterior cervicals, accessory intervertebral joints, and a variety of distinctly avian modifications of the manus. Possible alternative hypotheses are less able to account for observed patterns of shared apomorphies; accordingly, Sauropodomorpha and Theropoda (including birds) are hypothesized to be sister-groups within Saurischia, and Ornithischia is considered to be the sister-group of Saurischia within Dinosauria.

II. Phylogenetic Relationships within Theropoda

Theropoda

(n. comb. = "Theropoda" Marsh, 1881*b*, plus Aves Linne, 1758)

TEMPORAL RANGE.—late TRIASSIC to Recent.

INCLUDED TAXA.—*Procompsognathus**, *Lihenstermus**, Ceratosauria, Carnosauria, Ornithomimidae, *Compsognathus*, Caenagnathidae, Elmsauroidea*, *Microvenator**, *Coelurus**, *Saurornitholestes**, *Hulsanpes*, *Ornitholestes**, Deinonychosauria, and Avialae. The reader is referred to Olshevsky (1978) and Welles (1984) for additional nonavian theropod taxa that were not considered in this investigation.

DIAGNOSIS.—Theropoda is defined ostensibly to include birds and all saurischians that are closer to birds than they are to sauropodomorphs. Sauropodomorpha, Ornithischia, Herrerasauridae*, Pterosauria-*Lagosuchus*, Ornithosuchidae, *Euparkeria**, and Pseudosuchia will be used as successively more remote outgroups in the following analysis. Theropods are distinguished from other saurischians by the following synapomorphies.

11) Reduced overlap of dentary onto postdentary bones and reduced mandibular symphysis. Many extant birds display some degree of intramandibular mobility, and several authors have noted that the construction of nonavian theropod mandibles also allows intramandibular mobility (e.g., Gingerich 1976). Extant Pseudosuchia have solidly constructed mandibles that show no indication of intramandibular mobility. That is to say, crocodylians display a broad overlap between dentary and postdentary bones (with the dentary extending to the level of the orbit), a process of the dentary passing dorsal to the mandibular fenestra, and a prominent mandibular symphysis. Each of these attributes indicates the absence of intramandibular mobility, and they are retained in nontheropod ornithosuchians, including Ornithischia (Fig. 1C, D; Romer 1956) and Sauropodomorpha (Fig. 1E, F; Galton 1984). In contrast, the mandibular symphysis is reduced in Theropoda and the overlap of the dentary onto the postdentary bones is very reduced, such that the anterodorsally sloping posterolateral margin of the dentary terminates antorbitally (Fig. 1G–L). This region of the mandible is poorly preserved in *Archaeopteryx**, but Gregory (1952) described the similarities between the intramandibular joints of *Ichthyornis* and *Hesperornithes* and those of some squamates with intramandibular kinesis. Many extant lineages of Aves retain the ancestral relations of theropod dentary and postdentary elements and intramandibular mobility (e.g., *Larus*). However,

birds with noncarnivorous diets, and short and stout jaws with broad mandibular symphyses, do not.

12) Lacrimal broadly exposed on skull roof. The lacrimal forms the posterodorsal and posterior margins of the antorbital fenestra, but does not participate in the formation of the skull roof in Pseudosuchia (Bonaparte 1981), *Euparkeria** (Fig. 1A), Ornithosuchidae (the lacrimal gains some exposure dorsally as part of the supraorbital cornice; Fig. 1B), Pterosauria (Wellnhofer 1978), Ornithischia (Fig. 1C, D), and Sauropodomorpha (Fig. 1F). In contrast to the ancestral condition, the lacrimal forms much of the skull roof anterior and lateral to the prefrontal above the orbit in *Procompsognathus** (pers. obs.), Ceratosauria (Welles 1984), Carnosauria (Fig. 1G, H), Ornithomimidae (Fig. 1I), Deinonychosauria (Fig. 1J, K), *Compsognathus* (pers. obs.), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), and Avialae (Fig. 1L; see Part V, character 67).

13) Presence of maxillary fenestra. An accessory fenestra within the antorbital fossa is absent in all Pseudosuchia (Krebs 1976), *Euparkeria** (Fig. 1A), Ornithosuchidae (Fig. 1B), Pterosauria (Wellnhofer 1978), Ornithischia (Fig. 1C, D), and Sauropodomorpha (Fig. 1E, F). Thus, a maxillary fenestra is absent in Saurischia ancestrally. In contrast, a small fenestra lies at the anterior margin of the antorbital fossa in Ceratosauria (T. Rowe, pers. comm.), and a larger fenestra lies in a more posterior position within the antorbital fossa in Carnosauria (Fig. 1G, H), *Ornitholestes** (Osborn 1917), *Compsognathus* (Ostrom 1978), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 1I), Deinonychosauria (Fig. 1J, K), and *Archaeopteryx** (Fig. 1L). This character is absent and has presumably been lost in Ornithurae (see Part III, character 37).

14) Vomers fused anteriorly. The vomers are short, narrow, and paired in Archosauria ancestrally (Gauthier 1984); to judge from the condition seen in Pseudosuchia (aside from the comparatively long vomers of aetosaurs, Walker 1961), *Euparkeria** (Fig. 2A), Ornithosuchidae (Fig. 2B), and Pterosauria (Wellnhofer 1978) this condition appears ancestral for Ornithodira (Appendix A). In contrast, the vomers are elongate, extending well posterior to the level of the anterior limit of the palatine in Ornithischia ancestrally (Galton 1974; Heaton 1972), Sauropodomorpha ancestrally (Huene 1906, 1908, 1932; Galton 1984), and Theropoda aside from Neognathae (pers. obs.), and this appears to be the ancestral condition in Dinosauria. Few nonavian theropod fossils have this region of the skull preserved. Theropoda differs from dinosaurs, other than thyrophan ornithischians (P. Sereno, pers. comm.), in that the vomers are indistinguishably fused anteriorly (although they may be paired in a few neognaths, pers. obs., and in *Hesperornis*, L. Martin, pers. comm.). Nevertheless, the presence of the apomorphic condition in theropods as diverse as *Procompsognathus** (Ostrom 1981), *Ceratosaurus* (T. Rowe, pers. comm.), *Deinonychus* (Ostrom 1969*b*), *Allosaurus* (Fig. 2C), *Tyrannosaurus* (Fig. 2D), *Oviraptor* (Osmolska 1976), *Gobipteryx* (Elzanowski 1977, 1981), and Ratitae and Tinami (Huxley 1867), suggests that the vomers are fused anteriorly in Theropoda generally. Walker (1964) described the enlarged, diamond-shaped anterior ends of the vomers in *Ornithosuchus* as being similar to the condition of the fused anterior third of the vomer in *Tyrannosaurus*. However, this similarity obtains between *Tyrannosaurus* and *Ornithosuchus* alone. Moreover, the paired and short vomers of the latter (Fig. 2B) are otherwise plesiomorphic

with respect to those of all other theropods, including *Tyrannosaurus* (Fig. 2D).

15) Expanded ectopterygoid with ventral fossa. Colbert and Russell (1969) argued that in early theropods (e.g., Ceratosauria) the ectopterygoid was "simple" and without a ventral fossa. However, I have observed this fossa in the ceratosaur *Coelophysis*. I agree with the observation that there is an expanded ectopterygoid with a more or less prominent fossa ventrally in the main body of the element in Carnosauria, Ornithomimidae, and Deinonychosauria (Colbert and Russell 1969), *Saurornitholestes** (Sues 1978), and in Caenagnathidae (Barsbold 1983). This character cannot be determined in *Archaeopteryx**, and the ectopterygoid has not been identified with certainty in Ornithurae (see McDowell 1978). In the context of all the evidence, birds are considered to have attained their current condition from an ectopterygoid like that seen in theropods generally.

16) First intercentrum with large occipital fossa and small odontoid notch. The occipital fossa on the anterior face of the first intercentrum is more than three times as wide as it is tall and the odontoid notch is consequently broad and deep in Pseudosuchia (pers. obs.), *Euparkeria** (Ewer 1965), Ornithischia (Fig. 3A), and Sauropodomorpha (Hatcher 1901). In contrast, the occipital fossa is only about twice as wide as it is tall and the odontoid notch is consequently smaller in Ceratosauria (Fig. 3B), Carnosauria (Madsen 1976), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Ostrom 1969b), and Avialae (Fig. 3C).

17) Second intercentrum with broad, crescentic fossa anteriorly for reception of first intercentrum. The articular surface on the anteroventral margin of the axial (2nd) intercentrum is convex in Pseudosuchia (pers. obs.). Dinosaurs differ from the ancestral condition in Archosauria in that this articular surface is at least partly concave (Fig. 3D). Compared to other dinosaurs, however, the articular surface on the axis for the first intercentrum forms a broad, deep, and concave fossa in Ceratosauria (Fig. 3E), Carnosauria (Gilmore 1920), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 3F), and Avialae (Fig. 3G).

18) Pleurocoelous presacral vertebrae, particularly in cervical region. Fenestra leading into hollow centra (=pleurocoels) are absent in Pseudosuchia (Romer 1956), *Euparkeria** (Ewer 1965), Ornithosuchidae (Walker 1964), *Lagosuchus** (Bonaparte 1975b), Herrerasauridae (Galton 1977), Ornithischia (Romer 1956), and Sauropodomorpha ancestrally (Cooper 1981a). Thus, nonpleurocoelous vertebrae are the ancestral condition for Saurischia. In contrast, pleurocoels are present in all Theropoda; Ostrom (1978) discussed the distribution of this character within the group, noting regional variations in the presacral column. Pleurocoels are present in Ceratosauria (Gilmore 1920), Carnosauria (Madsen 1976), Ornithomimidae (Osmolska et al. 1972), *Saurornitholestes** (Sues 1978), *Coelurus** (Marsh 1884a), *Microvenator** (Ostrom 1970), Deinonychosauria (Ostrom 1969b), and Avialae (Ostrom 1976a). Analogous modifications are known in Pterosauria (Wellnhofer 1978) and Sauropoda (Marsh 1896), but this is considered convergence because pleurocoels are absent in their respective outgroups among sauropodomorphs, ornithischians, herrerasaurs*, and *Lagosuchus**.

19) At least two additional vertebrae incorporated into sacrum (including at least one from the caudal series and at least one from the trunk). As argued above, three sacrals are present

in Dinosauria ancestrally. In contrast, no theropod in which the sacrum is coossified and intact has fewer than five sacrals. Among theropods, the character has been reported in Ceratosauria (Raath 1969), Carnosauria (Steel 1970; Madsen 1976), Ornithomimidae (Osborn 1917), Deinonychosauria (Barsbold 1974), and Avialae (Ostrom 1976a). Ornithurae has many more vertebrae in the sacrum, a character that is by no means unique to Theropoda. As noted above, a sacrum consisting of at least four to five vertebrae may also be ancestral for Ornithischia. The *Heterodontosaurus* (Santa Luca 1980) and ornithopod (Galton and Jensen 1973) lineage of Sereno (1984) has at least five or six, which is also the lowest number reported in pachycephalosaurs and ceratopsians, with the latter group possessing as many as eleven sacrals (Steel 1969). In addition, subgroups within Pterosauria (Wellnhofer 1978) and Sauropoda (Berman and McIntosh 1978) have five or more sacrals.

20) Transition point in tail (sensu Russell 1972). In Dinosauria ancestrally, the caudal zygapophyses are short and vertically oriented, and the transverse processes are present posterior to the middle of the caudal series (Santa Luca 1980; Cooper 1981a). In contrast to the condition retained by Sauropodomorpha, however, in Theropoda the neural arches and the transverse processes are reduced posteriorly so that they are absent in most of the posterior half of the tail. In addition, the caudal prezygapophyses in the posterior half of the tail are elongate, pointed anteriorly, and clasp the elongate, blocklike postzygapophysial moiety. Finally, the caudal haemal arches in at least the posterior third of the tail are depressed and boat-shaped in lateral outline (e.g., Fig. 3E, F). The degree of transformation in each of these aspects of caudal morphology is not precisely correlated. Although the zygapophyses may begin elongation prior to complete loss of transverse processes, with modified haemal arches subsequently appearing further posteriorly, these transformations take place within a few vertebrae of one another; accordingly, they are described collectively as the "transition point." The least-modified tails seen among theropods are present in Ceratosauria (Raath 1969). However, the transformation in caudal form is more profound and the transition point begins closer to the base of the tail in Carnosauria (Lambe 1917), *Compsognathus* (Ostrom 1978), *Ornitholestes** (Osborn 1917), Ornithomimidae (Osmolska et al. 1972), Caenagnathidae (Barsbold 1983), Deinonychosauria (Ostrom 1969b), and *Archaeopteryx** (see Part III, character 40). The tail is further modified in Ornithurae, in that the proximal caudal zygapophyses are lost, but the tail still retains mobile proximal and stiff distal portions (i.e., the pygostyle). Moreover, in Hesperornithes that possess a multisegmented pygostyle in the adult, these caudal vertebrae have lost the neural spines and transverse processes. Although lacking the ventral keel, boat-shaped haemal arches are retained in the proximal caudals in Hesperornithes (L. Martin, pers. comm.) and in several other ornithurine birds, such as *Ichthyornis*, penguins, and loons (Marsh 1880). A similarly stiffened posterior part of the tail arose convergently in *Staurikosaurus** (Galton 1977); and vaguely similar modifications are present in ankylosaurs, in which the distal extremity of the tail bears a club (Coombs 1978a). An analogous condition, although highly modified in a fashion similar to dromaeosaurs, arose convergently within Pterosauria (i.e., the tail in *Scleromochlus** is not stiffened). The tail of *Staurikosaurus** could be construed as evidence of a relationship to theropods. How-

ever, so far as *Staurikosaurus** is preserved, it lacks the diagnostic characters of Saurischia, and it shares an expanded distal end of the pubis with *Herrerasaurus** (Galton 1977; and see Gauthier 1984).

21) Enlarged distal carpal I overlaps bases of metacarpals I and II. Few early archosaurs have well-preserved hands, but aetosaur (Sawin 1947) and embryo crocodylian pseudosuchians (pers. obs.) are like Ornithischia (e.g., Fig. 4H) in retaining the ancestral saurian condition, in which the distal carpals are restricted to the bases of their respective metacarpals. This region is not preserved in *Efraasia**. In *Thecodontosaurus** distal carpal I is also confined to the base of metacarpal I, but the base of metacarpal II and its associated distal carpal are not preserved (Huene 1914c). The only reasonably complete hands of early sauropodomorphs are those of *Massospondylus* and some platanosaurs (e.g., Huene 1932; Young 1941, 1947, 1958; Galton and Cluver 1976:135, fig. 7). Based on published illustrations, personal communications from P. Galton, and personal observation of *Plateosaurus*, it appears that distal carpal I is restricted to the base of metacarpal I in Sauropodomorpha ancestrally. *Massospondylus* may be an exception, in that distal carpal I overlaps distal carpal II, although the former is separated from metacarpal II by the latter (Fig. 4J; and see Cooper 1981a:737, fig. 32). In contrast, *Halticosaurus** (Huene 1934), Ceratosauria (Fig. 4K), Carnosauria (Fig. 4L), *Coelurus** (Ostrom 1976a), Caenagnathidae (Barsbold 1983), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O) are distinguished from other archosaurs in that an enlarged distal carpal I overlaps the bases of the inner two metacarpals, thus functionally integrating digits I and II in the wrist, just as in extant birds. In theropods in which distal carpals I and II are present, a small distal carpal II lies distal and largely posterolateral to distal carpal I; thus distal carpal II lies at least partly between distal carpal I and metacarpal II (Madsen 1976). Distal carpals I and II are fused in *Syntarsus rhodestensis*; the adult status of the type-specimen is indicated by several other fusions in the postcranial skeleton marking the cessation of growth (Raath 1969). According to Madsen (1976), in *Allosaurus fragilis* the larger distal carpal I and the smaller distal carpal II fuse to one another very late in postnatal development. Ornithomimidae is an exception in that its wrist is composed of small and poorly ossified carpals that lack articular facets (Osborn 1917). Ornithomimids are thus like tyrannosaurid carnosaurs (Barsbold 1983) in that the carpals appear to be arrested at a juvenile stage of development. No separate distal carpal II has been reported in any adult deinonychosaur or bird; the elements are said to arise separately in bird embryos (Heilmann 1926), although Hinchliffe and Hecht (1984) have been unable to identify more than a single condensation in *Gallus*.

22) Manal digit V reduced to a vestige or absent. The fifth manal digit is present in all Pseudosuchia (e.g., Fig. 4G), *Euparkeria** (Ewer 1965), and Ornithosuchidae (Bonaparte 1975a). And, although the digit is reduced in Dinosauria ancestrally, it is retained by Ornithischia (Fig. 4H) and Sauropodomorpha (Fig. 4I, J). Thus, a fifth manal digit is present in Saurischia ancestrally. In contrast, all that remains of the fifth manal digit in Ceratosauria is the small metacarpal splint lying at the base of the palmar surface of metacarpal IV in *Coelophysus* (Colbert, pers. comm.). No other ceratosaurs are reported to have a vestigial fifth digit, but *Coelophysus* is the only ceratosaur that is well enough preserved to be able to discriminate between ab-

sence and nonpreservation. No vestige of the fifth manal digit has been reported in Carnosauria (Fig. 4L), *Compsognathus* (Bidar et al. 1972), *Saurornitholestes** (Sues 1978), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Elmsauridae* (Osmolska 1981), Ornithomimidae (Fig. 4M), Deinonychosauria (Fig. 4N), or Avialae (Fig. 4O). The fifth manal digit is also missing in the ontogeny of extant birds (Heilmann 1926). *Lilienstermus** is described as retaining a reduced fifth digit, but Huene's (1934) description and illustration of what remains of the hand speaks against such an interpretation; the metacarpals he interpreted as being III and IV were capped by an enlarged carpal, thus corresponding to metacarpals I and II of other theropods, and there is no evidence of a fifth digit. Loss of the fifth manal digit arose convergently in Pterosauria (Wellnhofer 1978).

23) Manal digit IV reduced or absent in adult. As discussed above, manal digits IV and V are reduced in Dinosauria ancestrally. Theropoda is unique, however, in that manal digit IV is never longer than metacarpal III, and it is never represented by more than a metacarpal with a vestigial phalanx on its distal extremity. Ceratosauria (Fig. 4K) retains the vestigial manal digit IV just described, but the fourth digit is reduced to a mere nubbin of bone or is absent in postembryonic development in Carnosauria (Fig. 4L), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), *Compsognathus* (Bidar et al. 1972), *Saurornitholestes** (Sues 1978), Elmsauridae* (Osmolska 1981), Ornithomimidae (Fig. 4M), Deinonychosauria (Fig. 4N), and in all birds beyond embryonic stages (Fig. 4O; Heilmann 1926). The ancestral theropod phalangeal formula is thus 2-3-4-1-0, rather than 2-3-4-3-2 as it is in the hands of Dinosauria and Saurischia ancestrally.

24) Manus with elongate penultimate phalanges. The penultimate phalanges are shorter than the more proximal elements in each digit in Pseudosuchia (Fig. 4G) and Ornithischia (Osborn 1924a; *Heterodontosaurus* is apomorphic among ornithischians in this regard, see Fig. 4H). The same can be said for digits two through five in Sauropodomorpha, except that like other saurischians the first metacarpal is relatively short (e.g., Fig. 4J). Thus, a hand with the same internal proportions as archaic sauropodomorphs such as *Thecodontosaurus** (Fig. 4I) appears to be ancestral for Saurischia. Theropods are further derived in that the penultimate phalanges on the functional digits are uniformly longer than the more proximal elements comprising their respective digits. This apomorphy appears in its most general form among Ceratosauria (Fig. 4K), but it is also present in Carnosauria (Fig. 4L); it is further developed in *Saurornitholestes** (Sues 1978), Caenagnathidae (Barsbold 1983), Elmsauridae* (Osmolska 1981), Ornithomimidae (Fig. 4M), *Ornitholestes** (Osborn 1917), Deinonychosauria (Fig. 4N), and *Archaeopteryx** (Fig. 4O). Ornithurine birds retaining an unmodified first digit usually maintain its ancestral proportions. However, the first phalanx in manal digit II may be subequal to or longer than the second phalanx, and the third digit often retains only one phalanx. The ornithurine carpometacarpus cannot be considered plesiomorphic, and the way in which the ornithurine manus differs from that of other theropods is considered to have arisen secondarily. Pterosaurs also have elongate penultimate phalanges in digits I through III, and this is considered yet another example of convergence between pterosaurs and theropods.

25) Manal digit III with short first and second phalanges. The third phalanx of digit III is shorter than either the first or second in Pseudosuchia (Fig. 4G), Ornithischia (Fig. 4H), and Sauropodomorpha (Fig. 4I, J), so this condition is ancestral for Saurischia. In contrast, the first and second phalanges of manal digit III are short, so that the third phalanx is the longest element in Ceratosauria (Fig. 4K) and Carnosauria (Fig. 4L), and this character is even more markedly developed in Ornithomimidae (Fig. 4M), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Elmsauridae* (Osmolska 1981), *Saurornitholestes** (Sues 1978), and Deinonychosauria (Fig. 4N). This condition is ancestral for Avialae (Fig. 4O), but it is absent in the diagnostically modified carpometacarpus of Ornithurae, in which only one phalanx remains in manal digit III (Heilmann 1926). This character has arisen convergently in Pterosauria, some of which may have very short first and second phalanges as in the subgroup of theropods of which birds are a part (see below), but others may have only the first phalanx shortened (Wellnhofer 1978); the level at which these characters arose within Pterosauria is unknown.

26) Manal unguals enlarged, compressed, sharply pointed, strongly recurved, and with enlarged flexor tubercles. As noted above, modification of the pollex in Ornithosuchidae indicates that the ability to grasp with the hands unites a more inclusive group of Ornithosuchia than Dinosauria alone. Nevertheless, with the possible exception of Pterosauria (Wellnhofer 1978), no archosaurs except theropods have manal unguals so modified as to indicate that they played an important role in securing prey (Ostrom 1969b). Impressions of claw sheaths are preserved only in *Compsognathus*, *Archaeopteryx** (pers. obs.), and *Chirostenotes** (Currie, pers. comm.) among Mesozoic theropods, and claw sheath morphology corroborates estimates of claw-form extrapolated from ungual morphology (Ostrom 1978). Based on ungual morphology, raptorial claws are present in the hands of *Liliensternus** (Huene 1934), Ceratosauria (Gilmore 1920; pers. obs.), Carnosauria (Madsen 1976), *Coelurus** (Ostrom 1976a), *Ornitholestes** (Osborn 1917), *Compsognathus* (Ostrom 1978), *Saurornitholestes** (Sues 1978), *Microvenator** (Ostrom 1970), Caenagnathidae (Barsbold 1983), Elmsauridae* (Osmolska 1981), Deinonychosauria (Russell 1969; Ostrom 1969b, 1974b), and *Archaeopteryx** (Ostrom 1976a). The juveniles, and occasionally the adults, of a wide variety of extant birds may retain clawed digits, but with the notable exception of juvenile Hoatzin (*Opisthocomus*) they are virtually nonfunctional in modern birds (Heilmann 1926). As noted above, an enlarged and sharply pointed first ungual is an ancestral condition for Saurischia; however, even this claw only approaches the level of specialization seen in Theropoda (compare *Masospondylus* in Cooper 1981a:748, fig. 45, with *Deinonychus* in Ostrom 1969b:108, fig. 63). In the context of all the evidence, the hands of Ornithomimidae and Ornithurae are considered secondarily modified in this regard.

27) Preacetabular part of ilium enlarged and extending far forward of acetabulum. A prominent iliac spine arose prior to the origin of Archosauria within Archosauromorpha (Gauthier 1984). The ancestral condition is retained by Pseudosuchia (Romer 1956), *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte 1975a), *Lagosuchus** (Bonaparte 1975b), and Sauropodomorpha (Fig. 5B). Ornithischians have a diagnostically elongate iliac spine (Fig. 5A). In contrast, Colbert (1964) noted

that an enlarged preacetabular portion of the ilium obtains in all theropods (e.g., Fig. 5C–I). The increased length of the theropod ilium is probably correlated in a general way with the added number of sacral vertebrae. The character is not entirely redundant, however, because the addition of sacral vertebrae has not been accompanied by the same modifications of the ilium in other archosaurs. Rowe (pers. comm.) pointed out that the *M. puboischiofemoralis internus* (2), which originates beneath the posterior transverse processes in crocodiles, has moved onto the enlarged anterior portion of the ilium in Theropoda. Both Walker (1977) and M. Parrish (pers. comm.) believe that this muscle originated from the medial part of the pubis and that the dorsal shift of origin of the pifi 2 (one of the so-called *M. ilirotrochantericus* group found in Aves) to the transverse processes appears to be correlated with reduction of the pubis in crocodilians. Their hypothesis strikes me as *ad hoc*, however, given that this muscle has a dorsal origin, rather than a ventral origin from the pubis, in the only archosaurs in which it can actually be observed.

28) Pronounced brevis fossa. The brevis fossa is a modified area of origin for the *M. caudofemoralis brevis* on the ventral surface of the postacetabular portion of the ilium (Romer 1923, 1927; Walker 1977). This muscle is largely a retractor of the hindlimb in archosaurs with long ilia (M. Parrish, pers. comm.). Possession of a brevis fossa (or shelf) is an ancestral condition in Dinosauria, although it is also present in cursorial Rauisuchia (Bonaparte, pers. comm.; and see Appendix A). However, the brevis fossa is most markedly developed in Theropoda, in which there is a broad, deep, and elongate fossa on the posteroventral margin of the ilium (see Madsen 1976:145, fig. 46b). The prominent shelf forming part of the brevis fossa often gives the posterior extremity of the iliac blade a squared-off, truncated profile in lateral view (Fig. 5C–E). An enlarged brevis fossa is present in *Liliensternus** (Huene 1934), Ceratosauria (Welles 1984), Carnosauria (Madsen 1976), *Ornitholestes** (Osborn 1917), Ornithomimidae (Osmolska et al. 1972), Elmsauridae* (Currie, pers. comm.), Caenagnathidae (Barsbold 1983), and Deinonychosauria (Ostrom 1969b, 1976a). The dinosaurian origin of this muscle is retained in birds (Romer 1923), but a brevis fossa as such appears to be absent in Avialae; in light of all the evidence it is simpler to accept reversal rather than plesiomorphy as an explanation for its absence in birds.

29) Femur bowed in a convex arc and sigmoidal curvature less prominent. The femur has a sigmoidal curvature in Archosauria ancestrally (Romer 1956), in that the shaft of the element is S-shaped in two planes (Padian, in press). Dinosaurs retain this condition, because a sigmoidal femur is present in Herrerasauridae* (Galton 1977), and in Ornithischia (Colbert 1981) and Sauropodomorpha ancestrally (Cooper 1981a), thus indicating that a sigmoidal femur is the ancestral condition for Saurischia. In contrast, the femur is bowed dorsally and the distal end is inflected laterally so there is little or no sigmoidal curvature in *Procompsognathus** (Ostrom 1981), *Liliensternus** (Huene 1934), Ceratosauria (Gilmore 1920; Raath 1969), *Coelurus** (Ostrom 1976a), *Compsognathus** (Ostrom 1978), *Ornitholestes** (Osborn 1917), *Microvenator** (Ostrom 1970), Ornithomimidae (Osmolska et al. 1972), Elmsauridae* (Currie, pers. comm.), Caenagnathidae (Barsbold 1983), Deinonychosauria (Ostrom 1976a), and Avialae (Ostrom 1976b). The femur is less bowed in large theropods, especially in Carnosauria, and

Ostrom (1976*b*) suggested that this reflects constraints imposed by large size. The bowed and nonsigmoidal femur arose convergently in Pterosauria (Padian 1983), and it appears to be ancestral for ornithopod ornithischians (Galton and Jensen 1973). This character is evidently related to small size and highly developed cursorial habits in Ornithosuchia (Coombs 1978*b*; Padian 1983).

30) Fibula closely appressed to tibia, and fibula attached to crest on lateral side of proximal end of tibia. The fibula is broadly separated from the tibia for most of its length, and there is no fibular crest on the tibia, in Pseudosuchia (Krebs 1976), *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte 1975*a*), and *Lagosuchus* (Bonaparte 1975*b*). This condition is retained in Ornithischia ancestrally (Romer 1956) and in Sauropodomorpha (Cooper 1981*a*). In large dinosaurs, the tibia and fibula are even more broadly separated from one another. However, regardless of size, the fibula is always closely appressed against the lateral face of the tibia in Theropoda. This character is unique to Theropoda among Saurischia (Ostrom 1976*a*), but it arose convergently in Pterosauria (Wellnhofer 1978) and it appears to be the ancestral condition for ornithopod ornithischians (Galton and Jensen 1973). Unlike either of the last mentioned taxa, however, only theropods possess the fibular crest on the tibia. This synapomorphy is present in *Liliensternus** (Huene 1934), *Procompsognathus** (Ostrom 1981), *Compsognathus* (Ostrom 1978), Carnosauria (Fig. 6A), *Microvenator** (Ostrom 1970), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 6C), Deinonychosauria (Fig. 6B), and Avialae (Bellairs and Jenkin 1960).

31) Metatarsus narrow and elongate. In Ornithodira ancestrally the metatarsus is narrow compared to its length owing to elongation of the metatarsals and reduction of the outer digits (Fig. 6K–P). Within Sauropodomorpha, the manus and pes are shortened, and they are broadened owing to enlargement of digit I (Fig. 6N; this appears to be developmentally correlated with modification of the pollex; Appendix A). In contrast, the theropod metatarsus is relatively long and narrow, and it is thus more like that of birds than is the case in Dinosauria ancestrally (Fig. 6O, P). The only other ornithosuchian with such a narrow and elongate metatarsus is *Lagosuchus** (Fig. 6K). *Lagosuchus** is considered to be convergent with theropods in this regard because the metatarsus is not so narrow in Sauropodomorpha (Fig. 6N), Ornithischia (Fig. 6M), or Herrerasauridae* (Fig. 6L), all of which are closer to Theropoda than is *Lagosuchus**. The proportions of the metatarsus vary with size; the larger dinosaurs possess relatively broad metatarsals compared to related, smaller dinosaurs. This difference appears to reflect scaling effects, and applies to large versus small theropods as well. Nevertheless, according to Ostrom (1976*a*), all theropods have a relatively narrower metatarsus when compared to other dinosaurs of equal size. A narrow, elongate metatarsus has been reported in *Procompsognathus** (Ostrom 1981), *Liliensternus** (Huene 1934), Ceratosauria (Raath 1969), *Compsognathus* (Ostrom 1978), *Ornitholestes** (Osborn 1917), *Hulsanpes* (Osmolska 1982), Caenagnathidae (Barsbold 1983), Elmisauidae* (Osmolska 1981), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Russell 1969), and Avialae (Ostrom 1976*a*).

32) Pes with pedal digit IV reduced and subequal to II in length, thus making pes symmetrical about digit III. As Ostrom (1981) argued, theropod feet are unlike those of dinosaurs gen-

erally; in other dinosaurs pedal digit IV is longer than II (Fig. 6M, N), but in theropods pedal digit IV is reduced and approaches the length of pedal digit II (Fig. 6O), thus making the pes even more symmetrical about digit III than in dinosaurs ancestrally. The symmetrical pes is present in *Procompsognathus** (Ostrom 1981), Ceratosauria (Gilmore 1920; Raath 1969), Carnosauria (Madsen 1976), Elmisauidae* (Sternberg 1932), and Ornithomimidae (Osmolska et al. 1972). In the context of all the evidence, it is more parsimonious to accept that the elongate pedal digit IV of Deinonychosauria (Ostrom 1969*b*) (and to a lesser extent that of *Ornitholestes** [Ostrom 1976*a*], *Compsognathus* [Ostrom 1978], Caenagnathidae [Barsbold 1983], and Avialae [Fig. 6P]) is a secondary modification (see Part V, character 84).

33) Fifth metatarsal reduced to no more than a spur of bone in adult. Pedal digit five is reduced and bears only a vestigial phalanx on the distal end of the fifth metatarsal in Dinosauria ancestrally (Fig. 6L, N). In contrast, no theropod has more than a vestigial metatarsal spur (Fig. 6O, P); the element has been lost in adult Ornithurae, and it may also have been lost in some ornithomimids, caenagnathids, and elmisauides*, although loss and nonpreservation cannot be distinguished in the extinct theropods. The fifth pedal digit is reduced to a spur of bone in Proterochampsidae, the sister-group of Archosauria (Gauthier 1984). Within Archosauria the same apomorphy appeared independently in four different groups: Crocodylomorpha, pterodactyloid Pterosauria, Ornithischia, and Theropoda. The fifth digit could have been reduced in the ancestral dinosaur and subsequently reevolved in Sauropodomorpha, which retains what appears to be the ancestral condition. Alternatively, the fifth digit could have been reduced twice, once in Ornithischia and once in Theropoda. Two evolutionary events are required in either case; unless one is willing to assume that convergence is more likely than reversal in evolution (or vice versa), the level of synapomorphy of this character must be considered ambiguous. Fortunately, this character is but one among many supporting theropod monophyly, and regardless of how it is optimized, it has no effect on the conclusions of this analysis. In this instance I accept convergence over reversal as an explanation of the distribution of this character among dinosaurs; this conclusion predicts that we will one day find a fifth digit like that seen in sauropodomorphs in either an ornithischian or a theropod (or both).

34) Theropod first metatarsal. In Archosauria ancestrally, metatarsal I articulates with the tarsus and it is proportioned much like the other metatarsals (Fig. 6J). This condition is retained in *Lagosuchus** (Fig. 6K), Pterosauria (Wellnhofer 1978), Herrerasauridae* (Fig. 6L), Ornithischia ancestrally (Fig. 6M), and Sauropodomorpha (Fig. 6N). In contrast, the proximal portion of metatarsal I fails to contact the tarsus and the compressed and triangular shaft of the element is bound by connective tissue to the medial side of metatarsal II in *Liliensternus** (Huene 1934), *Procompsognathus** (Ostrom 1981), and Ceratosauria (Fig. 6O). Metatarsal I is even more broadly separated from the tarsus in Carnosauria (Osborn 1906; Lambe 1917; Gilmore 1920), *Compsognathus* (Fig. 6Q), Elmisauidae* (Sternberg 1932), Caenagnathidae (Barsbold 1983), Ornithomimidae (Barsbold 1983), Deinonychosauria (Ostrom 1969*b*), and Avialae (Fig. 6P). Tarsitano and Hecht (1980) argued that in Theropoda with an intact pes, metatarsal I is attached about half-

way down metatarsal II (Fig. 6O), and birds are further derived in that the element attaches about three-quarters of the way down metatarsal II (Fig. 6P). Ostrom (1976a) argued that a reversed hallux was ancestral for Theropoda. Tarsitano and Hecht (1980) took exception, noting that in the few articulated theropod feet, the hallux is short, unreversed, and metatarsal I lies medial to metatarsal II. I agree with Tarsitano and Hecht that the condition of the first digit as they describe it is indeed ancestral for Theropoda. However, the articulated feet of *Compsognathus* show that metatarsal I in this taxon is like that of birds, and unlike that of early theropods, in that it is short and displaced to the posterior side of metatarsal II (Fig. 6Q). The reversal, elongation, and posterior displacement of the hallux presumably relate to the perfection of the grasping function of the foot in Avialae (see Part V, character 84). Tarsitano and Hecht (1980) argued that this functional complex is not ancestral for Theropoda and I quite agree. Nevertheless, it is clear that certain modifications that are prerequisite to the reversed hallux of Avialae apply to more inclusive groups of Theropoda than to birds alone. In this regard, it is interesting to note that the first pedal digit recapitulates its phylogenetic history in the development of the pes in extant Aves (Heilmann 1926). The position of the first pedal digit as preserved in early theropods indicates that this digit was unreversed, at least at rest. However, as Thulborn (1984) has noted, Triassic theropod trackways displaying impressions of reversed first digits stand as mute testaments to our inability to infer function from structure alone.

35) Thin-walled long bones (=hollow skeleton). This character has long been recognized as a theropod synapomorphy (see diagnosis of "Theropoda" in Marsh 1881b, 1884a) and it is present in all taxa here considered to be theropods except for Hesperornithes and a few other diving birds. The walls of the long bones are thicker in *Dilophosaurus* and *Ceratosaurus*, and even thicker in Carnosauria, as their larger size demands. Even so, the limb bones of the largest theropod, *Tyrannosaurus rex*, are thin-walled in comparison to the same elements of contemporaneous large dinosaurs, such as *Triceratops* and *Anatosaurus* (pers. obs.). The limb bones are hollow in Dinosauria ancestrally, but aside from Pterosauria (Bramwell and Whitfield 1974), no other archosaurs have long bones that are quite as thin-walled as those of Theropoda (Romer 1956). Moreover, T. Rowe (pers. comm.) has pointed out that in theropods the entire skeleton, including the phalanges and caudal vertebrae, are hollow and lightly constructed in comparison to other dinosaurs of equal size. This may partly explain why theropods in general and birds in particular are so uncommon in the fossil record.

III. Phylogenetic Relationships within Tetanurae

Tetanurae (n. tax.)

(Gr.: *tetanos*, stiff; *ourae*, tails)

TEMPORAL RANGE.—late Jurassic to Recent.

INCLUDED TAXA.—Carnosauria, *Compsognathus*, *Ornitholestes**, *Coelurus**, *Microvenator**, *Saurornitholestes**, *Hulsanpes*, *Elmisauridae**, *Caenagnathidae*, *Ornithomimidae*, *Deinonychosauria*, and *Avialae*.

DIAGNOSIS.—Tetanurae is defined here to include birds and all other theropods that are closer to birds than they are to Ceratosauria. In the following analysis, Ceratosauria, Sauropodomorpha, Ornithischia, Herrerasauridae*, Pterosauria-*Lagosuchus**, Ornithosuchidae, *Euparkeria**, and Pseudosu-

chia will be used as successively more remote outgroups. Tetanurine theropods are diagnosed by the following synapomorphies.

36) Absence of enlarged fanglike tooth in dentary. Gauthier (1984) proposed that an unnamed taxon including erythrosuchids, proterochampsids, and archosaurs (n. comb.) can be distinguished among Archosauromorpha by an enlarged anterior dentary tooth (e.g., Fig. 1A, B). The fanglike tooth projects dorsally between teeth in the upper tooth-bearing bones, and it may be received in a more or less pronounced notch between the premaxilla and maxilla. The ancestral condition is retained by *Liliensternus** (Huene 1934) and, in a modified form, by Ceratosauria. The fang is very large in ceratosaur theropods, and it is received into the diagnostic subnarial gap in all ceratosaurians except *Ceratosaurus* (pers. obs.; Welles 1984). In contrast, an enlarged dentary fang is absent in Carnosauria (Fig. 1G, H), *Compsognathus* (Ostrom 1978), *Elmisauridae** (Gilmore 1924), *Ornitholestes** (Osborn 1917), *Deinonychosauria* (Fig. 1J, K), and *Avialae* (Fig. 1L). This character is considered indeterminable in the toothless *Ornithomimidae* (Fig. 1I) and *Caenagnathidae* (Osmolska 1976).

37) Maxillary fenestra large and posteriorly placed. An antorbital fenestra was present in the ancestral archosaur, and this condition was retained by the ancestral dinosaur (Romer 1956). Theropods differ in that they possess an additional fenestra anterior to the antorbital fenestra, here termed the maxillary fenestra (=second antorbital fenestra of various authors; see Madsen 1976:65, plate 6). In contrast to the small, slitlike fenestra confined to the anterior margin of the antorbital fossa in Ceratosauria (Welles 1984), however, the maxillary fenestra is large, circular, and more posteriorly placed in Carnosauria (Fig. 1G, H), *Ornithomimidae* (Fig. 1I), *Caenagnathidae* (Barsbold 1983), *Ornitholestes** (Osborn 1917), *Compsognathus* (Ostrom 1978), *Deinonychosauria* (Fig. 1J, K), and *Archaeopteryx** (Fig. 1L). The maxillary fenestra is absent in the highly modified antorbital region of Ornithurae. A second pre-antorbital fenestra is present in some Rausisuchia (Sill 1974) and in a single erythrosuchid, *Shansisuchus* (Young 1964). However, this fenestra lies between the premaxilla and maxilla, and it is not considered homologous with the maxillary fenestra present in Tetanurae.

38) Antorbital tooth row. In Saurischia ancestrally the upper and lower tooth rows terminate below the center of the orbit (Fig. 1A-F). The ancestral condition is retained in *Procompsognathus** (pers. obs.) and Ceratosauria (Colbert and Russell 1969). In contrast, the tooth rows are entirely antorbital in Carnosauria (Fig. 1G, H), *Deinonychosauria* (Fig. 1J, K), *Ornitholestes** (Osborn 1903, 1917), *Compsognathus** (Ostrom 1978), and *Avialae* ancestrally (Fig. 1L). In the context of all the evidence, the most parsimonious explanation for the edentulous *Ornithomimidae*, *Caenagnathidae*, and Aves is that they each achieved their toothless condition separately, and that they did so via the condition seen in other tetanurine theropods. Antorbital tooth rows arose independently in several groups of diapsids, most of which are carnivores (e.g., McDowell and Bogert 1954). However, some herbivores, for example some sauropods and ceratopsian ornithischians, have also acquired this condition. An antorbital tooth row also occurs in a variety of other archosaurs that are thought to have been carnivorous, such as some erythrosuchids (Charig and Reig 1970), rausisuchians (Bonaparte 1981), and some pterosaurs (Wellnhofer 1978), but it

is absent in others, such as ornithosuchids (Walker 1964) and proterosuchids (Cruickshank 1972). Thus, while the character is not an infallible indicator, it appears to be correlated with macropredaceous habits (sensu McDowell and Bogert 1954).

39) Spine table on the axis. Spine tables are present in the posterior cervicals and anterior trunk vertebrae in Archosauria ancestrally (Gauthier 1984). However, spine tables are absent in the anterior cervicals including the axis in Pseudosuchia (Rommer 1956), *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte 1975b), *Lagosuchus** (Bonaparte 1975b), Pterosauria (Wellnhofer 1978), Herrerasauridae* (Galton 1977), Ornithischia (Santa Luca 1980), Sauropodomorpha (Fig. 3D), *Liliensternus** (Huene 1934), and Ceratosauria (Fig. 3E). Thus, anterior spine tables are absent in theropods ancestrally. In contrast, an expanded distal end of the neural spine (=spine table) is present, at least on the axis, in Carnosauria (Madsen 1976), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 3F, H), and Avialae (Fig. 3G, I).

40) Transition point begins closer to proximal half of tail. With the exception of a few birds lacking the pygostyle, all theropods have tails that are mobile proximally and stiffened distally. The transition between these regions is marked by roughly coincident changes in neural spines, transverse processes, haemal arches, and pre- and postzygapophyses, which are referred to collectively as the transition point. As noted above, although ceratosaurs display the transition point, it is less marked, and they retain the ancestral condition of the caudal haemal arches well into the posterior half of the tail. In contrast to ceratosaurs, however, the transition between the stouter and more mobile proximal and stiffened and thinned distal portions of the tail is more pronounced and begins closer to the base of the tail in tetanurine theropods. In addition, unlike the case in Ceratosauria (Gilmore 1920), the haemal arches in Carnosauria (Madsen 1976), Ornithomimidae (Fig. 2E), Deinonychosauria (Fig. 2G), and Avialae ancestrally (Fig. 2F) become progressively shorter dorsoventrally and elongate anteroposteriorly from the proximal to the distal end of the tail. Russell (1972) noted some variation in the position of the transition point in the tails of taxa that I include in Tetanurae, and detailed comparisons of theropod caudal series may provide further characters for phylogenetic analysis. Analogous modifications of the caudal region are present in sand lizards, such as *Callisaurus*, *Cophosaurus*, and *Holbrookia* (pers. obs.). The zygapophyses are not deeply imbricate as in theropods, but they are vertically disposed (as in most ornithodiran archosaurs); the tail is stout basally, but it tapers abruptly in a region analogous to the theropod transition point, and the greater part of the tail is thin, with short haemal arches that are expanded fore and aft. Thus, the base of the sand lizard tail would correspond to the mobile proximal portion, and the remainder of the tail to the stiff distal portion, of the tetanurine tail. Sand lizards typically curl their comparatively short tails dorsally, particularly during bipedal progression when the tail acts as a dynamic stabilizer. The tail is also used for display, with side-to-side wagging of the curled distal portion playing a role in social interaction. The stiffened distal portion of the theropod tail probably could not have been curled as in sand lizards, owing to the deeply imbricate zygapophyses. Although the theropod tail's paramount role may have been as a dynamic stabilizer, one cannot overlook the possibility of accessory roles in social display.

41) Scapula straplike. As in Diapsida generally, the distal end of the scapula is flared anteroposteriorly in Dinosauria ancestrally (Fig. 4A, B). This condition is retained by Ceratosauria (Raath 1969; Welles 1984) and from what remains of the scapula in *Liliensternus** (Huene 1934), it appears to retain the ancestral condition as well. In contrast, the distal expansion is reduced or absent and the scapula is thus straplike in Carnosauria (Madsen 1976), *Compsognathus* (Ostrom 1978), *Ornitholestes** (Ostrom 1976a), Ornithomimidae (Fig. 4C), Deinonychosauria (Ostrom 1976a), and Avialae (Fig. 4D). This modification is further enhanced in Ornithurae, in which the scapula tapers distally (Elzanowski 1981). The carnosaur *Tyrannosaurus* is unusual among tetanurines in the possession of a flared distal end of the scapula (Osborn 1906); rather than symmetrical, however, the scapula is flared mainly at its anterior margin, suggesting that this condition is secondary.

42) Coracoid tapers posteriorly in profile. In Ornithodira ancestrally the profile of the coracoid is subcircular below its articulation with the scapula, although the element may taper to a blunted point posteroventrally. The ancestral condition is retained in Ornithischia (Fig. 4A), Sauropodomorpha (Fig. 4B), and in Theropoda ancestrally in that the coracoid has a subcircular profile in *Liliensternus** (Huene 1934) and Ceratosauria (Welles 1984). In contrast, the pointed posteroventral margin of the coracoid is more pronounced in that it extends well beyond the rims of the glenoid when the scapulocoracoid is oriented vertically in Carnosauria (Madsen 1976), *Compsognathus* (Bidar et al. 1972), and Ornithomimidae (Fig. 4C). The rectangular profile of deinonychosaurs and avialans is here considered a further modification of the form of the coracoid seen in other tetanurine theropods. A posteriorly tapering coracoid appeared independently in ornithopod ornithischians (e.g., Galton 1974).

43) Manus forms more than two-thirds of combined lengths of radius plus humerus. Ostrom (1969b) pointed out that the manus is less than half the length of the humerus plus radius in Ceratosauria (47% in *Coelophysis* and *Syntarsus*), as it is in Dinosauria ancestrally. *Heterodontosaurus tucki* is exceptional among ornithischians in that the manus is over half (i.e., 56%) of the humerus plus radius length (Santa Luca 1980). In contrast, Tetanurae possesses conspicuously enlarged hands. The manus is 77% of the length of the radius plus humerus in Carnosauria ancestrally (i.e., *Allosaurus*), although the forearm is greatly reduced in Tyrannosauridae (Lambe 1917). The manus is modified in Ornithomimidae, but it is still at least 58% of the length of the radius plus humerus. In Caenagnathidae (Osborn 1924b), *Ornitholestes** (Osborn 1917), Deinonychosauria (Ostrom 1969b), and Avialae (Ostrom 1976a) ancestrally, the manus is 67–75% of the humerus plus radius length. Tetanurae in general and coelurosaurs in particular are unique among Dinosauria in the relative size of the hand. Although *Scleromochlus** does not appear to be so modified (Huene 1914a), pterosaurs are the only other archosaurs whose hands exceed the relative size seen in Tetanurae. Even the highly modified hands of Ornithurae are enormous relative to those of most other archosaurs.

44) Basal half of metacarpal I closely appressed to metacarpal II. As in Diapsida ancestrally, the metacarpals overlap one another proximally, and this condition is retained in Pseudosuchia (Fig. 4G), Ornithosuchidae (Walker 1964), Pterosauria (Wellnhofer 1978), Ornithischia (Fig. 4H), Sauropodomorpha

(Fig. 4I, J), and Ceratosauria (Welles 1984). In contrast, the bases of metacarpals I and II are closely appressed for at least half the length of metacarpal I in Carnosauria (Fig. 4L), Ornithomimidae (Fig. 4M), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Elmsauridae* (Osmolska 1981), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O).

45) Base of metacarpal III set on palmar surface of hand below base of metacarpal II. As was argued in Part I, character nine above, the bases of metacarpals IV and V (and thus their associated digits), were set on the palmar surface of the hand in Saurischia ancestrally. Tetanurine theropods are further specialized within this assemblage in that metacarpal III is also displaced ventrally with respect to metacarpal II. Ceratosauria retains the ancestral condition (Fig. 4K), but the derived condition is present in Carnosauria (Fig. 4L), Ornithomimidae (Fig. 4M), Elmsauridae* (Osmolska 1981), Caenagnathidae (Barsbold 1983), *Ornitholestes** (Osborn 1917), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O). Even in disarticulated specimens, the beveled articular surface of the proximal end of metacarpal III is sufficient to identify this character.

46) Fourth manal digit absent beyond embryonic stages. As argued above, the fourth manal digit is reduced in all Theropoda and probably plays no role in the function of the hand (Galton 1971). Unlike Ceratosauria, however, the fourth digit is absent in Carnosauria (Fig. 4L), *Compsognathus* (Ostrom 1978), *Saurornitholestes** (Sues 1978), Elmsauridae* (Osmolska 1981), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 4M), and Deinonychosauria (Fig. 4N). Osborn (1917) and Ostrom (1969b) identified a fragment of bone near the proximal end of metacarpal III in *Ornitholestes** that may represent a vestige of metacarpal IV. The fourth digit is absent in all adult Avialae (Fig. 4O) but the precursor of the element is reported in embryonic Aves (Heilmann 1926; see Hinchliffe and Hecht 1984, for an alternative view).

47) Obturator process on ischium. An obturator process on the ischium is absent in Pseudosuchia, Ornithosuchidae, *Lagosuchus**, Pterosauria, and Herrerasauridae* (Gauthier 1984). An obturator process is also absent in all Ornithischia (Fig. 5A) except for *Lesothosaurus* (Thulborn 1972) and Ornithopoda (sensu Santa Luca 1980), and it is absent in Sauropodomorpha (Fig. 5B), *Liliensternus** (Huene 1934), *Procompsognathus** (Ostrom 1981), and Ceratosauria (Fig. 5C). In contrast, an obturator process is present on the ischium of Carnosauria (Fig. 5D), Ornithomimidae (Fig. 5E), *Ornitholestes** (Osborn 1917), *Compsognathus* (Ostrom 1978), Elmsauridae* (P. J. Currie, pers. comm.), Caenagnathidae (Barsbold 1983), and Deinonychosauria (Fig. 5F, G). Ostrom (1976a:129) may be correct in interpreting the anterior of the two processes at the ventral extremity of the ischium of *Archaeopteryx** as an obturator process (Fig. 5H). The ischium of *Archaeopteryx** is, however, difficult to assess because the element is in several ways different from that seen in other Theropoda, including Ornithurae (Fig. 5I; Tarsitano and Hecht 1980). Unlike the pubis in *Archaeopteryx**, the morphology of the ischium has not received much attention, and this element needs further study. Nevertheless, even if the lower process on the ischium is not homologous with the obturator process of other Tetanurae, it is still more parsimonious to accept that birds lost, rather than never had, an obturator process.

48) Expanded pubic foot. An expanded distal extremity of

the pubis is present in Herrerasauridae* (Reig 1963; Benedetto 1973; Cooper 1981a; Galton 1977). However, the apomorphy is unknown elsewhere among Dinosauria, including *Liliensternus** (Huene 1934) and Ceratosauria (Fig. 5C). Thus, an expanded pubic foot applies to Herrerasauridae* on one hand, and Tetanurae on the other, but not to a group including both. An expanded foot at the distal end of the pubis is present in Carnosauria (Fig. 5D), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 5E), *Microvenator** (Ostrom 1970), *Compsognathus** (Ostrom 1978), *Coelurus** (Marsh 1896), Deinonychosauria (Fig. 5F, G), and *Archaeopteryx** (Fig. 5H). Thus, the absence of a pubic foot in Ornithurae is considered secondary (Fig. 5I).

49) Femur with winglike anterior (=lesser) trochanter. The anterior trochanter is a spikelike ridge in Dinosauria ancestrally, and this condition is retained in *Liliensternus** (Huene 1934) and in a modified form in Ceratosauria (Raath 1969). In contrast, the anterior trochanter is prominent and winglike in Carnosauria (Madsen 1976), Elmsauridae* (P. J. Currie, pers. comm.), Ornithomimidae (Osmolska et al. 1972), *Microvenator** (Ostrom 1970), and in a modified form in Deinonychosauria and Avialae (Ostrom 1976a, 1976b; Padian 1982). It is interesting to note at this point that a discrete, winglike lesser trochanter occasionally appears as a variant in a few extant birds. A winglike anterior trochanter arose convergently in Ornithischia, and it is particularly prominent in Ornithopoda (sensu Santa Luca 1980; e.g., Galton 1974). Evidently, the dorsal migration and posterior displacement of the area of insertion of the so-called M. iliiochantericus group of Aves (Cracraft 1971), is associated with perfection of bipedal, cursorial habits (Coombs 1978b; see further discussion in Part V, character 82).

50) Ascending process of astragalus tall, broad, and superficially placed. Welles and Long (1974) provided a detailed description of the theropod tarsus. The distribution of characters in their classification of theropod tarsi (p. 197) indicates that their five "distinct kinds" are phenetic, rather than phylogenetic, concepts. For example, they note that one of the characters, the "free medial component" (=superficial part of ascending process) is absent both in dinosaurs ancestrally and in their "ceratosauroid" group of theropods (= *Liliensternus** and Ceratosauria of this work). The "free medial component" is, however, present in all members of their "allosauroid" (Fig. 6A), "albertosauroid," "tyrannosauroid," and "ornithomimid" (Fig. 6B, C) groups, as well as in *Compsognathus*, *Ornitholestes**, and *Microvenator**. Moreover, an ascending process is present in all birds (Fig. 6D), and although its height and width may vary with size and the presence of a tendinal groove in birds, it is relatively larger in birds than it is in theropods ancestrally (pers. obs.). Accordingly, the development of a larger ascending process is considered to be a synapomorphy of Tetanurae. Although the ascending process, which arises as a separate ossification center in Theropoda (Heilmann 1926; Welles 1983; pers. obs.), retains its ancestral relations with the tibia, it has shifted its association with the proximal tarsals in Neognathae (pers. obs.).

51) Metatarsals II and IV with broader participation in ankle and metatarsal III compressed between them to a variable degree. Using the ornithopod ornithischian *Hypsilophodon** (Fig. 6E), the sauropodomorph *Massospondylus* (Cooper 1981a), the early theropod *Liliensternus** (Huene 1934), and the ceratosaur *Dilophosaurus* (Fig. 6F) to assess the ancestral condition of the

metatarsus in Saurischia, neither metatarsal II or IV contributes as much to the surface area of the ankle joint as does metatarsal III in proximal view. In contrast, metatarsals II and IV participate more broadly in the ankle relative to metatarsal III, and metatarsal III is more or less compressed between II and IV. The width of metatarsal III is more than 33% of the width of metatarsals II–IV on the midline in Ornithischia (Fig. 6E) and Ceratosauria (Fig. 6F) and it is less than 26% of the width of the proximal ends of these metatarsals in Carnosauria (Fig. 6G), *Hulsanpes* (Osmolska 1982), Elmsauridae* (Osmolska 1981), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 6H), and Avialae (Fig. 6I; see Part IV, character 67, for further discussion).

52) Metatarsal I short. As noted above, metatarsal I does not reach the tarsus in theropods ancestrally. In the ancestral condition, the compressed shaft of metatarsal I is relatively long, as can be seen in *Liliensternus** (Huene 1934), *Procompsognathus** (pers. obs.), and Ceratosauria (Fig. 6O) with the possible exception of *Ceratosaurus* (see Gilmore 1920). By contrast, metatarsal I in Tetanurae is relatively short (e.g., Fig. 6P). The apomorphic tetanurine condition is reported in Carnosauria (Lambe 1917), *Compsognathus* (Fig. 6Q), Caenagnathidae (Barsbold 1983), Elmsauridae* (Sternberg 1932), Ornithomimidae (Barsbold 1983), Deinonychosauria (Ostrom 1969b), and Avialae (Fig. 6P).

IV. Phylogenetic Relationships within Coelurosauria

Coelurosauria (n. comb.)

TEMPORAL RANGE.—late Jurassic to Recent.

INCLUDED TAXA —*Ornitholestes**, *Compsognathus*, *Microvenator**, *Coelurus**, *Saurornitholestes**, *Hulsanpes*, Elmsauridae*, Caenagnathidae, Ornithomimidae, Deinonychosauria, and Avialae.

DIAGNOSIS.—As defined here, Coelurosauria includes birds and all other theropods that are closer to birds than they are to Carnosauria. This concept differs fundamentally from that of previous workers, all of whom applied “coelosaurs” to a paraphyletic group including all theropods except for carnosaurs. In the following analysis, Carnosauria, Ceratosauria, Sauropodomorpha, Ornithischia, and Herrerasauridae* will be used as successively more remote outgroups. The remaining outgroups, Pterosauria-*Lagosuchus**, Ornithosuchidae, *Euparkeria**, and Pseudosuchia, will be referred to as the “nondinosaurian archosaurs” or “other archosaurs” to facilitate the following discussion. Coelurosauria possesses the following synapomorphies distinguishing it among Theropoda.

53) Subsidiary fenestra between pterygoid and palatine. A subsidiary fenestra is absent in nondinosaurian archosaurs (Romer 1956), Ornithischia (e.g., Heaton 1972), and Sauropodomorpha (Galton 1984). According to Colbert and Russell (1969), this character is also absent in taxa here referred to Ceratosauria and Carnosauria. In contrast, a subsidiary fenestra between the pterygoid and palatine is present in Ornithomimidae (Osmolska et al. 1972), Caenagnathidae (Osmolska 1976), and Deinonychosauria (Colbert and Russell 1969). The palate is not exposed in *Archaeopteryx**, and the palate of other birds is too transformed to interpret in this regard (McDowell 1978). In the context of all the evidence, birds are considered to have modified the palatal elements from the condition seen in other coelosaurs.

54) Deeply excavated pocket on ventral surface of ectopterygoid flange. As noted above (Part II, character 15), a relatively smaller excavation is present on the ventral surface of the ectopterygoid in Carnosauria (Colbert and Russell 1969). According to Sues (1978) this pocket is deeper in *Saurornitholestes**, Ornithomimidae, and Dromaeosauridae, and the apomorphic condition appears to obtain as well in Troodontidae (Barsbold 1983) and Caenagnathidae (Osmolska 1976). As in the case of the previous character, modification of the avian palate precludes a simple conclusion regarding the presence or absence of this character, especially since the ectopterygoid has not been identified in birds. Nevertheless, in view of their relationships within Coelurosauria it would still be simpler to accept secondary modification in birds. Another modification in this region of the palate may also be diagnostic of Coelurosauria: a conspicuous oval depression, subdivided by a ridge, that lies on the dorsal surface of the pterygoid process of the ectopterygoid in the dromaeosaur *Deinonychus* and in *Saurornitholestes** (Sues 1978). Although at present this character has been reported only in these taxa, it is absent in Carnosauria, indicating that it arose within theropods after the divergence of carnosaurs; more information will be necessary to establish its level of synapomorphy.

55) Cervical ribs fused to centra in adults. Cervical ribs remain unfused throughout ontogeny in nondinosaurian archosaurs aside from some Pterosauria (Romer 1956). Both Ornithischia and Sauropodomorpha retain the ancestral condition, although fusion between ribs and vertebrae in the cervical region arose within Sauropoda. Fully adult ceratosaurs, such as the specimens of *Syntarsus* and *Ceratosaurus* described by Raath (1969) and Gilmore (1920) respectively, retain free ribs, and this appears to be the case in *Allosaurus* as well (Madsen 1976). Thus, the ancestral condition in tetanurine theropods appears to be the retention of free cervical ribs in adults. Fused cervical ribs have so far been reported only in *Coelurus** (Marsh 1881a), fully adult specimens of ornithomimids such as *Gallimimus* (Osmolska et al. 1972) and *Struthiomimus* (Osborn 1917), and in fully adult ornithurine birds (Marsh 1880). *Coelurus** is too poorly known to allow placement beyond Coelurosauria *incertae sedis*, and will for that reason be ignored in the following discussion.

At first glance, it seems that fused cervical ribs arose (at least) twice, once in Ornithomimidae and once in Ornithurae, because neither *Archaeopteryx** nor deinonychosaurs are reported to have fused cervical ribs. This interpretation itself depends on assuming that there are fully adult examples among the known specimens of the latter two taxa, and according to the criteria here used to determine cessation of growth, this does not appear to be the case. The situation is further complicated by the fact that *Deinonychus* is the only deinonychosaur for which any portion of the cervical region has been described, and these specimens represent subadult individuals. For example, the axial intercentrum remains suturally distinct from both the first and second centrum (Fig. 3F), while in fully adult reptiles (sensu Gauthier et al., in prep.) the second intercentrum is always fused, at least to the first centrum. Although this fusion takes place earlier in ontogeny in some reptiles (e.g., in extant crocodylomorph embryos), it may be a near terminal event in the skeletal ontogeny of others (e.g., most squamates), but by the cessation of growth it is in any case fused. Fusion of the axial intercentrum

takes place prior to fusion of the cervical ribs in extant birds (pers. obs.); thus the absence of fused cervical ribs in the currently known *Deinonychus* may simply reflect the relative immaturity of the specimens, not the retention of an ancestral condition. The presence or absence of this character will be scored as unknown in Deinonychosauria.

For similar reasons, I also consider this character indeterminate in *Archaeopteryx**. If the five *Archaeopteryx** skeletons are ranked according to measures of homologous structures, the relative size from largest to smallest specimens would be the subequal-sized London, Maxberg, and Haarlem specimens, followed by the Berlin, and then the Eichstätt specimens (see Wellnhofer 1974). The first three specimens are of comparable size, the Berlin specimen is about 15% smaller than the London specimen, and the Eichstätt is about 45% smaller than the London specimen, based on the length of the humerus (data from Wellnhofer 1974). The scapula and coracoid are unfused in all specimens, although they are firmly attached to one another in the London specimen, indicating by extrapolation that the London, Maxberg, and Haarlem specimens are near to full maturity (also corroborated by fusion of tarsometatarsus). Unfortunately, the cervicals are either poorly preserved or absent in these apparently full-grown specimens. Free cervical ribs are present in the smaller specimens from Berlin and Eichstätt, but this is to be expected in view of the apparent immaturity of these specimens. Thus, until this character can be determined in new and fully adult specimens of *Archaeopteryx** and Deinonychosauria, it is simpler to accept that fusion of cervical ribs, at least by maximum adult size, is synapomorphic of Coelurosauria among Theropoda.

56) Cervical zygapophyses flexed. In nondinosaurian archosaurs, the cervical zygapophyses are planar (pers. obs.), and this condition is retained in Ornithischia (e.g., Ostrom 1970), Sauripodomorpha (Huene 1908), Ceratosauria (Gilmore 1920), and Carnosauria (Madsen 1976). Thus, planar zygapophysial facets in the cervical region are the ancestral condition in Tetanurae. In contrast, the zygapophysial facets are sharply flexed about a line dividing the facet into larger lateral and smaller medial components in Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Ostrom 1969b), and Avialae (this character is not determinable in *Archaeopteryx**, but it is present in other birds).

57) Anterior cervical vertebrae broader than deep anteriorly, with kidney-shaped articular surfaces that are taller laterally than on the midline. Amphicoelous intervertebral joints are the ancestral condition for Archosauria (Romer 1956). Either the ancestral condition, or a more or less prominent opisthocoely derived from it, is retained in Ornithischia (Galton 1974), Sauripodomorpha (Huene 1932), *Lilienstermus** (Huene 1934), Ceratosauria (Gilmore 1920), and Carnosauria (Madsen 1976). Unfortunately, the placement within the neck of isolated cervicals referred to *Coelurus** (Marsh 1881a) and *Microvenator** (Ostrom 1970) is unknown. In contrast to the ancestral condition, the anterior articular surfaces in the anterior cervical vertebrae of Ornithomimidae (Osmolska et al. 1972) and Deinonychosauria (Fig. 3H) are modified in a distinctly avian manner, although the posterior surfaces remain amphicoelous (Ostrom 1969b; posterior amphicoely led de Beer 1954, to the erroneous conclusion that the London *Archaeopteryx** was amphicoelous throughout the column). The kidney-shaped anterior surfaces

display the initial stages of avian heterocoely. They are not much less modified in this respect than are homologous vertebrae of *Ichthyornis* (Marsh 1880), early Hesperornithes such as *Baptornis* (Martin and Tate 1976), and embryos of extant birds (pers. obs.). L. D. Martin (pers. comm.) notes that heterocoely becomes more pronounced and extends further posteriorly in the vertebral column within Hesperornithes, and that these same modifications arose in parallel in Aves ancestrally. Thus, the fully heterocoelous condition so characteristic of extant birds (e.g., Fig. 3I), arose twice within Ornithurae.

58) Furcula. In Dinosauria ancestrally the clavicles are reduced and gracile, and they are difficult to distinguish from ribs in all but perfectly articulated fossils (Ostrom 1976a). Clavicles are present in the ceratosaur *Segisaurus** (Camp 1936; pers. obs.), but they have yet to be identified in Carnosauria, in which the forelimbs and girdles are reduced (Lambe 1917). Fused clavicles (=furcula) have been reported in Caenagnathidae and Ornithomimidae (Barsbold 1983), and these furcula are like those of *Archaeopteryx** in that they are very robust, unlike clavicles in dinosaurs ancestrally, or for that matter in Ornithurae of equivalent size (see following character for comments on functional implications of a robust furcula). Fusion of the clavicles takes place during postnatal ontogeny in extant birds (pers. obs.). The timing of this event is unknown in coelurosaurians ancestrally, but fusion of the clavicles would probably have occurred no earlier in the ontogeny of extinct than extant coelurosaurians. Clavicles have yet to be described in Deinonychosauria, although they are said to be present in *Velociraptor* (Kielan-Jaworowska and Barsbold 1972). Fused clavicles are also present in Avialae ancestrally (Heilmann 1926), although the elements may be reduced and unfused, or absent, via paedomorphosis, in flightless taxa within this group (Marsh 1880; Glenny and Friedmann 1954; Van Tyne and Berger 1959). Based on the development of *Coturnix*, Lansdown (1968) suggested that the avian furcula may be a neomorph because at least part of the element forms from a cartilaginous precursor. Clavicle development in *Coturnix* was, however, recently reconsidered by Russell and Joffe (1985), and they reaffirmed that the element was dermal rather than endochondral in origin.

59) Bony sternal plates fused, at least in fully adult individuals. Another character that may be functionally related to the development of the furcula, namely, a fused, bony sternum, may have originated at a level more inclusive than Ornithurae within Coelurosauria. Olson and Feduccia (1979) argued that the robust furcula of *Archaeopteryx**, together with the coracoclavicular membrane, acted as the point of origin of the muscle providing the power stroke for the wing, a hypertrophied *M. pectoralis*. They further noted that the posterior portion of this muscle also originates from the area of the sternum that is not preempted by the underlying *M. supracoracoideus* in Ornithurae. They presumed this portion of the *M. pectoralis* to be absent in *Archaeopteryx**, because *Archaeopteryx** was thought to lack a bony sternum. More recent finds allow us to modify Olson and Feduccia's conclusions.

Although the sternum may calcify in fully adult specimens, ossified sternal plates are absent in all nondinosaurian archosaurs (except Pterosauria). Paired ossifications within the cartilaginous sternum homologous with the pleurosteons of extant Aves have been reported in some subgroups of Ornithischia and Sauripodomorpha; but it is not clear if such ossifications were

present in these groups ancestrally (Romer 1956). Ossified sterna are unknown in early theropods, but more complete knowledge of this region in well-preserved ceratosaurs, such as *Coelophysis*, is necessary before absence can be distinguished from nonpreservation. The sternum becomes well ossified fairly late in post-hatching ontogeny, it is superficially placed, and it is not attached to the remainder of the skeleton; this combination of factors makes the sternum a poor candidate for preservation. To date, paired sternal plates have only been reported in a single specimen of Carnosauria (Lambe 1917) and in a few specimens of Caenagnathidae, Ornithomimidae, and Deinonychosauria (Barsbold 1983). With the possible exception of the London specimen (de Beer 1954), bony sternal plates are unknown in *Archaeopteryx**. However, they remain as pleurosteons in juvenile Ornithurae, and may be accompanied by additional ossification centers, the lophosteon and metosteon, in the keel and xiphoid processes respectively (Bellairs and Jenkin 1960). Current knowledge of the distribution of this character among ornithosuchian archosaurs precludes a firm decision regarding the level of synapomorphy of this character. The boldest hypothesis would be that bony sternal plates arose in ancestral Ornithodira. An ossified sternum has long been considered synapomorphic for Ornithurae, especially since a bony sternum was thought to be absent in *Archaeopteryx**. However, in view of the presence of a bony sternum in other tetanurines, if not all ornithodirans, the sternum was probably present in *Archaeopteryx**; whether its absence results from nonpreservation or immaturity of the specimens, or a combination of both factors, cannot yet be determined. Whether or not fusion between the sternal plates is synapomorphic of Ornithurae is also questionable, because some caenagnathids (*Oviraptor*) and ornithomimids (*Ingema*) also have fused sternal plates, at least in fully mature specimens (Barsbold 1983). Thus, this character appears to have arisen within Coelurosauria at a more inclusive level than birds alone. A sternum has so far been reported in only one deinonychosaur (*Velociraptor*; Barsbold 1983). The paired and apparently ancestral condition of the sternum in this taxon may not be conclusive, however, because the specimen has not been described completely enough to determine its stage of development. Full ossification of the sternal plates in extant birds occurs late in ontogeny, followed by coossification near maximum adult size (Bellairs and Jenkin 1960). Thus, the unfused sterna of *Velociraptor* may simply reflect immaturity. In view of the scant evidence, it may be too early to consider fusion of the sternum synapomorphic for Coelurosauria. In the context of the present hypothesis, however, I predict that a fused sternum will be found to have arisen outside of Ornithurae within Coelurosauria.

Such a find would have interesting consequences in light of arguments made by Olson and Feduccia (1979) regarding flight capability in *Archaeopteryx**. If, as seems to be the case, the basic pattern of the pectoral apparatus of *Archaeopteryx** applies to all Coelurosauria rather than to the immediate ancestor of Avialae, then some aspects of pectoral function must be equally general. That is to say, it would be inaccurate to consider the modifications of the pectoral girdle of *Archaeopteryx** solely in terms of flight. Thus, the presence of a hypertrophied M. pectoralis, as indicated by a robust furcula, enlarged coracoid, and fused sternum, suggests the presence of powerful forelimb adductors in all coelosaurs. These modifications may have served initially to enhance the raptorial capabilities of coelosaur fore-

limbs and only later been conscripted to serve the power stroke in avian flight. Aside from Coelurosauria, the only other archosaurs possessing a coossified, bony sternum are pterosaurs (Wellnhofer 1975, 1978), and this is hypothesized to be a case of convergence.

60) Elongate forelimb exceeds half the length of hindlimb and/or presacral vertebral column. Ostrom (1969b) pointed out that the forelimb is no more than 45% of the hindlimb length in Theropoda ancestrally. In Carnosauria, the forelimb varies from 25–42% of the hindlimb length. In contrast, Ornithomimidae (Russell 1972), Caenagnathidae (Barsbold 1983), *Ornitholestes** (Ostrom 1969b), Deinonychosauria (Ostrom 1969b), and Avialae (Ostrom 1976a) are unique among Theropoda in that the forelimb exceeds 51% of the hindlimb length (Ostrom 1969b) and 52% of the presacral vertebral column (Cooper 1981a). The forelimbs of *Ornitholestes** and Deinonychosauria are at least 66% of hindlimb length and 75% of the presacral column, and the extremely long arms seen in many flying birds exceed the lengths of both the hindlimbs and the presacral vertebral column (Ostrom 1976a). Ostrom (1978) estimated the forelimbs of *Compsognathus* to be only 38% of hindlimb length. Yet in the context of all the evidence, the short forelimbs of *Compsognathus* are most parsimoniously interpreted as a secondary modification within coelosaurs.

61) Manus gracile and elongate, especially digits two and three and their metacarpals, and metacarpal I only one-third the length of metacarpal II. As argued above, in Saurischia ancestrally metacarpal I is about half the length of metacarpal II. Moreover, the length of its second digit and its metacarpal is always less than seven times the width across the bases of metacarpals I and II. These relationships are retained in Ceratosauria (Fig. 4K) and Carnosauria ancestrally (Fig. 4L). In contrast, the hands are enormously elongate, and the length of the second digit and its metacarpal is at least nine times the width of metacarpals I and II in *Ornitholestes** (estimated from Ostrom 1976a), Caenagnathidae (Barsbold 1983), Elmsauridae* (Osmolska 1981), Deinonychosauria (Fig. 4N), and Avialae ancestrally (Fig. 4O). The characteristically modified manus of Ornithomimidae makes interpretation of the manus difficult. The length of the second digit and its metacarpal is over seven times the basal width of metacarpals I and II. However, metacarpal I is elongate and subequal in length to metacarpals II and III (Fig. 4M). This condition is unique among Theropoda in general and coelosaurs in particular, because metacarpal I is only one-third of the length of metacarpal II in all other coelosaurs, and it is no more than one-half of the length of metacarpal II in Saurischia ancestrally. In the context of all the evidence, the diagnostic modifications of the ornithomimid hand are hypothesized to be secondary.

62) Combined lengths of first and second phalanges of manal digit three less than or equal to length of third phalanx. As argued above, in Tetanurae ancestrally the first and second phalanges are relatively short compared to the length of the third (e.g., Fig. 4K, L). In contrast, the third phalanx equals or exceeds the combined lengths of the first and second phalanges in Ornithomimidae (Fig. 4M), Caenagnathidae (Barsbold 1983), Elmsauridae* (Osmolska 1981), *Ornitholestes** (Ostrom 1969b), Deinonychosauria (Fig. 4N), and Avialae ancestrally (Fig. 4O). The loss of all but the first phalanx of digit three in Ornithurae is considered secondary, but it is interesting to note that the

remaining phalanx is very short relative to the length of its metacarpal, just as in other coelurosaurs. This apomorphy arose convergently within Pterosauria (Wellnhofer 1978).

63) Fourth trochanter feebly developed or absent. A prominent fourth trochanter is the ancestral condition for Archosauria (Romer 1956). Moreover, an aliform fourth trochanter is the ancestral condition for Ornithodira (see Appendix A), and this condition is retained in *Procompsognathus** (Ostrom 1981), Ceratosauria (Welles 1984), and Carnosauria (Madsen 1976). In contrast, the fourth trochanter is represented by a feeble ridge in Ornithomimidae (Osmolska et al. 1972), or it may be absent, as in *Microvenator** (Ostrom 1970), Deinonychosauria (Ostrom 1976b), and Avialae ancestrally (Heilmann 1926; Tarsitano and Hecht 1980). This apomorphy arose convergently in Pterosauria (Wellnhofer 1978).

64) Moundlike greater trochanter (=posterior trochanter of Ostrom 1976b). The greater trochanter is represented by a rugose area on the posterolateral margin of the proximal end of the femur (in vertical pose) in Archosauria ancestrally (Romer 1923). The ancestral condition is retained by Ornithischia (Santa Luca 1980), Sauropodomorpha (Cooper 1981a), Ceratosauria (T. Rowe, pers. comm.), and Carnosauria (Madsen 1976). In contrast, a moundlike eminence develops within the greater trochanter in Ornithomimidae (pers. obs.) and Ostrom (1976a) has noted its presence in *Microvenator**, Deinonychosauria, and *Archaeopteryx**. Although lacking in many small birds, the greater trochanter appears to be modified with a moundlike eminence in at least some large ratites, such as *Dromaeus* (pers. obs.); thus the development of this feature may in part be size-related in extant birds.

65) Ascending process of astragalus enlarged both in height and width to cover most of anterodistal quarter of tibia. Welles and Long (1974) pointed out the synapomorphic resemblance among their "ornithomimoid" group (e.g., Fig. 6B, C), which with the addition of Avialae is equivalent to Coelurosauria as here defined. Birds present a problem in this regard, because several authors have claimed that the avian ascending process is not homologous with that seen in other Dinosauria (Whetstone and Martin 1979; Tarsitano and Hecht 1980; Martin et al. 1980; Martin 1983a, b). Tarsitano and Hecht (1980) even claimed that *Archaeopteryx** did not have an ascending process. My observations support the generally held view that an ascending process is present in *Archaeopteryx**. Moreover, Martin et al. (1980) used ultraviolet light to determine that the structure in question was not calcite as had been suggested by Tarsitano and Hecht (1980).

The development of the ascending process in Neognathae was most recently reviewed by Martin et al. (1980), who argued that the ascending process of birds is not homologous with that of other dinosaurs, because the ascending process arose in birds from a separate ossification center that fused to the calcaneum, rather than to the astragalus as in dinosaurs. This proposition requires reevaluation in light of further study. First, comparable developmental evidence from fossil theropods is lacking. Welles (1983) has, however, described a suture between the ascending process and astragalus in *Dilophosaurus*. Having examined the *Dilophosaurus* tarsi, it is difficult to distinguish the suture from cracks in the specimens. However, the orientation of the bone fibers on one margin of the so called "suture" are distinctly different from those in the underlying bone. Moreover, the as-

ending process appears to overlap the astragalus on the medial side of the proximal astragalus surface. In addition, Welles's interpretation of *Dilophosaurus* has been supported by examples of other nonavian theropod tarsi (pers. obs.). More observations of other theropod fossils are necessary before we can confidently distinguish between cracks and sutures. Further examination of the ascending processes of other dinosaurs should be undertaken. Second, Martin et al. (1980) based their conclusion on the development of the tarsus in Neognathae, but the work of McGowan (1984) and my work with K. Warheit and K. de Queiroz shows that the condition in Neognathae is not ancestral for Aves. Indeed, all birds are like other dinosaurs in the possession of an ascending process; Ratitae and Tinami retain the ancestral condition in which the ascending process fuses to the astragalus, but Neognathae is specialized in that at least part of it fuses instead with the precociously developed calcaneum. Both Martin et al. (1980) and McGowan (1984) used the position of the ascending process with respect to the proximal tarsals as the only test for homology, and neglected the fact that this process has maintained its phylogenetic and ontogenetic association with the anterolateral margin of the distal end of the tibia throughout Dinosauria. Based on the study of avian tarsal ontogeny (Gauthier, Estes, and de Queiroz, in prep.), it is clear that the ancestral avian ascending process differs from that of other Coelurosauria only in that it is not so broad, although it may be as tall (e.g., *Struthio*).

The differences between the ascending processes of avialans (e.g., Fig. 6D) and other coelurosaurs appear to depend on two factors. One is that the size of the ascending process may vary with the size of the organism in question; the ossification center appears in the usual dinosaurian position, and during ontogeny this center grows both dorsally and medially, so that given enough time it would eventually cover the entire distal end of the tibia. This would account in part for the variation in size of the ascending processes of large and small birds.

The other factor affects the width but not the height of the ascending process in Ornithurae; that factor is the development of a prominent tendinal groove on the distal end of the tibia, which would limit the medial spread of the ascending process during ontogeny. The only other theropods with ascending processes with proportions like those of coelurosaurs are tyrannosaurid carnosaurs, and they are here considered to have acquired this condition separately.

It must be emphasized that even if Martin et al. (1980) were correct in assuming that the neognath condition was general among Aves, this assumption would not preclude close relationship between birds and other coelurosaurs. To argue that this region is "different" in birds, rather than ancestral to the condition of these elements in Theropoda, does not remove the possibility that birds possess a transformation of the condition seen in coelurosaurs generally. Birds are unlike other Diapsida in many details of the shape of the tibiotarsus and their ankles are in no sense ancestral to the condition seen in other Theropoda. In view of the numerous synapomorphies supporting the dinosaurian and coelurosaurian relationships of Aves, and the dearth of discordant data, it is more parsimonious to conclude that the smaller ascending process and its association with the enlarged calcaneum in Neognathae are secondary modifications.

66) Metatarsal I lies more on the posterior than the medial side of metatarsal II. As described above, coelurosaurs are fur-

ther derived within theropods (metatarsal I lies on the medial side of metatarsal II ancestrally) in that metatarsal I lies in a posteromedial position (e.g., Fig. 6Q). Wellnhofer (1974), Osborn (1976a), and Tarsitano and Hecht (1980) noted the posterior position of metatarsal I in Avialae, although there was some disagreement among them as to the level at which this transformation took place within Theropoda. Once again, the controversy stems from different interpretations of the original positions of dissociated elements in fossils. This transformation is here considered to have taken place in the ancestral coelurosaur, because the apomorphic condition is known to be present in articulated examples of *Compsognathus* and Avialae. Moreover, articulated ceratosaurs demonstrate that this condition is not ancestral for Theropoda (pers. obs. of *Segisaurus**). The position of this element, however, remains a matter of conjecture in carnosaurs, and future finds may show that the apomorphic condition applies to a more inclusive taxon than to coelurosaurs alone among theropods. S. Hope (pers. comm.) notes that corvids have reversed the ancestral coelurosaur condition, because metatarsal I lies on the medial side of metatarsal II, as it does in Theropoda ancestrally.

67) Proximal surface of metatarsal IV subequal to II in size and metatarsal III more or less pinched between them. As argued above, the enlargement of the fourth metatarsal and the constriction of the proximal end of the third is the ancestral condition for Tetanurae. In contrast to Carnosauria ancestrally (Fig. 6G), however, metatarsal IV is subequal to III in size and metatarsal II forms no more than 22% of the width of the transverse axis of the ankle joint in Ornithomimidae (Osmolska et al. 1972), *Hulsanpes* (Osmolska 1982), *Compsognathus* (pers. obs.), Elmisauidae* (Osmolska 1981), Deinonychosauria (Fig. 6H), and Avialae (Fig. 6I). A further derived condition, in which the third metatarsal is so pinched between the second and fourth metatarsals that it barely contributes to the ankle joint, has arisen independently in tyrannosaurid carnosaurs, ornithomimids, *Hulsanpes*, troodontids, and elmisauidids*. Ornithurine birds are unusual in that the proximal end of metatarsal II lies behind the plane of metatarsals II and IV, but ornithurines are otherwise coelurosaurlike in sharing these apomorphies in metatarsal morphology.

V. Phylogenetic Relationships within Maniraptora

Maniraptora (n. tax.)

(Gr. *manus*, hand, *raptus*, to seize)

TEMPORAL RANGE.—late Jurassic to Recent

INCLUDED TAXA.—This taxon is erected to emphasize that all the characters listed below were shared by a common ancestor of Avialae and Deinonychosauria (or at least dromaeosaurs) that was not also an ancestor shared with Ornithomimidae. However, some of these characters also appear to be present in some of the less well known coelurosaurs, such as *Coelurus**, *Ornitholestes**, *Microvenator**, *Saurornitholestes**, *Hulsanpes*, Caenagnathidae, Elmisauidae*, and *Compsognathus*. Unfortunately, these taxa are too incompletely preserved to determine the sequence in which the maniraptoran synapomorphies appeared (see Fig. 9). A more precise determination of the level of synapomorphy of these characters must await future finds (see Conclusions, part I for further comment).

Diagnosis.—This section will examine the phylogenetic relationships between Deinonychosauria and Avialae. As in previous sections, evidence derived from less well known coelurosaurs listed above will be included. In the following analysis, Ornithomimidae, Carnosauria, Ceratosauria, and Sauropodo-

morpha will be used as successively more remote outgroups. Maniraptora possesses the following synapomorphies distinguishing this taxon among Theropoda.

68) Prefrontal reduced or absent. As in amniotes generally, both the lacrimal and prefrontal are present in Sauropodomorpha (Galton 1984). In Theropoda ancestrally the lacrimal gains broad exposure on the skull roof, thus partly replacing the prefrontal. The ancestral condition of the theropod lacrimal is retained by Ceratosauria (Gilmore 1920) and Carnosauria (Madsen 1976). This condition is also retained in Coelurosauria ancestrally, as is indicated by the presence of both elements in the growth series of the ornithomimid *Gallimimus* (Osmolska et al. 1972), and in all other ornithomimids in which this region is well preserved (Russell 1972). In contrast to the ancestral condition in coelurosaurs the prefrontal, if not absent, is at least reduced, its role in the construction of the skull roof having been supplanted by the lacrimal. The prefrontal is absent from all stages of ontogeny in Aves (Bellairs and Jenkin 1960), and no separate element is reported from this region in *Ornitholestes** (Osborn 1917) or Caenagnathidae (Barsbold 1983).

Currie (in press a) may have identified a prefrontal, albeit reduced and no longer in contact with the nasal, in *Troodon*. He notes that no clear suture remains because of coossification with the frontal. Nevertheless, he concludes that the structure is a prefrontal because its rugose dorsal surface bears shallow channels for blood vessels and its so-called "sutural contact" with the frontal is marked by several foramina. Currie notes further that at least remnants of sutural scars indicate the presence of a small and narrow prefrontal in *Dromaeosaurus*, *Saurornitholestes**, and perhaps in *Compsognathus*. However, the criteria Currie used to identify a prefrontal in *Troodon* may also be observed along the anterolaterally in ratites with subtriangular frontals. Moreover, the lateral margins of the frontal are similarly demarcated in tinamous; the dorsolateral surface is rugose and an apparent suture is formed by a series of foramina. The demarcated area often falls off when preparing the specimen, leaving traces of what could be considered a sutural surface. There is, however, no evidence that this structure represents a prefrontal bone. In both ratites and tinamous, the demarcation of the frontal in this region appears to be associated with the external nasal gland.

Aves is distinguished among extant tetrapods by the synapomorphic displacement of the external nasal gland to a position above the orbit. In birds in which the frontal reaches broadly over the orbits, the external nasal gland appears to induce the changes in frontal form noted above, including a linear array of more or less complete foramina marking the gland's position below the frontal margins (pers. obs.). (In some marine birds the dorsal surface of the frontal may display a foramen-filled trough that marks the dorsal displacement onto the frontal of a hypertrophied, salt-excreting external nasal gland.) Resolution of the problem of the identity of this structure will require more evidence. Nevertheless, whether one considers the structure a reduced prefrontal, or modification of the frontal induced by an avianlike position of the external nasal gland in maniraptorans, these theropods must be considered more birdlike in this respect than are other theropods.

Wellnhofer (1974), like some earlier authors, thought a separate prefrontal bone may have been present in the Eichstätt *Archaeopteryx**. Having examined this specimen, I am not con-

vinced of this interpretation, because the skull in general and the prefrontal region in particular are crushed and incompletely preserved. I agree with other authors that the portion of an element in the antorbital region on the counterslab is the remains of the lower ramus of the lacrimal, and I see no evidence of a separate prefrontal. Parts of the lacrimal remain in the antorbital region of the main slab, and there is a division between a fragment of the antorbital ramus and another fragment lying on the skull roof. The dispute centers on the identity of the latter fragment, and the conclusion that the division between the fragments on the main slab represents a suture rather than a break in an originally intact element. Given the direction in which the skull was compressed during preservation, the position and orientation of the division corresponds to a natural fracture plane between the skull roof and antorbital moieties of the usual maniraptoran lacrimal. Moreover, the shape and relationships of the so-called prefrontal are unlike those of other theropods, particularly since the "prefrontal" would exclude the lacrimal from the skull roof, unlike the case in any other theropod, including all other birds. Although there is some question about this character, it appears safe to conclude that unlike other theropods, the prefrontal is either reduced or lost in maniraptorans.

69) Axial epiphyses prominent. Epiphyses are present on the anterior cervicals in Saurischia ancestrally. In general the prominence of the epiphyses varies both with their position in the column and with the size of the saurischian in question. Nevertheless, in contrast to the condition of the axial epiphyses in Saurischia ancestrally (Fig. 3D, E), these structures are most prominent in Deinonychosauria (Fig. 3F) and Avialae (Fig. 3G), regardless of size.

70) Hypapophyses on vertebrae from cervicothoracic region. In Archosauria ancestrally the cervical vertebrae bear a more or less prominent midventral keel. The keel is commonly most prominent in the anterior elements of the cervical series, but it has become reduced or lost several times within Archosauria (Romer 1956). The keel is produced ventrally to form hypapophyses in eusuchian crocodylomorph pseudosuchians, but hypapophyses are otherwise absent in nondinosaurian archosaurs (Romer 1956). Hypapophyses are also absent in Sauropodomorpha (e.g., Galton and Cluver 1976), Ceratosauria (e.g., Gilmore 1920), and Carnosauria (e.g., Madsen 1976). The ancestral condition is retained in Coelurosauria in that hypapophyses are absent in Ornithomimidae (Osmolska et al. 1972) and *Compsognathus* (Ostrom 1978). In contrast, midventral keels in the anterior trunk vertebrae (i.e., cervicothoracic region) are produced ventrally to form discrete hypapophyses associated with the attachment of the *M. longus colli ventralis* in Deinonychosauria (Ostrom 1969b). The condition is not determinable in any of the *Archaeopteryx** specimens, but more or less prominent hypapophyses are present throughout Ornithurae (Bellairs and Jenkin 1960). In some groups of birds, such as loons and grebes, the hypapophyses may be large and elaborate, and they may extend well into the cervical region (Zusi and Storer 1969). However, in other birds, such as *Apteryx*, the hypapophyses are comparatively simple, feebly developed, and they are confined to the anterior few trunk vertebrae as in deinonychosaurs (pers. obs.).

71) Modifications associated with transition point begin close to base of tail. As argued above, Tetanurae is apomorphic compared to Theropoda ancestrally in that the modifications as-

sociated with the transition point are more marked. Compared to *Compsognathus* (Ostrom 1978) and Ornithomimidae (Fig. 2E), however, the transition point is more proximally placed in that the transition takes place between caudals 7 and 11 in Deinonychosauria (Fig. 2G) and Avialae (Fig. 2F). Fairly complete caudal series are known from both *Deinonychus* (Ostrom 1969b) and the Eichstätt *Archaeopteryx** and they differ from the tails of ornithomimids and other theropods in several ways. First, the neural spines and transverse processes are confined to the first seven to nine vertebrae, although like other archosaurs both structures are more prominent in the larger *Deinonychus* compared to the smaller *Archaeopteryx**. Second, the first 5 caudals have short, boxlike centra and vertically oriented zygapophysial facets. And third, both have modified haemal arches that are longer than deep in lateral view extending nearly to base of the tail. Thus, maniraptorans are the most derived among Theropoda in the development of the dynamic stabilizer tail (Ostrom 1969b; Padian 1982). Following Wellnhofer (1974), L. D. Martin (pers. comm.) agrees that long, tapered prezygapophyses are present posteriorly, but argues that only the postzygapophyses are elongate in the anterior portion of the tail in *Archaeopteryx** (Eichstätt). After examining a cast of the specimen in Martin's lab, I have, however, concluded that *Archaeopteryx** had elongate prezygapophyses on caudals beyond those in the base of the tail as in other maniraptorans for two reasons. First, the prezygapophyses in the middle of the tail are variable in length and shape as preserved; if these variations are natural, *Archaeopteryx** would be unlike all other saurians. Second, elongate postzygapophysial articular facets are uniformly present in this region, and this modification seems superfluous without concomitant elongation of the prezygapophyses with which the facets articulate. Taking these factors into account, variation in prezygapophysial shape and length in the midcaudals is here attributed to removal of the counterslab and consequent damage to the narrow and superficial portions of the prezygapophyses.

Although the caudal series is quite modified in Ornithurae, principally by the reduction and fusion of the distal segments and the loss of the zygapophyses, a number of the maniraptoran synapomorphies in tail form have been retained. For example, the short and boxlike centra in the proximal series are widespread among Aves. In addition, although they may be modified and fused to the centra, boat-shaped haemal arches that are longer than deep and flat-bottomed in lateral view are retained in the caudal region of some groups, such as Hesperornithes (Marsh 1880), and loons and penguins (pers. obs.). Like all birds, *Archaeopteryx** has enlarged feathers along the lateral margins of the tail (Ostrom 1976a), but then it is the only nonornithurine maniraptoran preserved in an environment of deposition in which feather impressions could be preserved. The orientation of the feathers and caudal zygapophyses in *Archaeopteryx** indicates that the tail was most mobile in the dorsoventral plane, as in dinosaurs generally. Evidently, the horizontal orientation of the tail feathers in extant birds cannot be accounted for in functional terms solely as an adaptation for flight.

72) Coracoid with subrectangular profile. The coracoid is subcircular in profile in Ornithodira ancestrally (see Appendix A). This condition is retained in Sauropodomorpha (Fig. 4B) and Ceratosauria (Raath 1969), and this appears to be the case judging from what remains of the element in *Lilienstermus** (Huene

1934). Except for the tapering posteroventral margin (see Part III, character 42), the coracoid is otherwise subcircular in Carnosauria (Madsen 1976) and in the coelurosaurs *Compsognathus* (Ostrom 1978), Ornithomimidae (Fig. 4C), and Caenagnathidae (Barsbold 1983). The coracoid in Deinonychosauria and Avialae is further derived relative to that seen in other Coelurosauria in that it is enlarged, particularly at the ventromedial and posterior margins; these modifications impart to the element a subrectangular profile (Fig. 4E). In addition, a pronounced "coracoid tubercle" lies just anterior to the glenoid rim and immediately ventral to the coracoid foramen. During ontogeny, the shoulder girdle of the chicken transforms from a subrectangular to an elongate coracoid characteristic of Ornithurae; I have been unable to determine if the coracoid was subcircular in outline at its initial stages of development. Interestingly, a subrectangular coracoid has re-evolved within Hesperornithes (compare coracoids of *Baptornis* with *Hesperornis* in Martin and Tate 1976) and in some other flightless birds such as the ratites (Feduccia 1980). This appears to be an example of pedomorphosis in that the subrectangular shape is a transitory stage in the transformation of the coracoid in the ontogeny of Aves. This is, however, the terminal stage in the ontogeny of the element in the two successively more remote outgroups of Ornithurae, namely Deinonychosauria and *Archaeopteryx**. Contrary to Tarsitano and Hecht (1980), the coracoid in *Archaeopteryx** is not ancestral with respect to the condition seen in other theropods. On the contrary, the shape and flexure of the element and the enlarged "coracoid tubercle" in *Archaeopteryx** (Fig. 4D) are matched in kind, if not degree, in deinonychosaurians (Fig. 4F) and elmsaurids* (P. J. Currie, pers. comm.). Ostrom (1974a, b, 1976a, b) and Padian (1982) have explored the significance of the transformations in coracoid morphology and their relationship to the function of the forearm and the origin of flight in the taxa here included in Maniraptora (see also Gauthier and Padian 1985).

73) Elongate forelimb nearly 75% of presacral vertebral column length, and elongate hand nearly equals or exceeds length of foot. As argued above, coelurosaurs are diagnosable in part on the basis of their elongate forelimbs and hands, although the hands of ornithomimids may be secondarily shortened. According to Ostrom (1976a), the forelimbs of *Ornitholestes** and Deinonychosauria are about 75% of the length of the presacral vertebral column, and those of *Archaeopteryx** are 120% to 140% of the presacral column length. Moreover, the hand is 92% of the length of the foot in Deinonychosauria (Ostrom 1969b, 1976a) and the hand exceeds the length of the foot in Avialae ancestrally (Bellairs and Jenkin 1960). Ostrom (1974b, 1976a), Padian (1982), and Gauthier and Padian (1985) have noted the synapomorphic resemblance between the forelimbs of deinonychosaurians and birds, and have explored the significance of these characters in the origin of flight within Coelurosauria.

74) Ulna bowed posteriorly. As in Archosauria ancestrally, the posterior margin is roughly straight and the element is not bowed posteriorly in Sauropodomorpha (Cooper 1981a: 736, fig. 31D), *Procompsognathus** (Ostrom 1981), *Liliensternus** (Huene 1934), Ceratosauria (Welles 1984), Carnosauria (Madsen 1976:137, fig. 42D), and *Compsognathus* (Ostrom 1978). The ulna is only slightly bowed in Ornithomimidae (Osmolska et al. 1972). In contrast, the ulna is strongly bowed posteriorly

in Caenagnathidae (Osborn 1924b), *Microvenator** (Ostrom 1970), troodontid (Russell 1969:603, fig. 9A) and dromaeosaur (Ostrom 1969b: 95, fig. 58A) deinonychosaurians, and *Archaeopteryx** (Ostrom 1976a). The ulna is even more prominently bowed in Ornithurae (Bellairs and Jenkin 1960). This apomorphy arose convergently within Pterosauria (Wellnhofer 1978).

75) Semilunate carpal. As argued above, distal carpal I caps the bases of metacarpals I and II in Theropoda ancestrally (Fig. 4K), and this condition is retained in Carnosauria ancestrally (Fig. 4L). The carpus in Ornithomimidae (Osborn 1917) and Tyrannosauridae (Barsbold 1983) is composed of small, poorly formed carpals lacking articular facets, and both taxa appear to be pedomorphic in this respect. Although it is clear that the tyrannosaurid condition derived from the ancestral condition, retained by other carnosaurians such as *Allosaurus*, the condition from which the ornithomimid hand derived is unclear. As in tyrannosaurids, the pedomorphic carpals of ornithomimids could have derived from the ancestral condition. However, because ornithomimids are closer to maniraptorans than carnosaurians are, it is also possible that the pedomorphic carpals could have derived from the condition here considered diagnostic of Maniraptora. I consider the former case to be correct, although I recognize that more information is needed to dispel the ambiguity regarding this point; in any case, this decision has no influence on the final outcome of the analysis.

In contrast to the ancestral theropod condition retained by the tetanurine ancestor, distal carpal I in Maniraptora was transformed into a depressed, semilunate-shaped carpal with a deep, horizontal groove proximally for reception of a reciprocally shaped ridge for articulation with the proximal carpal, and two prominent fossa distally for reception of the bases of metacarpals I and II (see Russell 1969; Ostrom 1976a). A semilunate carpal is present in *Coelurus** (Ostrom 1976a), Caenagnathidae (Barsbold 1983), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O). The integration of manual digits I and II in the wrist was initiated in Saurischia ancestrally. Functional integration was further advanced in Theropoda when distal carpal I capped both metacarpals. With the development of a semilunate carpal, the carpus reached a kind of functional equivalence with that of Ornithurae in ancestral Maniraptora. As noted by Russell (1969) and Ostrom (1969b), the resulting mesocarpal joint permitted increased mediolateral excursion of the hand relative to the forearm (=190°), a prerequisite to the development of avian powered flight (J. Rayner, pers. comm.).

76) Metacarpal III bowed laterally and very thin compared to metacarpal II. Metacarpal III is neither very thin nor bowed in Sauropodomorpha (Fig. 4I, J), Ceratosauria (Fig. 4K), and Ornithomimidae (Fig. 4M). The third digit and its metacarpal are reduced, but never bowed, in Carnosauria (Fig. 4L). In contrast, metacarpal III is very thin compared to metacarpal II, and it is bowed laterally in Deinonychosauria (Fig. 4N), *Archaeopteryx** (4O; based on pers. obs. of Eichstätt specimen) and most Ornithurae (Bellairs and Jenkin 1960). A gracile third metacarpal is also present in *Ornitholestes** (Osborn 1917) and Caenagnathidae (Osborn 1924b). I am unable to determine from the published figures if the element is bowed, and examination of the specimens will be necessary to decide if a thin and a bowed third metacarpal are one and the same character. As in all tetanurines, the third metacarpal lies ventral to the level of second, and the bowed nature of the third metacarpal may only

be apparent in dorsal or ventral view; thus, the preserved orientation of the element is critical in recognizing this character. Differences in orientation as preserved may account for why the third metacarpal of the Berlin *Archaeopteryx** appears bowed in the left hand but not in the right.

77) Posterodorsal margin of ilium curves ventrally in lateral view. The dorsal margin of the ilium is gently arched in profile in Saurischia ancestrally (Fig. 5B, C), although very early in sauropodomorph phylogeny the arching becomes more prominent. The gentle dorsal arc is retained in Theropoda, however, the posterior margin of the ilium is truncated vertically in *Liliensternus** (Huene 1934), Ceratosauria (Fig. 5C), Carnosauria (Fig. 5D), and Ornithomimidae (Fig. 5E). In contrast, the dorsal margin of the ilium curves posteroventrally in profile in Caenagnathidae (Barsbold 1983), *Ornitholestes** (Osborn 1917), Deinonychosauria (Fig. 5F, G), and Avialae (Fig. 5H, I).

78) Pubic peduncle of ilium extends ventrally beyond level of ischiadic peduncle, and pubis directed posteroventrally. The pubic and ischiadic peduncles terminate at about the same level and the pubis points anteroventrally in Sauropodomorpha ancestrally (Fig. 5B). The ancestral condition is retained in *Liliensternus** (Huene 1934), Ceratosauria (Fig. 5C), Carnosauria (Fig. 5D), Caenagnathidae (Barsbold 1983), *Ornitholestes** (Osborn 1917), and Ornithomimidae (Fig. 5E). In contrast, the pubic peduncle extends further ventrally and the pubis is directed more or less posteroventrally in Deinonychosauria (Fig. 5F, G) and Avialae (Fig. 5H, I). Ostrom (1976b) was the first to note that both the morphology of the pubic peduncle of the ilium and the preserved orientation of the pubis in *Deinonychus* indicated that the pubis could not have projected anteroventrally as in dinosaurs ancestrally. This observation has been corroborated by finds of articulated dromaeosaur pelvises (Barsbold 1977, 1979, 1983; Barsbold and Perle 1979). Of course, in the absence of articulated pelvises the precise orientation of the pubis is difficult to determine, as the variety of restorations of pubic orientations in *Archaeopteryx** and dromaeosaurs graphically illustrates (Fig. 5F, G). Tarsitano and Hecht (1980) argued that Ostrom's (1976a) restoration of the *Archaeopteryx** pelvis was incorrect, and that the pubes of *Archaeopteryx** were in fact oriented more as in Ornithurae. Regardless of the degree of reversal, however, the point to be emphasized is that Deinonychosauria and Avialae are like one another and unlike all other Theropoda in the great length of the pubic peduncle and that the pubis no longer points anteroventrally. If *Archaeopteryx** is in fact more birdlike in this respect than other theropods, that is consistent with our belief that it is a bird, but this observation has no bearing on the question of relationship between birds and deinonychosaurs.

Troodontids present a potentially more serious problem when trying to optimize the character "reversed pubis" on the most parsimonious tree for all the data. That is to say, an outline drawing of a pelvis said to be from *Saurornithoides* first appeared in Barsbold (1977), and the pubis was figured in the unreversed, ancestral condition. Subsequently, dashed lines included in another outline drawing of the same pelvis in Barsbold (1983) revealed that both drawings represented an incomplete specimen. A formal description of this specimen, including adequate illustrations and rationale for its referral to *Saurornithoides*, has yet to be published. If the ancestral form of the pubis and its attachment to the ilium can be verified in Troo-

odontidae, then one might question the monophyly of Deinonychosauria, which would require independent origins (i.e., convergence) to explain the similarities between the raptorial second pedal digits and didactyl pes in troodontids and dromaeosaurs. Alternatively, if one accepts the raptorial second pedal digit and didactyl pes of Deinonychosauria as synapomorphic, then reversal of the pubis took place twice among maniraptorans: once in dromaeosaurs and once in avialans. Yet another and equally parsimonious hypothesis would be the appearance of the reversed pubis in ancestral Maniraptora, with its subsequent reversal to the ancestral condition in troodontids; once again one must assume that troodontids are most closely related to dromaeosaurs on the basis of shared apomorphies in the raptorial second pedal digit and didactyl pes.

Each of these interpretations requires three evolutionary events to account for the distribution of these two characters among these three taxa. There is thus no basis for choice among the possible alternatives. Accordingly, until there is firmer evidence to the contrary, I will consider the pubis to have been reversed in the immediate common ancestor of deinonychosaurs and birds. Assuming this to have been the case, a reversed and posteroventrally oriented pubis must have arisen three times within Ornithosuchia, because this condition also obtains in Ornithischia (Fig. 5A) and segnosaurs (Barsbold and Perle 1979; Barsbold 1983; segnosaurs are here considered sauropodomorph dinosaurs of uncertain relationships, see Appendix A).

79) Pubic foot reduced anteriorly. As noted above, a pubic foot is present in Tetanurae ancestrally. However, it is expanded both fore and aft in Carnosauria (Fig. 5D), Caenagnathidae (Barsbold 1983), and Ornithomimidae (Fig. 5E). In contrast, the pubic foot is much less developed anteriorly than it is posteriorly in *Compsognathus* (Ostrom 1978), *Microvenator** (Ostrom 1970), *Coelurus** (Marsh 1896), Deinonychosauria (Fig. 5F, G), and *Archaeopteryx** (Fig. 5H; Padian 1982). The absence of a pubic foot in Ornithurae is considered a secondary modification (Fig. 5I). This character, like the preceding one and the following two characters, has yet to be determined in troodontids. The condition of the pubic foot in caenagnathids presents certain problems; the profile of the structure differs in each of Barsbold's figures (e.g., 1979, 1983), but it is usually portrayed as being longer anteriorly than posteriorly. In light of the evidence under consideration, caenagnathids are part of Maniraptora; thus their pubic foot must have been modified from the anteriorly abbreviated condition seen in other maniraptorans. This may, however, simply reflect inaccuracies in Barsbold's reconstructions.

80) Ischium two-thirds or less of pubis length. The ischium is at least three-quarters of the length of the pubis in Sauropodomorpha ancestrally (Fig. 5B), as it is in *Liliensternus** (Huene 1934), Ceratosauria (Fig. 5C), Carnosauria (Fig. 5D), and Ornithomimidae (Fig. 5E). In contrast, the ischium is no more than two-thirds of the length of the pubis in *Compsognathus* (Ostrom 1978) and Caenagnathidae (Barsbold 1983), and although the pubis is incomplete distally, this appears to be the case in *Ornitholestes** as well. As noted by Ostrom (1976a, b) and Padian (1982), the ischium is only half or less of the pubic length in Deinonychosauria (Fig. 5F, G) and *Archaeopteryx** (Fig. 5H). Ornithurae is hypothesized to be secondarily modified owing to reduction in the length of the pubis (Fig. 5I).

81) Obturator process distally placed on ischium. As argued

above, an obturator process on the ischium is the ancestral condition for Tetanurae. In Carnosauria the process is proximally placed (Fig. 5D), and this condition is retained in Ornithomimidae (Fig. 5E). *Ornitholestes** (Osborn 1917) appears to have a large and distally placed obturator process but its pelvis is not well enough preserved to allow further interpretation. The obturator process is distally placed in *Compsognathus* (Ostrom 1978) and Caenagnathidae (Barsbold 1983), and it is both enlarged and distally placed in Deinonychosauria (Fig. 5F, G). As discussed above, the condition in *Archaeopteryx** is difficult to interpret; either an obturator process is absent, or it is represented by the ventral of the two processes at the distal end of the ischium (Fig. 5H). This process is absent in Ornithurae, but in any case its absence in birds is here hypothesized to represent a phylogenetic loss rather than retention of an ancestral condition.

82) Anterior trochanter nearly confluent with proximal head of femur. As noted above, the anterior (=lesser) trochanter is a tall flange that is separated by a deep cleft from the femoral shaft in Carnosauria (Madsen 1976) and Coelurosauria ancestrally. Ornithomimidae (Osmolska et al. 1972) and *Microvenator** (Ostrom 1970) retain the ancestral tetanurine condition. The femoral head in Deinonychosauria (Ostrom 1976b) and *Archaeopteryx** (Ostrom 1976a) is like that of other coelurosaurs in that the anterior trochanter extends to the femoral head (Padian 1982). However, maniraptorans are distinguished from other coelurosaurs in that the anterior trochanter is separated from the femoral head by no more than a shallow groove, and the anterior trochanter is thus nearly to completely confluent with the femoral head. Ostrom (1976a:124, 125) described and figured the proximal end of the femur of *Microvenator**, *Archaeopteryx**, and *Cathartes*, and argued that the femur of *Archaeopteryx** is intermediate between that of "theropods" and Recent birds, in which there is no separate anterior trochanter (except as an occasional variant among neognaths). As is evident from Romer (1927), birds recapitulate the phylogenetic history of this transformation during ontogeny; the *pif* 2 attaches in the ancestral archosaurian position and subsequently migrates proximally through various theropod attachment points, eventually arriving at the position seen in extant birds. Thus, the five (or four) muscles inserting on the avian major trochanter yield a composite anterior plus greater trochanter (T. Rowe, pers. comm.).

83) Absence of fourth trochanter on femur. Tarsitano and Hecht (1980) noted that *Archaeopteryx** and other nonswimming birds are unusual among archosaurs in the loss of the fourth trochanter. As noted above, however, the fourth trochanter is feebly developed among coelurosaurs ancestrally, and it is absent in Deinonychosauria and birds. Pterosaurs also lost the fourth trochanter (Wellnhofer 1978), and this area of muscle attachment is also reduced in a number of very large quadrupedal dinosaurs, such as Sauropoda (see Appendix A).

84) Pedal digit IV longer than II and closer to III in length. Pedal digit IV is longer than II and closer to III in length in archosaurs ancestrally (Fig. 6J–N). As argued above, however, theropods are apomorphic in that pedal digit II is only a little shorter than IV, and the foot is thus more symmetrically developed about digit III (Fig. 6O). The symmetrical theropod foot is retained in *Procompsognathus** (Ostrom 1981), Cerautosauria (Raath 1969), Carnosauria (Madsen 1976), and

Ornithomimidae (Osmolska et al. 1972). However, the ancestral theropod condition appears to have reversed within Coelurosauria in that pedal digit IV approaches III in length, and thus is longer than digit II in *Ornitholestes** (Ostrom 1969b), *Compsognathus* (Ostrom 1978), Caenagnathidae (Barsbold 1983), Deinonychosauria (Russell 1969; Ostrom 1969b), and Avialae (Fig. 6P). Tarsitano and Hecht (1980) argued that birds were plesiomorphic compared to other theropods owing to the greater length of pedal digit IV. However, in view of the data presented here, this character is hypothesized to be an apomorphic reversal rather than a plesiomorphic retention in birds and other maniraptoran theropods.

Another aspect of the construction of the pes that may be related functionally to a lengthened fourth digit is the development of a raptorial second pedal digit, an attribute that is taken to extreme in troodontids and dromaeosaurs. No other theropods aside from cariamid neognaths approach the degree of specialization characteristic of deinonychosaurs. However, a few other extinct maniraptoran coelurosaurs appear to show incipient specializations to this end. For example, an enlarged articular surface indicating a greater radius of excursion between the second and third phalanx in the second pedal digit is apparent in *Elmisaurus** (Osmolska 1981) and *Ornitholestes** (Osborn 1917); unfortunately, the more distal portion of this digit, including the ungual, were not preserved in either specimen. As pointed out by D. Yalden (pers. comm.), the claw impressions encasing the pedal unguals of *Archaeopteryx** resemble the claws of arboreal mammals more than they do the claws of raptors using the foot to secure prey. The claw impressions of *Archaeopteryx** are also unlike those of *Compsognathus*, in that the impressions of the latter display a flat-bottomed shape that would have been better suited to running than climbing. Yalden's evidence is compelling; nevertheless, *Archaeopteryx** clearly has an enlarged articular surface on the distal end of the first phalanx of the second digit (pers. obs. of Eichstätt specimen), accompanied by an enlarged claw (Wellnhofer 1974). This indicates that *Archaeopteryx** possessed some ability to pin and secure prey with its foot (or use this toe as a defensive weapon), and this attribute may have been present in maniraptorans ancestrally. To be sure, none of these specimens is as specialized as are deinonychosaurs in this respect. Nonetheless, the foot of *Archaeopteryx** appears to be intermediate between the functionally tridactyl foot of theropods ancestrally and the functionally didactyl and raptorial foot of deinonychosaurs.

If the use of the foot to grasp prey is ancestral for maniraptorans, it might explain the initial advantage of a reversed first digit (the hallux), especially in an organism whose formerly raptorial forelimbs had been preempted to serve the demands of powered flight. Because the hallux opposes the action of the second digit, the pincerlike action of both digits would have enhanced the ability to grasp with the foot. This interpretation need not contradict Yalden's conclusions regarding the use of the feet in *Archaeopteryx**. By the stage of avian evolution represented by *Archaeopteryx**, the pes may have played a critical role in its ability to climb. However, the ability to grasp with the pes, so necessary to an arboreal biped, may simply have been inherited from a more distant and nonavian ancestor. As noted above, a lengthened fourth toe is common among extant birds. However, aside from the deinonychosaurlike pes of cariamids, I am not aware of any other ornithurine bird that

has a similarly modified second pedal digit (although a number of ratites are nonetheless able to inflict severe damage with this toe; Ostrom 1969b). Accordingly, this attribute is considered to have been lost in Ornithurae ancestrally, and to have re-evolved in the common ancestor of cariamid neognaths.

CONCLUSIONS

I. Summary of the Main Phylogenetic Conclusions of this Work

As implied by their name "lizard-hipped" dinosaurs, saurischians have always been grouped on the basis of their plesiomorphic resemblances. However, compared to alternative hypotheses, such as monophyly of Ornithischia-Sauropodomorpha or Ornithischia-Theropoda, the taxon Saurischia provides a better summary of the evidence pertinent to hypotheses of monophyly. Accordingly, Saurischia is herein defined ostensibly to include birds and all dinosaurs that share a more recent common ancestor with birds than they do with Ornithischia. The most obvious of the ten synapomorphies uniting Saurischia is their elongate, mobile, and S-shaped necks, a character that distinguishes birds among extant amniotes. Other birdlike attributes present in the ancestral saurischian include a variety of modifications of the manus, such as digit II being the main axis of the hand, a uniquely modified pollex, the palmar displacement of the lateral digits, and the relatively large size of the hand. To these may be added other synapomorphies in the skull and postcranial skeleton, such as the modification of the premaxilla, the spread onto the frontals of the area of origin of the temporal musculature, the modification of the atlanto-axial joint, the development of cervical epiphyses, and the presence of hyosphene-hypantra accessory intervertebral articulations.

Saurischia is composed of two principal lineages, the extinct Sauropodomorpha and extant Theropoda. Twenty-five synapomorphies unite Theropoda within Saurischia. Intact skulls are known from few extinct theropods, and the only synapomorphies so far identified from this region of the skeleton are the characteristically modified vomers and intramandibular joint. The vomers in Ratitae and Tinami are little changed from the ancestral condition in theropods. Most extant birds retain the basic theropod shape of the dentary-postdentary articulation and some degree of intramandibular mobility, although they are unlike theropods ancestrally in that they possess a fused mandibular symphysis. Intramandibular mobility has been lost in birds that have short, powerful jaws with broad mandibular symphyses. From the perspective of the ancestral condition in Theropoda, these birds invariably have unusual diets. Most theropod synapomorphies are derived from the more completely known postcranial skeleton. The ancestral theropod was well suited to cursorial habits and was distinctively birdlike, as is indicated by a light, hollow skeleton, a broader area of origin of muscles arising from the ilium, a variety of modifications of the hindlimbs and feet, and a tail that was thinned and stiffened distally to enhance its role as a dynamic stabilizer. The ancestral theropod retained the carnivorous habits ancestral for Archosauria, but its raptorial hands indicate further specialization toward this end. Moreover, the intramandibular joint suggests macrocarnivorous habits in that it would enable theropods to ingest relatively larger prey.

The late Triassic *Procompsognathus** and *Halticosaurus** are

of uncertain relationships, and they are therefore placed *incertae sedis* within Theropoda. Among the early theropods are several taxa, including the well-represented *Coelophysus*, *Syntarsus*, and *Ceratosaurus*, that are included here in a modified version of Marsh's Ceratosauria. As constituted here, Ceratosauria is the sister-group of a new taxon, Tetanurae, which includes birds and all theropods that are closer to birds than they are to either Ceratosauria or to the other early theropods. The monophyly of Tetanurae is supported by 17 synapomorphies, including a profound difference between the larger, mobile proximal and the narrow, stiffened distal parts of the tail. Other birdlike attributes of Tetanurae include the presence of a large maxillary fenestra, antorbital tooth row, loss of dentary caniniform tooth, spine tables in the anterior cervicals, enlarged hand, basal appression of metacarpals I and II, palmar displacement of metacarpal III, loss of manal digit IV beyond embryonic stages of development, pubic foot, enlarged ascending process, and shortened metatarsal I.

Coelurosauria is ostensibly defined to include birds and all theropods that are closer to birds than they are to carnosaurs. Coelurosauria is thus removed from its classical and paraphyletic status; and in keeping with evolutionary theory, Coelurosauria is applied instead to a monophyletic taxon encompassing *Ornitholestes**, *Coelurus**, *Compsognathus*, *Microvenator**, *Saurornitholestes**, *Hulsanpes*, *Elmisauridae**, *Caenagnathidae*, *Ornithomimidae*, *Deinonychosauria*, *Avialae*, and their immediate common ancestor. Fifteen synapomorphies distinguish *Ornithomimidae*, *Deinonychosauria*, and birds from *Carnosauria*, and at least some of these apomorphies are shared by the remaining coelurosaurs listed above. Several characters distinguishing extant birds among archosaurs are seen in the skull and hindlimb of all coelurosaurs, but from the standpoint of powered flight, the most interesting of these are the modifications of the forelimb and pectoral girdle. These modifications, normally thought to be related to powered flight, include a fused and bony sternum, furcula, elongate forelimb and hand, and the beginnings of medial enlargement of the coracoid.

A new taxon, Maniraptora, is proposed for the group of theropods including birds and all coelurosaurs that are closer to birds than they are to *Ornithomimidae*. The immediate common ancestor of birds and deinonychosaurs may be distinguished from ornithomimids by possession of 17 synapomorphies. Even nonavian maniraptorans are essentially birdlike in many details of their morphology, including reduction (or loss) of the prefrontal, stiffening and thinning of all but the proximal part of the tail, a characteristically modified coracoid, very long forelimb, bowed ulna and third metacarpal, several modifications of the pelvis including a reversed pubis (at least in dromaeosaurs and birds), absence of discrete fourth and anterior trochanters on the femur, birdlike proportions of the relative lengths of pedal digits II, III, and IV, and at least the incipient development of a raptorial second pedal digit. Various specializations indicate that the raptorial function of theropod forelimbs reached its apex in ancestral maniraptorans. These modifications played an important role in the origin of flight, because the essential elements of the flight stroke are realized in the manner of folding and unfolding the hands, and extending and retracting the forelimbs and hands during prey capture (Padian 1982; Gauthier and Padian 1985).

The precise diagnosis and contents of Maniraptora are prob-

lematic. *Compsognathus* presents particular difficulties; it shares maniraptoran characters 79, 80, 81, and 84 that are absent in ornithomimids, but it retains the ancestral condition, an unbowed ulna, indicating that caenagnathids, *Microvenator**, deinonychosaurs, and birds are more closely related to one another than any of them is to *Compsognathus*. The anomalously short forelimbs of *Compsognathus* present further problems; the hand in particular is incomplete and after examining the specimen I do not feel secure with Ostrom's (1978) conclusions regarding the number of digits. Also, the ornithomimid tail appears in some ways more maniraptoranlike than is that of *Compsognathus*. Thus, it appears that *Compsognathus* is outside the remaining maniraptorans, and it is also possible that it is outside a possible ornithomimid-maniraptoran group.

Caenagnathidae, *Coelurus**, *Microvenator**, Elmsauridae*, and *Saurornitholestes**, and especially *Ornitholestes**, are closer to birds and deinonychosaurs than are ornithomimids. Although this conclusion seems secure, these taxa are so incompletely known that the details of their phylogenetic relationships remain obscure. Accordingly, these taxa are placed *incertae sedis* within Maniraptora, and with some reservations, *Compsognathus* is also included in this taxon. Compared to *Compsognathus*, it is clear that deinonychosaurs and birds are more closely related in that they share characters 69, 71, 72, and 78, but because of incomplete data it is not clear when these attributes arose within Maniraptora. The distinctly birdlike pelvis of dromaeosaurs appears to be absent in most other maniraptorans, thus indicating that this character arose within the group. If, as Barsbold (1983) suggests, these modifications are absent in troodontids, then the monophyly of Deinonychosauria would be brought into question; in any case, the precise level at which these modifications arose is at present indeterminable. Future discoveries and reanalyses will decide which among the 17 synapomorphies listed for Maniraptora are diagnostic of all, as opposed to some, members of this group. The cladograms in Figures 8 and 9 depict the phylogenetic relationships among Theropoda proposed here.

II. The Problem of the Definition of the Name Aves

Aves was initially applied to extant birds alone (Linne 1758). Subsequent finds of other feathered theropods from outside the immediate ancestry of all extant birds (i.e., *Archaeopteryx**, *Hesperornithes*) resulted in the term Aves being applied to a more inclusive taxon. Although this decision accurately reflects phylogenetic relationships, it also has the unfortunate side effect of diminishing the phylogenetic informativeness and stability of the name Aves. That is to say, Aves currently summarizes only those synapomorphies diagnostic of what I call Avialae, because it restricts the diagnosis of Aves to those characters that are determinable in the fossil *Archaeopteryx**.

An example of the kind of problem that this decision has generated is evident in Wellnhofer and Whetstone's disagreement over the identity of a particular bone in *Archaeopteryx**. Wellnhofer (1974) considered the element in question a squamosal, whereas Whetstone (1983) claimed it to be an opisthotic; surely, neither would have difficulty identifying these elements in the skulls of extant birds. This raises the issue of whether or not such an easily recognizable taxon as extant Aves should be left to the vagaries too often inherent in interpreting the mor-

phology of fossils. One must bear in mind that all synapomorphies present in *Archaeopteryx** must also be present in extant birds, although perhaps in a modified form. However, the reverse cannot be the case; not only do extant birds share a more recent common ancestor with one another than any of them does with *Archaeopteryx**, but extant birds share numerous apomorphies that are not preservable in fossils. Furthermore, it is exceedingly unlikely that any fossil would lead to the conclusion that Recent birds are not most closely related to each other among extant amniotes. After all, Appendix A and the text above record over 100 synapomorphies that distinguish the skeletons of extant birds from their nearest living relatives, the crocodiles; and there are numerous characters in soft anatomy, behavior, physiology, and biochemistry that are diagnostic of this taxon as well.

Another drawback of current practice is that it treats characters as if they were defining, in the sense that if an organism has feathers, it must be a bird. Not only is this perspective typological and thus antievolutionary, but one can envision the difficulties resulting from the possible discovery of feathers in deinonychosaurs, which most certainly did not fly. Moreover, under current practice how would one classify a group of birds that lost feathers during their evolution? In the phylogenetic system, this presents no problem, for if an organism is born to a bird, it is a bird, regardless of the characters it may or may not possess. Characters may aid recognition of ancestry, but they do not define it (Gauthier et al., in prep.). Accordingly, it is recommended that the taxon Aves be standardized in the phylogenetic system by applying this name only to that portion of Theropoda that includes the most recent common ancestor of Ratitae, Tinami, and Neognathae, and all of its descendants.

To reflect the more complex relationships that are of interest mainly to paleontologists, new or less widely used names are applied to taxa including Aves and one or more of its extinct sister-groups. The name Ornithurae is applied to Aves plus all extinct maniraptorans that are closer to Aves than is *Archaeopteryx**, and the name Avialae is applied to Ornithurae plus all extinct maniraptorans that are closer to Ornithurae than they are to Deinonychosauria. Thus, although the meaning of Avialae and Ornithurae is expected to vary according to the discovery of new fossils, the contents and diagnosis of the taxon Aves in the context of extant amniotes will remain unchanged.

Birds are poor candidates for fossilization and the paucity of their fossil record is widely recognized. This unfortunate circumstance is not confined to birds alone, but applies to Theropoda generally, all of which have lightly constructed skeletons for their size. Nevertheless, theropod stratigraphic occurrences are concordant with the phylogenetic hypothesis offered here. For example, Ceratosauria first appears in the late Triassic, although most ceratosaurs are reported from the early Jurassic, and they persist until the late Jurassic. Continental deposits of mid-Jurassic age are rare, so it is not until the late Jurassic that theropods once again become relatively common in the fossil record. By the late Jurassic most of the major tetanurine lineages have appeared: carnosaurs, ornithomimids, and maniraptorans, including birds, are reported from Upper Jurassic sediments. Indeed, the only major coelurosaur lineage that is not yet represented in the late Jurassic is Deinonychosauria, whose earliest appearance in the fossil record is in the early Cretaceous. Or-

nithurines are also reported from the early Cretaceous, and the earliest record of Aves is in the late Cretaceous.

III. Implications for the Origin of Flight

The above-hypothesized relationships among Theropoda have important implications for hypotheses concerning the origin of flight. Most of the skeletal modifications enabling *Archaeopteryx** to fly are present in all maniraptorans, although only avialans are able to fly. This requires that any functional explanation for the origin of flight must also account for the apomorphic similarities shared by *Archaeopteryx** and coelurosaurs in general and deinonychosaurs in particular (Gauthier and Padian 1985). One may not agree with the particular explanation initially offered by Ostrom (1974a, i.e., the insect net hypothesis), but one must appreciate that insofar as he sought to develop a general explanation for the function of the forelimbs and pectoral girdle in Maniraptora, his approach was basically sound. Those who favor other hypotheses should begin to analyze the evolution of flight in theropods in the context of the independent line of evidence afforded by their phylogenetic history (Gauthier and Padian 1985).

In view of the evidence placing birds within Maniraptora, Coelurosauria, Tetanurae, Theropoda, Saurischia, Dinosauria, Ornithodira, Ornithosuchia, and Archosauria, it should be clear that birds are neither the sister-group of mammals (Gardiner 1982), nor are they the sister-group of crocodiles (Walker 1972; Martin 1983a). Likewise, this evidence provides a new perspective on Walker's (1964) suggestion that theropods are polyphyletic. Walker's hypothesis can be rejected on two counts: (1) *Ornithosuchus* is not a carnosaur, and (2) the alternative hypothesis of separate origins of "carnosaurs" and "coelurosaurs" from within "theodonts" is uninformative, because it claims no more than that "carnosaurs" and "coelurosaurs" are archosaurs. A similar line of reasoning can be applied to Chatterjee's (1985) postulated connection between the poposaurid raiuisuchian pseudosuchian *Postosuchus* and tyrannosaurid carnosaur; in the context of all the evidence, their shared apomorphic resemblances beyond those common to all archosaurs must be considered convergent.

A popular misconception is that all dinosaurs were huge lumbering beasts that long ago became extinct. To be sure, only one lineage of dinosaurs survived the end of the Cretaceous. Nevertheless, this lineage currently accounts for nearly half of the total species diversity of extant Amniota. Birds are living dinosaurs, and as such they have extended the preeminence of Dinosauria among terrestrial vertebrates from the late Triassic to the present day.

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APPENDIX A

ARCHOSAUR PHYLOGENY: ON THE RELATIONSHIPS OF CERTAIN EXTINCT ARCHOSAURS TO EXTANT CROCODILES AND BIRDS

The hypotheses of relationship discussed below derive mainly from Gauthier (1984 and references therein). They provide the context in which the present analysis of saurschian phylogeny was undertaken. As used here, *Sauria*, n. comb., is restricted to the least inclusive taxon encompassing extant diapsids, and the name *Diapsida* is applied to the taxon including extant *Sauria* and its extinct sister-group, *Araucoscelidia*. The more inclusive groups of Recent *Amniota* recognized in this work follow the usage in Gauthier (1984) and Gauthier et al. (in prep.): *Mammalia* is the sister-group of *Reptilia* within *Amniota*; *Reptilia* includes the sister-taxa *Chelonia* and *Sauria*, and *Sauria* includes the sister-taxa *Lepidosauria* and *Archosauria*.

Archosauria (n. comb.) is redefined to encompass all the descendants of the most recent common ancestor of crocodiles and birds. So defined, some taxa previously included within *Archosauria* are now excluded from it. Thus, *Proterochampsidae*, *Erythrosuchidae*, and *Proterosuchidae* are here considered successively more remotely related outgroups of *Archosauria* (s.s.), rather than "proterosuchian-grade archosaurs." Defining *Archosauria* in this way provides a more fruitful perspective from which to examine archosaur phylogeny. Rather than proceeding from a position of less evidence—by trying to determine which group of "theodonts" gave rise to birds or crocodiles—we may now regard more precisely stated hypotheses from the position afforded by more secure knowledge (i.e., no one has ever confused a living crocodile with a living bird). That is to

say, by defining *Archosauria* and its major subgroups on the basis of the ancestry of extant archosaurs, an extinct and diagnosable archosaur can have only one of two possible relationships; it could be more closely related to birds, or it could be more closely related to crocodiles. *Pseudosuchia* (n. comb.) is redefined to include extant crocodiles and all extinct archosaurs that are closer to crocodiles than they are to birds. Likewise, *Ornithosuchia* (n. comb.) is redefined to include extant birds and all extinct archosaurs that are closer to birds than they are to crocodiles.

I realize that it is not enough simply to list supposed "synapomorphies" in support of a particular hypothesis. To make the hypothesis most vulnerable to test, one should proceed through the entire system of Hennigian argumentation for each character and array this evidence in a taxon/character matrix. Furthermore, I have had to consider many specimens of taxa that I have not had the opportunity to study first-hand, and I have relied instead on published illustrations and descriptions. Finally, I have not had the time to consider several recent publications on archosaur phylogeny (e.g., Paul 1984a, b) in the detail that they deserve. Accordingly, the following can only be considered a preliminary analysis (or as R. Bakker [pers. comm.] put it, an exercise in "armchair cladistics"). To balance these caveats, I should add that the hypothesis presented below is broadly concordant with those arrived at by other workers in this area (e.g., Benton 1985, Parrish 1984 and pers. comm.).

As defined here, *Pseudosuchia* and its major subgroups can be diagnosed as follows (cases of homoplasy will only be listed if they occur between, rather than within, basic taxa).

Pseudosuchia

(n. comb. = *Parasuchia*, *Aetosauria*, *Rauisuchia*, and *Crocodylomorpha*—including crocodiles)

- 1) Crocodile-normal crurotarsal ankle joint, in which the peg is on the astragalus and the socket is on the calcaneum.
- 2) Calcaneal tubercle enlarged (also in *Ornithosuchidae*).
- 3) Cervical ribs short and stout.
- 4) Discrete postparietal confined to early juvenile or prehatching ontogenetic stages (also in ornithosuchians aside from *Euparkeria**—see discussion below).
- 5) Palatal teeth absent (also in ornithosuchians aside from *Euparkeria**).

Unnamed Taxon Including Aetosauria, Rauisuchia, and Crocodylomorpha

- 6) Septomaxilla absent.
- 7) No separate postparietal at any time in posthatching ontogeny.
- 8) Fusion of second intercentrum and first centrum in juvenile or earlier stages of ontogeny.
- 9) Triradiate pelvis (also in ornithosuchians; see Parrish 1984).
- 10) "Screw-joint" tibio-astragalar articulation (R. Long, pers. comm.; also in *Ornithosuchidae*, M. Parrish, pers. comm.).
- 11) Fully developed crocodile-normal crurotarsal joint (Krebs 1963; Brinkman 1981).
- 12) Osteoderms on ventral surface of tail.

Unnamed Taxon Including Rauisuchia and Crocodylomorpha

- 13) First (atlantal) intercentrum much longer than wide.
- 14) Axial diapophysis reduced or absent (or corresponding process of axial rib reduced; J. Clark, pers. comm.).
- 15) Enlarged, pneumatic, basiptyergoid processes (J. Zawiskie, pers. comm.).
- 16) Length of pubis exceeds three times width of acetabulum (also in ornithosuchians aside from *Euparkeria**).
- 17) Fewer than four phalanges in pedal digit five.

Crocodylomorpha

- 18) Quadratojugal extends to dorsal surface of skull.
- 19) Quadrate and quadratojugal inclined anterodorsally.
- 20) Quadrate contacts prootic.
- 21) Postfrontal absent (also in ornithosuchians aside from *Euparkeria** and *Ornithosuchidae*).
- 22) Maxillaries contact to form secondary palate anteriorly.
- 23) Internal jugular vein absent.
- 24) Squamosal without ventral ramus.
- 25) Post-temporal fenestra very small (analogous modification achieved by separate means within *Ornithosuchia*).
- 26) Fenestra "pseudorotunda" present (also appearing at some unknown level within ornithosuchians and theropods).

- 27) Entire deltopectoral crest distally placed.
- 28) Clavicles absent.
- 29) Coracoid ventromedially elongate (also in pterosaurs).
- 30) Radiale and ulnare elongate and columnar.
- 31) Pedal digit five with fewer than four phalanges (also in ornithosuchians).

M. Parrish (pers. comm.) noted some interesting characters indicating a closer relationship between aetosaurs and rousuchians than is suggested by the characters listed above. Crocodylomorphs may turn out to be the sister-group of a rousuchian-aetosaur group, or they may be the sister-group of rousuchians as suggested above. Nevertheless, it must be emphasized that the analyses of Parrish and Gauthier agree on two points: 1) Pseudosuchia is monophyletic, and 2) Parasuchia is the sister-group of the crocodile-aetosaur-rousuchian group.

Ornithosuchia

(=*Euparkeria*?, Ornithosuchidae, *Lagosuchus**, Pterosauria—including *Scleromochlus**, Herrerasauridae*, Ornithischia, Sauropodomorpha, and Theropoda—including birds)

One might question whether or not *Euparkeria** is inside or outside of Archosauria (s.s.). Evidence presented below indicates that *Euparkeria** is closer to birds than to crocodiles. This early Triassic archosaur is, however, exceedingly primitive, and some evidence supports an alternative hypothesis in which Pseudosuchia and Ornithosuchia (excluding *Euparkeria**) are most closely related. For example, unlike *Euparkeria**, all other archosaurs share the apomorphic absence of palatal teeth, absence of discrete intercentra throughout the trunk and in most of the cervical region, and absence of a discrete postparietal and exoccipitals beyond juvenile stages of development. Thus, four potential synapomorphies could unite all archosaurs with respect to *Euparkeria**. However, discrete trunk intercentra are also absent in the two successively more remote outgroups of Archosauria, Proterochampsidae and Erythrosuchidae; the presence of discrete trunk intercentra in *Euparkeria** must then be interpreted as either a reversal, or as further evidence of the immaturity of the known specimens. Six potential synapomorphies unite *Euparkeria** with the birdlike archosaurs. I have been unable to discover any evidence that *Euparkeria** is closer to crocodiles.

Looking again at the evidence, it is interesting to note that intercentra, postparietals, and exoccipitals are present in juvenile archosaurs ancestrally (e.g., Camp 1930; de Beer 1937). That *Euparkeria** could be represented by juvenile or at least incompletely grown specimens is also indicated by unfinished articular surfaces on long bones, an ossified distal tarsal II, an unfused scapuloacromioid, neural arches that are unfused with their respective centra, and separate sacral ribs. Thus, rather than character discordance arising from convergence, the apparent discordance may arise instead from comparing nonequivalent ontogenetic stages. If one disregards the apparently age-related characters, and accepts the evidence indicating that *Euparkeria** is an ornithosuchian archosaur, then one need only invoke a single ad hoc hypothesis of convergence, namely, the independent loss of palatal teeth in Pseudosuchia on the one hand, and in Ornithosuchia aside from *Euparkeria** on the other, to account for the available evidence. This problem should be given further consideration, but for the present the following characters are accepted as diagnostic of Ornithosuchia. Fortunately, *Euparkeria** is so plesiomorphic that its ultimate placement makes little difference in determining character polarity in the following analysis.

- 1) Squamosal reduced and descending ramus gracile (reversed in large-headed, carnivorous ornithosuchians such as tyrannosaurs).
- 2) Centra steeply inclined in at least the first four postatlantal cervicals.
- 3) Modifications in the hindlimb and girdle correlated with semierect gait (also in pseudosuchians aside from Parasuchia; see Parrish 1984).
- 4) Ventral flange of astragalus absent.
- 5) Crocodile-reversed ankle joint, with peg on calcaneum and socket on astragalus (including loss of perforating foramen; see Cooper 1980, 1981b; Brinkman 1981; Thulborn 1982).
- 6) Pedal digit five with fewer than four phalanges (also in rousuchian-crocodylomorph group).

Unnamed Taxon Including Ornithosuchidae, *Lagosuchus**, Pterosauria, Herrerasauridae*, Ornithischia, Sauropodomorpha, and Theropoda

This taxon might more profitably be considered Ornithosuchia, in that the distribution of characters among archosaurs leaves little doubt as to the monophyly of this taxon. Until the position of *Euparkeria** is better understood, however, this taxon will remain unnamed. Should *Euparkeria** be shown to be outside of Archosauria (s.s.), then by definition the name Ornithosuchia would be restricted to this taxon. This group of archosaurs is diagnosed by the following synapomorphies (if indeterminable owing to nonpreservation or profound transforma-

tion, character will be followed by L? for *Lagosuchus** and Pt? for pterosaurs, including *Scleromochlus**).

- 7) Discrete postparietal absent in post-hatching ontogeny (L?; also in pseudosuchians).
- 8) Palatal teeth absent (L?; also in pseudosuchians).
- 9) Coracoid tubercle lies close to glenoid fossa and coracoid foramen.
- 10) First metacarpal with offset distal condyles, and pollex directed medially and bearing enlarged ungual (L?;Pt?).
- 11) Manus more asymmetrical than in pseudosuchians, with inner digits much larger than outer digits (L?;Pt?).
- 12) Supra-acetabular buttress.
- 13) Prominently triradiate pelvis, with pubis length at least three times width of acetabulum (also in crocodylomorph-rousuchian group, and to a lesser extent aetosaurs).
- 14) Anterior trochanter on femur appears early in posthatching ontogeny.
- 15) Aliform fourth trochanter (Pt?; characters 13–16 correlated with erect posture; see Parrish 1984).
- 16) Fifth metatarsal gracile.

Ornithodira (n. tax.)

(Gr. *ornithos*, bird; *deire*, neck)

(=*Lagosuchus**, Pterosauria, Herrerasauridae*, Ornithischia, Sauropodomorpha, and Theropoda)

The possession of the following synapomorphies makes it clear that ornithodiran monophyly is one of the most highly corroborated hypotheses in archosaur phylogeny. Indeed, the immediate common ancestor of Ornithodira was fundamentally more birdlike than were ornithosuchids, *Euparkeria**, or pseudosuchians. Unfortunately, the precise level at which the following characters arose is problematic in some instances, because *Lagosuchus** is incompletely known and pterosaurs are so specialized. If a character listed as diagnostic of Ornithodira is only questionably present due to incomplete preservation or profound modification, this fact will be denoted by either (L?) for *Lagosuchus** or (Pt?) for pterosaurs, following the character in question. It is not yet clear if *Lagosuchus** or Pterosauria is the immediate sister-group of dinosaurs, although the femur is, at least in *Dimorphodon*, more dinosaurlike than is that of *Lagosuchus** (Gauthier 1984).

- 17) Postfrontal absent (L?; also in crocodylomorphs).
- 18) Atlantal intercentrum enlarged, completely surrounding odontoid ventrally and laterally and fitting into prominent recessed area below odontoid on axis.
- 19) Axial intercentrum, and then odontoid, fuses to axis at cessation of growth.
- 20) Modification of cervical centra and zygapophyses that combine to yield an S-shaped neck (compared to dinosaurs, rudimentary in both *Lagosuchus** and in Pterosauria ancestrally; although within pterosaurs the neck may be in some ways more birdlike than is the neck of *Archaeopteryx**).
- 21) Zygapophysial facets nearly vertically disposed in all but proximal part of tail (L?).
- 22) Interclavicle absent (L?).
- 23) Clavicle reduced and gracile (L?; enlarged in coelurosaurs).
- 24) Glenoid facet on scapuloacromioid faces posteroventrally (Pt?).
- 25) Coracoid small, with subcircular profile, and lying in nearly the same plane as the scapula (Pt?).
- 26) Forelimbs less than 55% of hindlimb length (Pt?), and hindlimb very long relative to length of trunk.
- 27) Apex of deltopectoral crest placed distally on humerus (Pt?).
- 28) Less than five phalanges in manal digit four and less than three phalanges in manal digit five (L?).
- 29) At least three vertebrae involved in sacrum (L?; also in Ornithosuchidae?).
- 30) Brevis shelf appears on ventral surface of postacetabular portion of ilium (Pt?).
- 31) Birdlike distal end of femur—prominent anterior and posterior intercondylar grooves, with the latter constricted by prominent external tibial condyle, and appearance of a discrete fibular groove and condyle—modifications in the knee joint played key roles in enabling a narrow-tracked, bipedal gait and erect stance (Stolpe 1932).
- 32) Tibia as long or longer than femur (reversed in all dinosaurs over a few meters in length, or larger in the case of theropods).
- 33) Fibula thin and strongly tapered distally and calcaneum reduced.
- 34) Astragalus transversely widened.
- 35) Astragalus and calcaneum with smooth, rollerlike articular surfaces abutting against depressed distal tarsals.
- 36) Metatarsals elongate and closely appressed.
- 37) Pes digitigrade.

- 38) Pes functionally tridactyl (Pr?).
- 39) Pedal digit five reduced, does not exceed length of metatarsal IV (Pr?), and composed of no more than two phalanges.
- 40) Parasagittal rows of osteoderms absent.

Dinosauria

(n. comb. = Herrerasauridae*, Ornithischia, Sauropodomorpha, and Theropoda—including birds)

Before proceeding with a diagnosis of Dinosauria, it will be necessary to briefly consider Herrerasauridae*, and the diagnoses of, and phylogenetic relationships within, Ornithischia and Sauropodomorpha.

Herrerasauridae* is represented by three very incompletely known taxa, *Staurikosaurus**, *Ischisaurus**, and *Herrerasaurus**, that are of uncertain relationships to one another. They nevertheless appear to be the sister-group(s) of all other dinosaurs (Gauthier 1984).

Diagnosis of Ornithischia

The diagnosis and contents of Ornithischia are unproblematic, which might be expected since the monophyly of this taxon has been accepted for nearly a century (Seeley 1887). The same cannot be said for phylogenetic relationships within Ornithischia. Using Saurischia as a sister-group, with herrerasaurs* and Pterosauria-*Lagosuchus** as successively more remote outgroups, the following characters are considered diagnostic of Ornithischia. The evidence discussed below is derived from Gauthier (1984) but modified in light of the studies of Sereno (1984, 1986) and Norman (1984). The only examples of relatively generalized ornithischians that were available for study were specimens of *Scutellostaurus** and a cast of *Heterodontosaurus*, and most of the characters listed below are derived from the literature (see review in Gauthier 1984).

Preauricular bone; mandibular condyle set slightly to deeply below tooth rows; cheek teeth with distinct crown and root, crowns of cheek teeth low, bulbous basally, subtriangular in profile, and bear enlarged accessory denticles on margins; quadratojugal dorsal process reduced, not in contact with squamosal; ossified palpebral cartilage; antorbital fenestra reduced and much smaller than orbit; maxillary process of premaxilla enlarged and lengthened posteriorly to separate maxilla from nasal for half or more of their former sutural contact; quadrate elongate and massive; dentary participates in coronoid eminence; gastralia absent, ossified tendons present at least above sacral region; four to five or more sacral vertebrae and sexual dimorphism in sacral number (see Galton 1974, 1982); pubis completely reorganized, with short anterior process and long, rodlike posterior ramus paralleling ischium; ilium with enormously elongate iliac spine; symphysis restricted to distal end of ischium, winglike anterior trochanter, pendant fourth trochanter, fifth pedal digit reduced to metatarsal spur.

For the sake of discussion, I recognize the following basic taxa within Ornithischia:

- 1) *Lesothosaurus*
- 2) Thyreophora, a taxon including *Scutellostaurus**, *Scelidosaurus*, stegosaurs, and ankylosaurs.
- 3) Following Sereno (1984, 1986), a taxon including *Heterodontosaurus* and Ornithopoda sensu Santa Luca (1980)
- 4) Following Sereno (1984), and Osmolska and Maryanska (pers. comm.), a taxon including pachycephalosaurs and ceratopsians (including psittacosaur).

Taxon 1, *Lesothosaurus*, is very incompletely known. Its current placement in "Fabrosauridae" is uninformative, as conceived in Galton (1978) "fabrosaurs" are paraphyletic in that some taxa included within this group appear to be more closely related to the entity composed of ornithischian taxa 2–4 (hereinafter termed higher ornithischians), than they are to one another. *Lesothosaurus* is said to possess an obturator process on the ischium (Thulborn 1972), which is otherwise known only in Ornithopoda (Santa Luca 1980). However, other evidence indicates that *Lesothosaurus* is the sister-group of higher ornithischians (Gauthier 1984, Sereno 1984, 1986). That is to say, groups 2–4 share a mandibular fenestra that is very small or absent, a spout-shaped mandibular symphysis, slightly to deeply inset marginal tooth rows (i. e., structures analogous to "cheeks" are thought to have been present, Galton 1973b), a distal condyle of the quadrate that is wider than the mandibular condyle, an enlarged facial process of the maxilla that further reduces the size of the antorbital fossa and fenestra, a robust jugal, fused parietals, and an anterior pubic process that is at least moderately developed. Thus, in light of current knowledge it appears that an obturator process arose twice within Ornithischia.

*Scutellostaurus** is very poorly known, but it shares with the other members of taxon 2 raised osteoderms on the dorsum, an ilium that exceeds the length of the femur, and longer forelimbs and trunk compared to hindlimb length (Colbert,

1981). Accepting this placement requires that development of more deeply inset tooth rows took place twice within Ornithischia: once in the scelidosaur-stegosaur-ankylosaur group, and once in the remaining ornithischians. From evidence presented by Thulborn (1977), the so-called "juvenile scelidosaur" appears to bridge the gap between *Scutellostaurus** and the type-specimen of *Scelidosaurus* (Galton, pers. comm., considers the scelidosaur specimens conspecific). *Scelidosaurus*, stegosaurs, and ankylosaurs appear to be more closely related in that they share an enlarged palpebral covering the orbit dorsally; a hindlimb to trunk ratio of 0.85 or less, a tibia that is less than 80% of femur length; a metatarsal III that is less than 35% of femur length (ratios from Thulborn 1977); a relatively short, broad, and stoutly constructed manus and pes; and a stout postcranial skeleton. Within this assemblage, ankylosaurs and stegosaurs appear to be most closely related, although acceptance of this conclusion must await full preparation and description of *Scelidosaurus*. Stegosaurs and ankylosaurs share two additional osteoderms above the orbit; the absence of an antorbital fossa; a reduced or absent upper temporal fenestra; an inclined quadrate, a short neck and long torso; thick-walled limb bones; a more uniform width of the scapular blade and an enlarged acromial region of the scapulocoracoid; absence of a supra-acetabular buttress; femora with reduced fourth and anterior trochanters; a tibia that is less than 70–75% of femur length; a metatarsus that is only 25% of tibia length (ratios from Thulborn 1977), and very short, broad, and stout manus and pes bearing hooflike unguals. Most of these characters are associated with graviportal habits, and they appeared independently within ceratopsians and ornithopods (s.s.). One could thus argue that these characters could be collapsed into a single character related to large size and quadrupedal habits. Nevertheless, whether few or many, these data are accepted as indicating recency of common ancestry until there is evidence to the contrary.

Diagnoses of taxa 3 and 4 are left to Paul Sereno (1986). At this time I only wish to point out that both might be most closely related within Ornithischia, in that they share asymmetrically enameled tooth crowns, more deeply inset marginal tooth rows, at least five to six sacra, and the absence of a supra-acetabular buttress. Moreover, these taxa are the only ornithischians in which a fully open acetabulum could be considered the ancestral condition. That is to say, although the acetabulum is completely perforate in some stegosaurs, it is only semiperforate in ankylosaurs, *Scelidosaurus*, *Scutellostaurus**, and *Lesothosaurus*. Thus, a semiperforate acetabulum with a supra-acetabular buttress is the ancestral condition for Ornithischia, and because this condition is also ancestral for Sauropodomorpha and Herrerasauridae*, a semiperforate acetabulum with a prominent supra-acetabular buttress also appears to be ancestral for Dinosauria.

The analysis of ornithischian phylogeny is not intended to be definitive. Nevertheless, the following conclusions appear secure.

- 1) Ornithischia is monophyletic.
- 2) *Lesothosaurus* *diagnosticus* appears to be the sister-taxon of all other ornithischians.
- 3) Although relationships among the major groups of ornithischians remain unclear, it is nonetheless evident that any character shared by *Hypsilophodon*-*Heterodontosaurus*, pachycephalosaurs-psittacosaur-*Microceratops*, and *Scutellostaurus** and *Scelidosaurus* that is also present in *Lesothosaurus*, represents the ancestral condition for Ornithischia.

Diagnosis of Sauropodomorpha

Sauropodomorph monophyly is more problematic than that of Ornithischia (e.g., Chang et al. 1965). Nevertheless, using herrerasaurs*, and Pterosauria-*Lagosuchus** as successively more remote outgroups, the following characters are considered diagnostic of Sauropodomorpha, including such taxa as *Thecodontosaurus**, *Efraasia**, *Anchisaurus**, *Ammosaurus*, *Plateosaurus*, *Lufengosaurus*, *Segnosaurus*, *Massospondylus*, *Riojasaurus*, *Fulcanodon*, *Barapasaurus*, and Sauropoda. The characters discussed below are derived primarily from the literature reviewed in Gauthier (1984), and were supplemented by examination of *Plateosaurus* specimens in Tübingen.

*Efraasia** and *Thecodontosaurus**, and to a lesser extent *Anchisaurus**, appear to be the most primitive sauropodomorphs. These taxa correspond to the "narrow-footed prosauropods" of Galton and Cluver (1976). Of course, the "broad-footed prosauropods" of Galton and Cluver (1976) are more closely related to sauropods, thus demonstrating the paraphyly of "Prosauropoda." *Efraasia** and *Thecodontosaurus** are too incompletely preserved to be very informative; nonetheless they share certain apomorphies diagnostic of Sauropodomorpha, first among them being the robust pollex and its enlarged claw noted above (also the hallux). In addition, the most recent common ancestor of *Efraasia**, *Thecodontosaurus**, *Anchisaurus**, and the more completely known sauropodomorphs, possessed lanceolate teeth with coarsely serrated crowns, a comparatively small skull suspended on a long neck composed of at least 10 cervicals, each of which is at least 25%

longer than are most of the trunk vertebrae, and a hindlimb that is subequal to or shorter than the trunk and in which the tibia is invariably shorter than the femur (reversed from ancestral condition in Ornithodira).

The remaining sauropodomorphs, including *Anchisaurus**, are further specialized compared to *Thecodontosaurus** in that they possess an even more robust first metacarpal and digit, wider-based neural spines on the anterior caudals, an arched dorsal margin of the ilium, and a completely open acetabulum.

Compared to *Anchisaurus**, and especially to *Thecodontosaurus**, the remaining sauropodomorphs are larger animals (this taxon will hereinafter be referred to as broad-footed sauropodomorphs). The broad-footed sauropodomorphs also share the following apomorphies: the mandibular condyle is set below the tooth row (also in *Efraasia**, which according to Galton [pers. comm.] actually represents a juvenile example of *Sellosaurus gracilis*); the internasal process of the premaxilla is compressed; the nares are very large owing to the previous character and emargination of the nasals; the teeth in the upper tooth row increase in height anteriorly and are especially long in the premaxilla (segnosaurs?); proximal caudal centra relatively compressed anteroposteriorly and with broad-based neural spines; robust forelimbs with a relatively shorter, broader, and stout manus, and to a lesser extent pes (i.e., broad-footed), with a greatly enlarged pollex; proximal carpals fail to ossify; acetabular fenestra is much larger than the size of the femoral head, and it was presumably filled with cartilage throughout life; and the initial development of a descending flange on the postero-distal end of the tibia (Cooper 1981a).

Although segnosaurs (*Erlhosaurus*, *Segnosaurus*) have been considered related to "theropods" (e.g., Barsbold 1983), or to represent relics of a transition between Ornithischia and "prosauropods" (Paul 1984a, b), segnosaur relationships appear to be with this subgroup of sauropodomorphs. Segnosaurs are remarkably specialized, with retroverted pubes, an edentulous and apparently beaked premaxilla like ornithischians, and very large ascending processes like coelurosaur and tyrannosaur theropods. In the context of all the evidence, however, these characters are here considered to have been acquired separately, and thus they are diagnostic of segnosaurs among sauropodomorphs.

Within the broad-footed sauropodomorphs, *Riojasaurus*, *Vulcanodon*, *Barapasaurus*, and Sauropoda appear to be most closely related. For example, the descriptions of *Vulcanodon* (Raath 1972) and *Barapasaurus* (Jain et al. 1975, 1979) reveal that these taxa share with Sauropoda the following characters that are absent in Sauropodomorpha ancestrally: spatulate teeth; strongly opisthocoealous cervical and anterior trunk vertebrae; cervical centra at least twice the length of midtrunk centra; deep, oval, "pleurocoelous excavations" below transverse processes; at least one more vertebrae added to sacrum (minimum of four sacrals); elongate neural spines confluent with one another in the sacrum; forelimb at least two-thirds of hindlimb length; ilium short anteroposteriorly and strongly arched in profile; brevis shelf reduced or absent; texture of articular surfaces of long bones indicates retention of thick pads of cartilage; distal tarsals fail to ossify; anterior trochanter reduced to a rugosity or absent; fourth trochanter reduced and displaced distally to near middle of femur; femur robust, thick-walled, wider laterally than anteroposteriorly, and with straight shaft; tibia to femur ratio less than 0.63; tibia compressed side to side and cnemial crest reduced; enlarged descending flange on posterior face of distal end of tibia; metatarsal III less than 37% of tibia length; metatarsals subequal in length and arranged in a shallow arch, with a broad, very short and stoutly constructed pes with a hooflike ungual on pedal digit three; fourth and fifth pedal digits without clawlike unguals.

As the following list of synapomorphies attests, sauropod monophyly is a highly corroborated hypothesis.

Relatively short postorbital region of skull that is strongly inclined posteroventrally, thus making the skull appear flexed about the braincase in lateral view; frontals and parietals wider than long; very long nasal process of premaxillae (absent in many diplococids); nasals deeply excavated to form posterior margins of retracted external nares; postorbital reduced to a thin, elongate bar extending nearly to ventral surface of orbit; posterior and postorbital processes of jugal reduced; dorsal process of quadratojugal reduced in that it fails to reach squamosal, but anterior process enlarged and nearly reaching maxilla; lacrimal thin and elongate posterodorsally, forming most of anterodorsal margin of orbit; narrow process of maxilla extends over antorbital fenestra nearly to anterodorsal margin of orbit, lower temporal fenestra inclined anteroventrally to extend well below orbit; palate abbreviate, with broad choana; pterygoid flanges blunt and well anterior to braincase; epipterygoid absent; tooth rows entirely antorbital and anterior teeth procumbent; mandibular fenestra absent; at least two vertebrae added to cervical series (minimum of 12 cervicals); cervical ribs fused to centra in fully adult specimens; vertebrae with highly cancellous to cavernously pleurocoelous centra surrounded by dense lamellar bone; tall neural spines in posterior part of trunk, over sacrum, and in anterior caudal vertebrae; at least one vertebra incorporated into sacrum (=five or six sacrals); relatively broad sacrum with enlarged sacral transverse processes that are level with top of deeply arched ilium; massive proximal

caudals; greatly enlarged acromial region of scapulothoracoid, resulting in pronounced demarcation between scapular blade and base of scapula; metacarpals stout and arranged in a hemispherical colonnade below the forearm (Note: The fourth and fifth metacarpals and digits are set on the palmar surface of the hand in Saurischia ancestrally, thus initiating the cupped metapodial unit that is taken to extreme in sauropods; compare *Massospondylus* in Cooper 1981a, fig. 37, with *Brachiosaurus* in Janensch 1922); manus elephantine, only digit one retains the ancestral phalangeal formula and a large, clawlike ungual, with the others being reduced to single phalanges supporting hooflike unguals (phalangeal formula 2-1-1-1-1, as opposed to 2-3-4-3-2, the ancestral condition for Dinosauria); pubis ventrally directed and more massively developed than ischium; puboischiadic junction robust; forelimbs at least three-fourths of hindlimb length (may be less in diplococids); limbs massive, vertically disposed, long bones nearly solid (sauropods appear to be one of the few dinosaur groups with a truly vertical, parasagittal, limb posture); tibia with narrow descending flange; pes stout, very short and broad, phalanges of outer digits short, with digit three losing three phalanges (phalangeal formula 2-3-4-2-1 as opposed to 2-3-4-5-1); gastralia absent.

Sauropoda may be divided into two principal groups, here referred to informally as camarasaur and titanosaurs. Camarasaur share a strongly arched internarial bar of the premaxilla, a snout that is sharply demarcated from the rest of the skull, a relatively elongate ischium that extends well posterior to the level of the ilium while twisting to become more horizontally disposed distally, and a relatively very deep puboischiadic contact.

Euhelopus (Wiman 1929) may be the sister-taxon of the titanosaurs, both taxa share a quadrate that slants up and back from the mandibular condyle, neural spines that are slightly to deeply bifurcate (convergent in *Camarasaurus*), and the incorporation of three or more trunk vertebrae into the cervical series.

For the sake of discussion, titanosaurs will be divided into two informal taxa: the antarctosaurs for such taxa as *Antarctosaurus*, *Alamosaurus*, *Laplatasaurus*, and *Titanosaurus*, that share a caudal series in which the first centrum is biconvex and subsequent caudals are procoelous; and diplococids for *Apatosaurus*, *Barosaurus*, *Cetiosaurus*, *Dicraeosaurus*, *Diplodocus*, *Mamenchisaurus*, and *Nemegtosaurus*, that share diagnostically modified haemal arches with fore-and-aft projections, midsacral neural spines that are deeply cleft, and ischia that are expanded distally.

The phylogenetic analysis of Berman and McIntosh (1978) established titanosaur monophyly in that antarctosaurs and diplococids possess the following synapomorphies: snout long, broad, and depressed; body of premaxilla and supraantorbital process of maxilla extend dorsally to level of orbit, internasal processes of premaxilla and nasals reduced or absent, and nasals very short, thus external nares are confluent on midline and situated high on skull; lacrimal very reduced; dorsal process of quadratojugal very reduced and anterior process broadly in contact with maxilla at anteroventral margin of orbit, very long basiptyergoid processes of basisphenoid; elongate, pencil-like teeth confined to anteriormost part of jaws; neural spines in posterior cervical and anterior trunk vertebrae deeply cleft and V-shaped in anterior view (convergent in *Camarasaurus*); sacral neural spines very tall; very long tail forming distal whip-lash consisting of a long series of cylindrical caudals; relatively short forelimbs that are approximately two-thirds of hindlimb length, and metatarsal IV exceeds the length of metatarsal III.

The preceding discussion of sauropodomorph phylogeny establishes the following points.

- 1) Broad-footed sauropodomorphs are monophyletic.
- 2) Evidence currently available indicates that *Anchisaurus** could be the sister-group of the broad-footed group, and that the group composed of both these taxa would form an unresolved trichotomy with *Efraasia** and *Thecodontosaurus**. Thus, Sauropodomorpha appears to be monophyletic.
- 3) Sauropoda is monophyletic.
- 4) Such as they are known, *Riojasaurus*, and especially *Vulcanodon* and *Barapasaurus*, appear more closely related to Sauropoda than are other broad-footed sauropodomorphs.
- 5) Thus, any character that is present in broad-footed sauropodomorphs, that is also present in *Anchisaurus**, *Efraasia**, and *Thecodontosaurus**, is considered to have been present in Sauropodomorpha ancestrally.

Diagnosis of Dinosauria

Given that (1) Ornithischia, Sauropodomorpha, and Theropoda are each monophyletic, and (2) accepting that any character shared by *Lesothosaurus* and higher ornithischians, *Efraasia**-*Thecodontosaurus** and broad-footed sauropodomorphs, and *Procompsognathus**-*Litlensternus** and ceratosaurs represents the ancestral conditions for Ornithischia, Sauropodomorpha, and Theropoda respectively; and (3) accepting that herrerasaur* and *Scleromochlus**-*Lagosuchus** rep-

resent successively more remote outgroups, Dinosauria can be diagnosed by the following synapomorphies.

- 41) Vomers elongate, reaching posteriorly at least to level of antorbital fenestra (also in actosauroids?).
- 42) Scapula at least three times longer than width at base, and entire scapulocoracoid further inclined posterodorsally (also in pterosaurs aside from *Scleromochlus**).
- 43) Increased asymmetry of hand, with small outer two digits having fewer phalanges (ancestral phalangeal formula for: Archosauria = 2-3-4-5-3, Ornithodira = 2-3-4-4-?; and Dinosauria = 2-3-4-3-2).
- 44) Semiperforate acetabulum and prominent supra-acetabular buttress (T. Rowe, pers. comm., notes that the inner wall of the acetabulum is thin in semi-erect archosaurs. Thus, it is not surprising to see the independent appearance of this character in fully erect ornithosuchids, and in some fully erect crocodylomorphs and rauisuchians. The acetabulum becomes fully perforate at least three times within Dinosauria, once in ornithischians, once in sauropodomorphs, and once in theropods. The degree to which the acetabulum is open also varies with absolute size: with the exception of ankylosaurs, the larger the dinosaur the more open the acetabulum).
- 45) Birdlike femur and antitrochanter: medial rotation about long axis of element of that portion of femur proximal to fourth trochanter (=returned head of femur); proportional elongation of femoral shaft distal to anterior trochanter; dorsal arc of entire femoral shaft; fore-and-aft compression of femoral head in proximal view; and femoral head more distinctly set off from shaft of femur. Also, modifications of the distal end of the femur noted above are more prominent in dinosaurs. These modifications are also accompanied by reorientation of the antitrochanter, which faces mostly dorsally in archosaurs ancestrally, but faces mainly ventrally in dinosaurs (T. Rowe, pers. comm.). The proximal end of the femur in pterosaurs like *Dimorphodon* (Padian 1983) is in some ways more birdlike than is that of *Lagosuchus** (Gauthier 1984).
- 46) Anterior trochanter enlarged
- 47) Dinosaur tibia: cnemial crest prominent and with weakly crescentic profile in dorsal view (size and shape of cnemial crest varies with size of animal and style of locomotion) Distal end of tibia broadened mediolaterally, thus element appears twisted nearly 90° with respect to proximal end. And with prominent fossa on anterolateral face of distal end of tibia for reception of ascending process.
- 48) Birdlike ankle: proximal tarsals fit caplike onto tibia and fibula; crurotarsal joint and calcaneal tubercle absent, ascending process of astragalus present (i.e., intermedium moves dorsally)—thus, motion within the ankle confined mainly to a simple, hingelike joint between the rollerlike proximal and the compressed, distal tarsals. (Like the femur, the ankle joint in pterosaurs appears to be more dinosaurlike than that of *Lagosuchus**, these apomorphic similarities suggest a monophyletic pterosaur-dinosaur group [Ornithotarsus, n. tax.], as argued in Gauthier 1984).
- 49) Pedal digit five shorter than metatarsal I, the foot is tridactyl in the typical dinosaurian condition.

One of the key elements in the dinosaur controversy is the problem presented by Sauropodomorpha. Charig et al. (1965) and Chang (1976a, b) argued that the erect, quadrupedal pose of Sauropoda was an ancestral condition for dinosaurs, and that theropods and ornithischians acquired their bipedal habits independently (Chang accepts that the quadrupedal pose of some ornithischians is secondary). As Cooper (1981a) pointed out, some taxa are easily relegated to particular locomotor categories. For example, sauropods are probably obligate quadrupeds, and theropods obligate bipeds, but a number of taxa are not so readily placed in either category (e.g., the sauropodomorph *Massospondylus*). Whether we view this problem from the perspective of observed morphology or from that of inferred functions, we are still left with Chang's problem: are sauropodomorphs ancestral or apomorphic in these regards? That is to say, the ancestral dinosaur could have been a cursorial biped (or considering the role of the tail, a tripod), and sauropodomorphs could subsequently have reacquired quadrupedal habits. Alternatively, the common ancestor of dinosaurs could have been a pachypodal quadruped, with ornithischians and theropods subsequently becoming bipedal cursors independently of one another as Chang suggested. Either hypothesis requires the same number of evolutionary events, and if one is unwilling to make assumptions about the probability of reversals versus convergences, these data alone do not afford a basis for choice. This question can, however, be evaluated by reference to additional outgroups (Maddison et al. 1984). Given that taxa such as *Staurikosaurus**, *Scleromochlus**, and *Lagosuchus** represent outgroups, it appears likely that the ancestral dinosaur was a small, erect-postured, cursorial biped.

The same kind of analysis can be used to address the question of the ancestral dinosaur morphology. Using the dinosaur foot as an example, it is interesting to

note that the foot is gracile, elongate, and functionally tridactyl in *Lagosuchus**, herrerasaurs*, theropods, and in ornithischians ancestrally. Although the fourth toe (and finger) and fifth toe are unusually long in pterosaurs, the proportions and lengths of the middle three toes are like those of birds and unlike those of either pseudosuchians or ornithosuchians ancestrally (Padian 1983; Gauthier 1984). Consequently, the simplest explanation for the shorter, stouter, and tetradactylous foot of Sauropodomorpha is that these conditions represent apomorphic reversals.

In fact, sauropodomorphs are unique among archosaurs in the size and shape of the first finger and toe. The hand in particular is strikingly modified even in early sauropodomorphs. Galton (1971) and Baird (1980) discussed the relations between the articular surfaces of the metacarpal and first phalanx in manal digit I (the pollex) in early sauropodomorphs ("prosauropods"). They noted that adjacent articulations within the pollex were modified so that upon maximum extension the enormous ungual phalanx was directed medially and thus was nearly horizontally oriented. Upon flexion, however, the claw was brought into the same line of action taken by the other digits.

Baird (1980) described a fossil trackway of an *Ammosaurus*-like sauropodomorph walking quadrupedally. In a most elegant test of a functional hypothesis based on an extinct organism, Baird used the morphology of the trackway to show that the manus functioned as predicted. Indeed, the manus was held in an essentially digitigrade pose, with the digits fully extended so that the enlarged claw was laid flat upon its side against the substrate. Perhaps the unusual modifications of the pollex reflect divergent functional demands placed on the hand in the larger sauropodomorphs (five meters and above). Stout forelimbs and powerful, grasping hands may have supported the role of the head and neck as cropping organs while in a bipedal (or tripod) feeding pose (Bakker 1971), by providing secure purchase on the trunks of trees. This and other possible roles of the grasping hand and enlarged first claw would have to be balanced against the role of the hand as a weight-bearing structure during quadrupedal locomotion. Perhaps these factors combined to yield the unusually modified pollex of sauropodomorphs.

With regard to the problem of the history of the tridactyl foot, it is most interesting to note that in sauropodomorphs the modifications of the first finger (pollex) apply as well, albeit less dramatically, to the first toe (hallux). The modifications shared by the pollex and hallux cannot be accounted for by invoking functional similarity. Rather, as Davis (1964) argued in the case of the panda's thumb, simultaneous modification of the hallux and pollex suggests that it was simpler to alter the developmental program of both limbs than to change that of the hand alone. Of course, whatever accessory roles the hand may have played early in sauropodomorph history, these functions were overwhelmed by the demands of weight-bearing in Sauropoda. Thus, the tetradactylous impressions of hind feet attributed to some sauropodomorphs do not represent an ancestral condition; on the contrary the modified hallux is as diagnostic of sauropodomorphs as is the uniquely modified pollex.

In conclusion, the ancestral dinosaur was essentially birdlike. It had a mobile, S-shaped neck, a short trunk, and long hindlimbs with modified joints that enabled a narrow-tracked gait. Its short forelimbs, together with other modifications in the hands and girdles, indicate that the forelimbs were suited less to performing roles in support and locomotion than they were to grasping and manipulating food. As argued by Bakker and Galton (1974), a variety of structural modifications indicate that the primary responsibility for support and locomotion had shifted to the hindlimbs and girdles in the ancestral dinosaur. That the ancestral dinosaur was a bipedal cursor is especially evident in the morphology of its tail, in the elongate and narrow distal portions of its hindlimbs, and in its functionally tridactyl and digitigrade pes. By the standard of typical Mesozoic dinosaurs, the ancestral dinosaur was quite small. Indeed, using other ornithodirans as outgroups, one might infer that it was certainly under two meters and perhaps under one meter in total length. Although small, the ancestral dinosaur would have had a broad visual horizon because of the birdlike pose of its neck and hindlimbs. Considering these modifications as a whole suggests that the ancestral dinosaur was small, cursorial, erect and normally bipedal. Its divergently specialized fore- and hindlimbs indicate that the ancestral dinosaur was capable of more than the mere facultative bipedality it inherited from its saurian ancestors. On the other hand, trackways indicate that forelimbs could still play a role in support and locomotion at low speed, so the ancestral dinosaur was not so locked into this mode of progression as are its obligately bipedal living relatives.

The main points of the foregoing discussion of archosaur phylogeny may be summarized as follows (and see Fig. 7).

- 1) Archosauria is composed of the sister-groups Pseudosuchia and Ornithosuchia
- 2) Parasuchia is the sister-group of all other pseudosuchians, and *Euparkeria** appears to be the sister-group of all other ornithosuchians.
- 3) Within Ornithosuchia, Ornithosuchidae is the sister-group of Ornithodira (n. tax.).

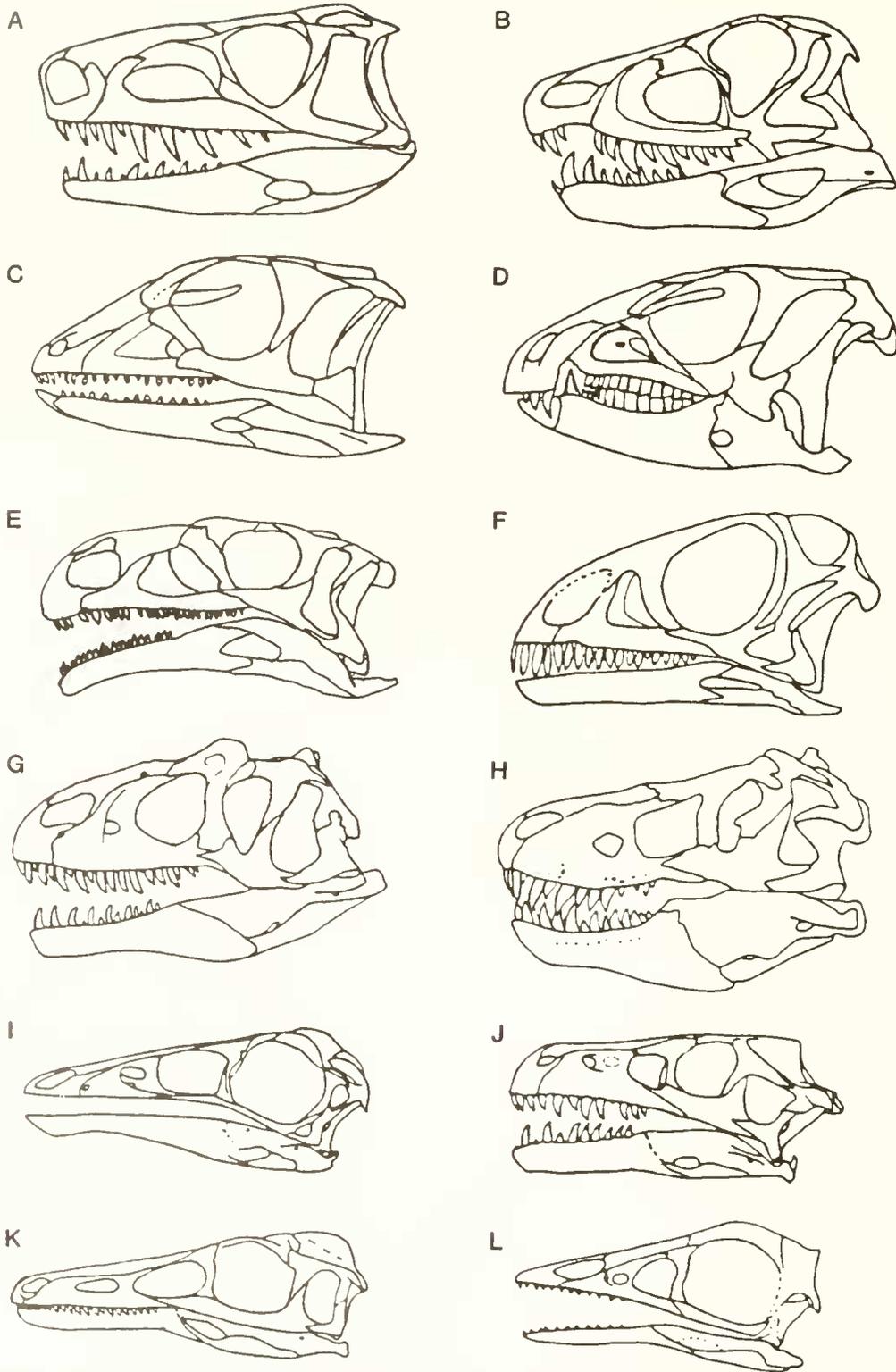


FIGURE 1. Skulls in lateral view: A) *Euparkeria capensis**, B) *Ornithosuchus longidens* (Ornithosuchidae), C) *Lesothosaurus diagnosticus* (Ornithischia), D) *Heterodontosaurus tucki* (Ornithischia), E) *Plateosaurus engelhardti* (Sauropodomorpha), F) *Massospondylus carinatus* (Sauropodomorpha), G) *Allosaurus fragilis* (Carnosauria), H) *Tyrannosaurus rex* (Carnosauria), I) *Dromiceiomimus breviterius* (Ornithomimidae), J) *Dromaeosaurus albertensis* (Dromaeosauridae), K) *Saurornithoides mongoliensis* (Troodontidae), L) *Archaeopteryx lithographica** (Avialae). Drawing A after Ewer (1965); B after Walker (1964); C after Galton (1978); D after Chang (1979), E after Galton (1984), F after Cooper (1981a), G after Madsen (1976); H after Romer (1956); I after Russell (1972); J after Colbert and Russell (1969); K after Russell (1969); L after Ostrom (1976a).

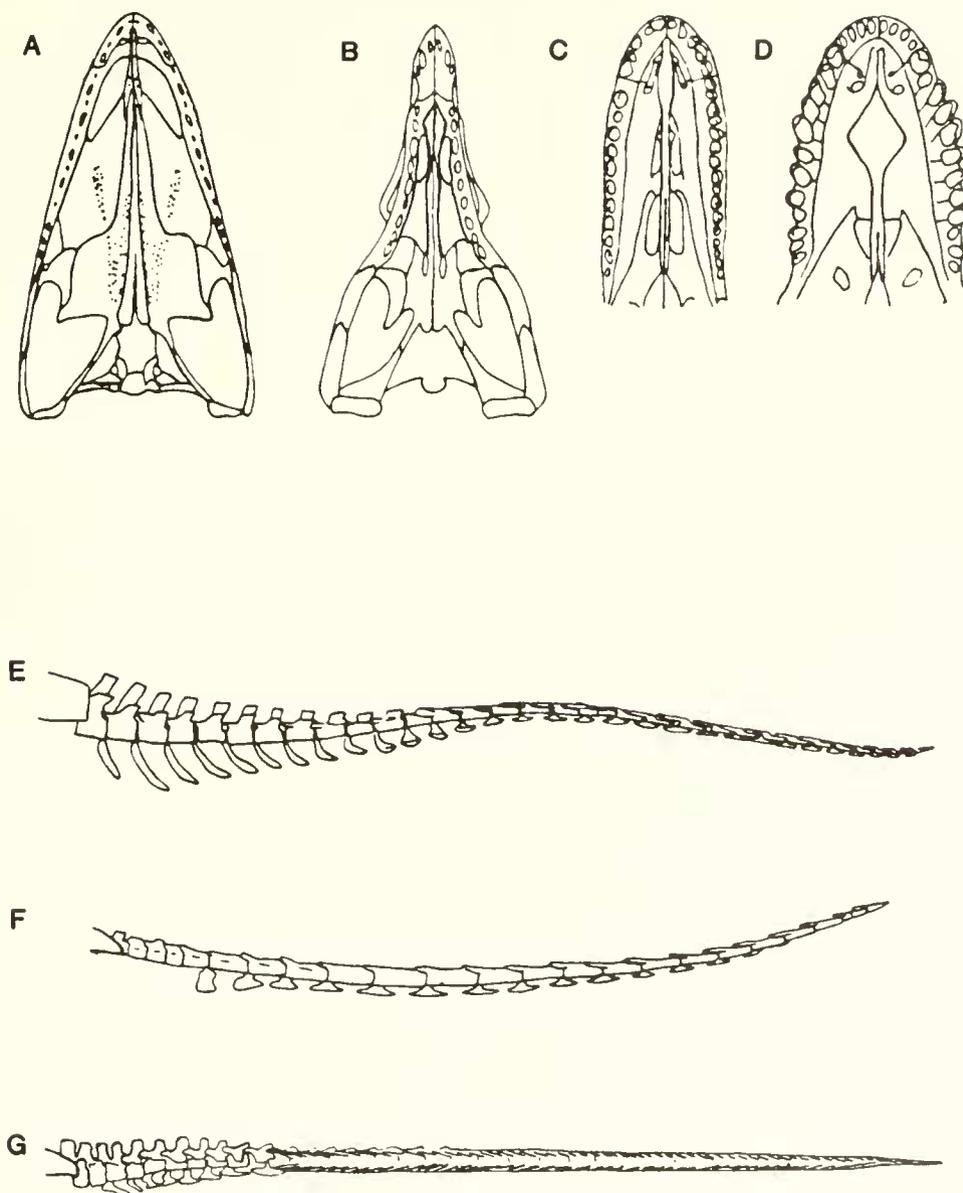


FIGURE 2. Skulls in ventral view: A) *Euparkeria capensis**; B) *Ornithosuchus longidens* (Ornithosuchidae); C) *Allosaurus fragilis* (Carnosauria); D) *Tyrannosaurus rex* (Carnosauria). Caudal series in lateral view: E) *Dromiceiomimus breviterius* (Ornithomimidae); F) *Archaeopteryx lithographica** (Avialae); G) *Deinonychus antirrhopus* (Dromaeosauridae). Drawing A after Krebs (1976); B after Walker (1964); C after Madsen (1976); D after Romer (1956); E after Russell (1972); F after Ostrom (1976a); G after Ostrom (1976b).

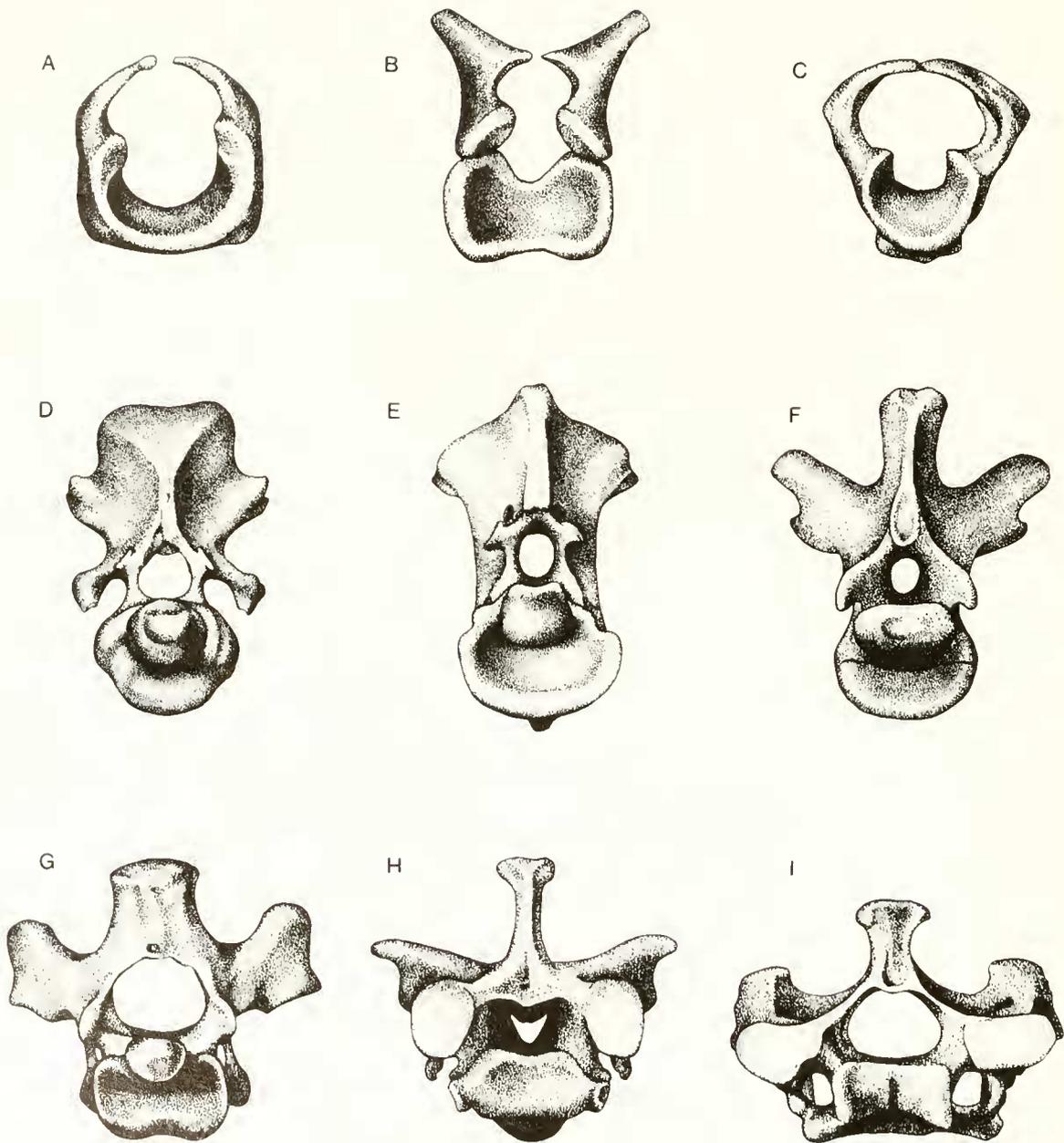


FIGURE 3. Anterior views of atlas (A-C), axis (D-G), cervicals 3-4 (H, I): A) *Stegosaurus stenops* (Ornithischia); B, E) *Ceratosaurus nasicornis* (Ceratosauria); C, G, I) *Apteryx australis* (Aves), D) *Camarasaurus grandis* (Sauropodomorpha); F, H) *Deinonychus antirrhopus* (Dromaeosauridae). Drawing A, D after Ostrom and McIntosh (1966), B, E after Gilmore (1920), F, H after Ostrom (1969b).

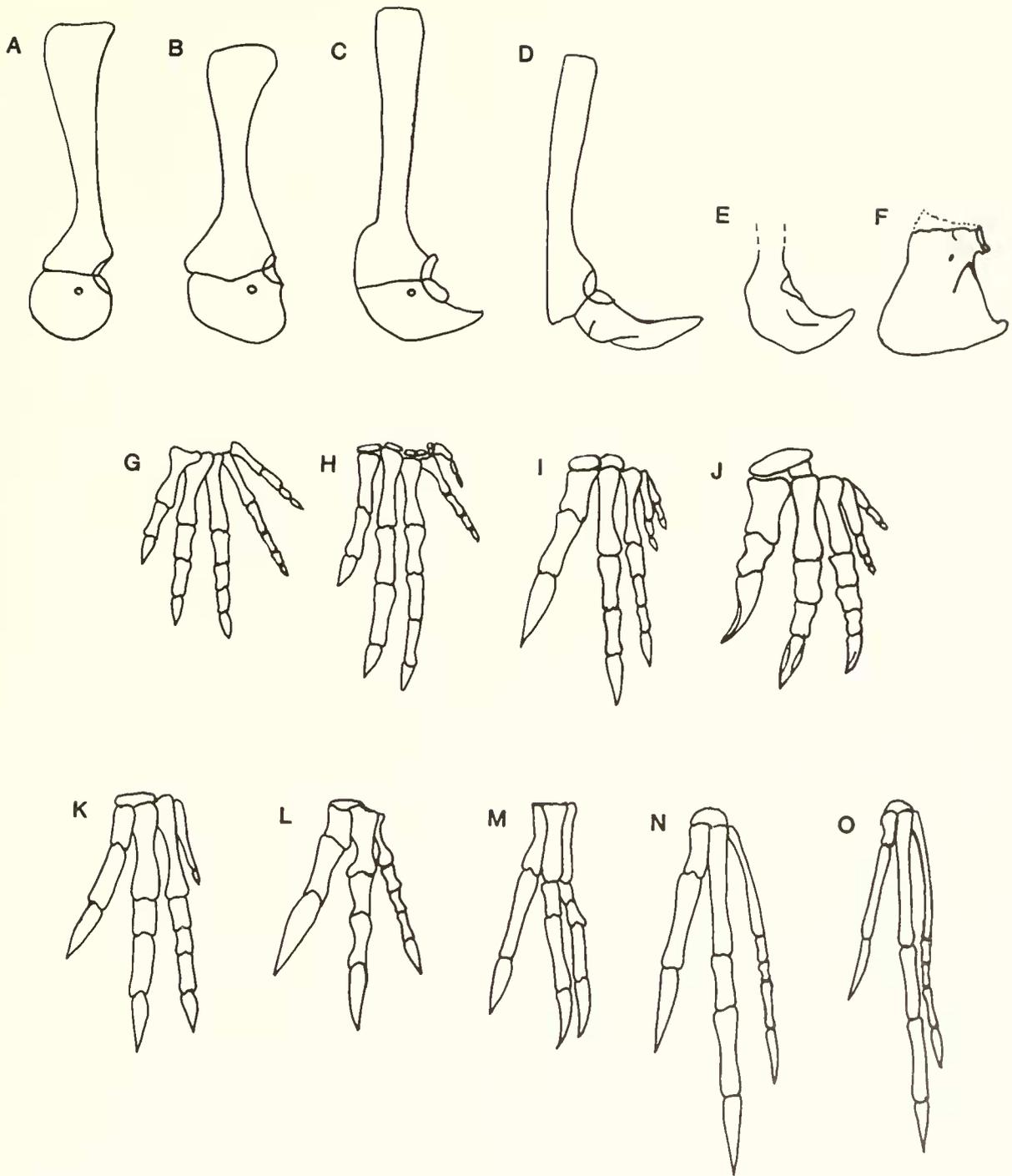


FIGURE 4. Scapulocoracoids in lateral view: A) *Heterodontosaurus tucki* (Ornithischia); B) *Massospondylus carinatus* (Sauropodomorpha); C) *Gallimimus bullatus* (Ornithomimidae); D) *Archaeopteryx lithographica** (Avialae); E, F) *Deinonychus antirrhopus* (Dromaeosauridae). Left manus in dorsal view: G) *Crocodylus* sp. (Crocodylomorpha); H) *Heterodontosaurus tucki* (Ornithischia); I) based on *Thecodontosaurus antiquus** and *Efraasia diagnostica** (Sauropodomorpha); J) *Massospondylus carinatus* (Sauropodomorpha); K) *Syntarsus rhodesiensis* (Ceratosauria); L) *Allosaurus fragilis* (Carnosauria); M) *Struthiomimus altus* (Ornithomimidae); N) *Deinonychus antirrhopus* (Dromaeosauridae); O) *Archaeopteryx lithographica** (Avialae). Drawing A, H after Santa Luca (1980); B, J after Cooper (1981a); C after Osmolska et al. (1972); D, E after Ostrom (1976a); F after Ostrom (1974b); G after Romer (1956); I partly after Bakker and Galton (1974) and Huene (1932); K after Raath (1969); L after Madsen (1976); M after Osborn (1917); N after Ostrom (1976a); O partly after Ostrom (1976a).

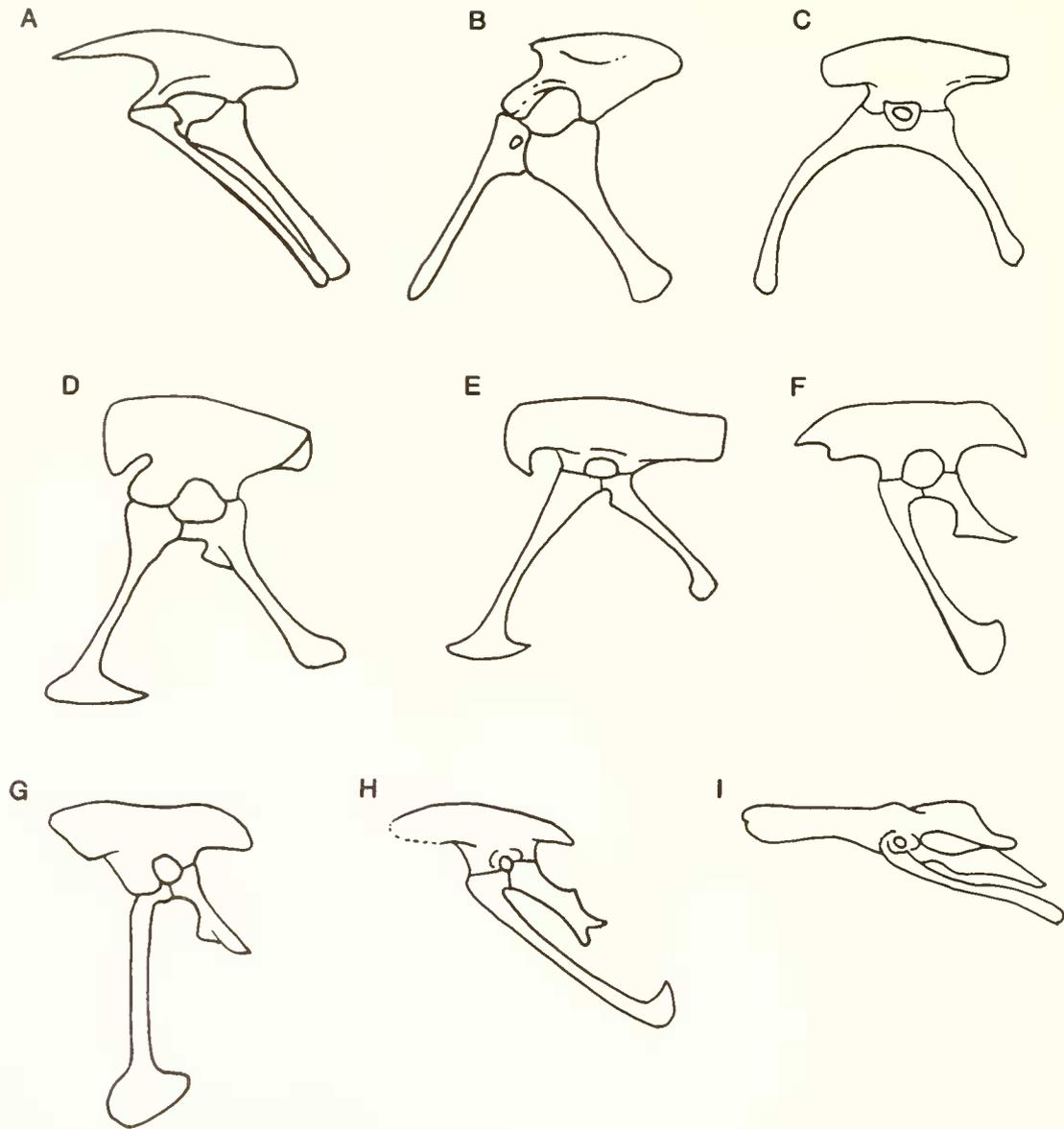
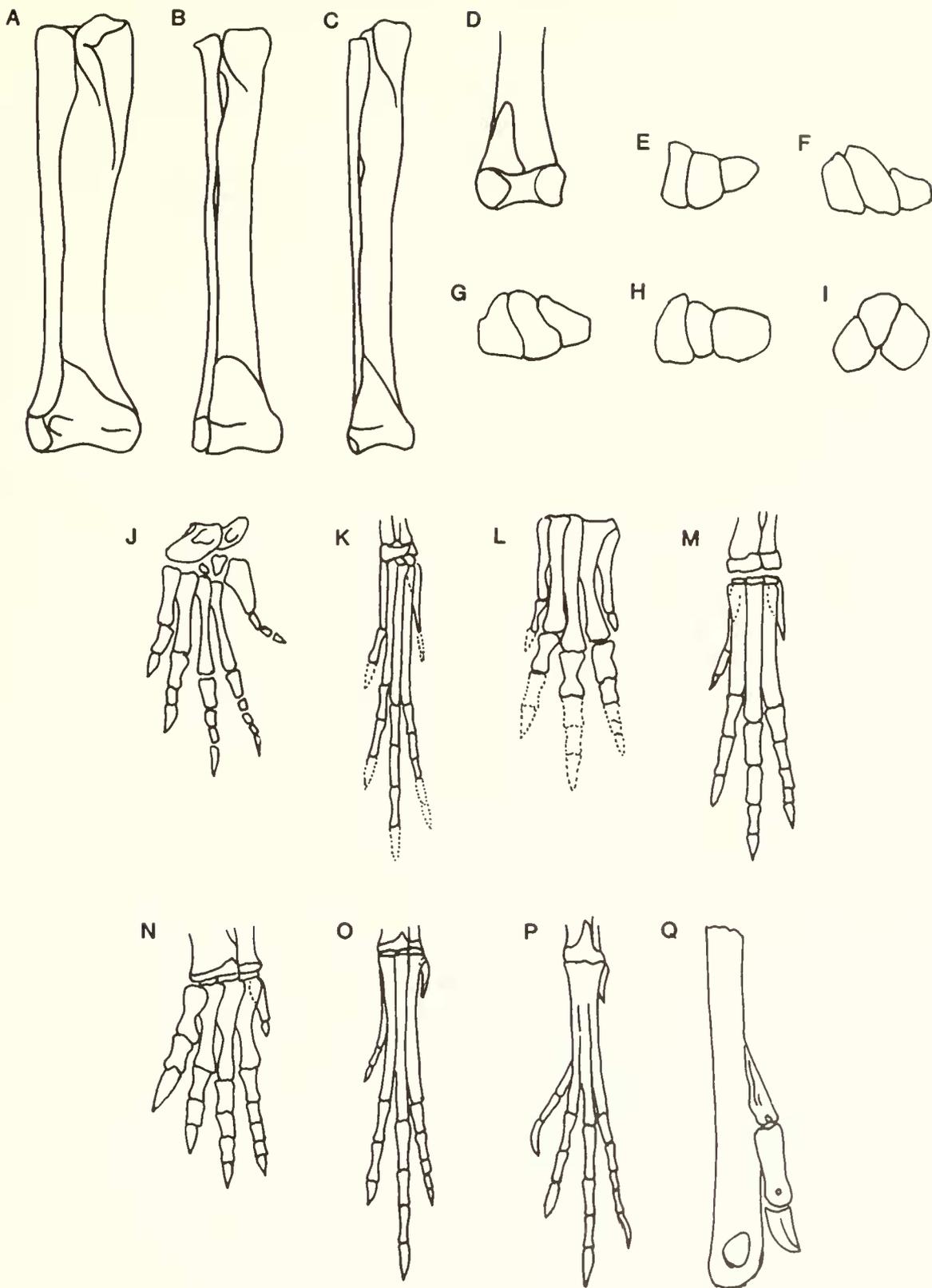


FIGURE 5. Pelvic girdle in lateral view: A) *Scelidosaurus* (Ornithischia), B) *Massospondylus carinatus* (Sauropodomorpha), C) *Coelophysis bauri* (Ceratosauria), D) *Allosaurus fragilis* (Carnosauria), E) *Gallimimus bullatus* (Ornithomimidae), F) *Adasaurus mongoliensis* (Dromaeosauridae), G) *Deinonychus antirrhopus* (Dromaeosauridae), H) *Archaeopteryx lithographica** (Avialae), I) *Apatornis celer* (Ornithurae). Drawing A after Charig (1976b), B after Cooper (1981a), C after Raath (1969), D after Madsen (1976), E after Osmolska et al. (1972), F after Barsbold (1983), G after Ostrom (1976b), H after Ostrom (1976a), I after Marsh (1880).

FIGURE 6. Tibia, fibula, and proximal tarsals in anterior view: A) *Allosaurus fragilis* (Carnosauria), B) *Deinonychus antirrhopus* (Dromaeosauridae), C) *Gallimimus bullatus* (Ornithomimidae). Distal end of tibiotarsus in anterior view: D) *Baptornis advenus* (Ornithurae). Metatarsals II, III, and IV in proximal view: E) *Hypsilophodon foxi** (Ornithischia), F) *Dilophosaurus wetherilli* (Ceratosauria), G) *Allosaurus fragilis* (Carnosauria), H) *Deinonychus antirrhopus* (Dromaeosauridae), I) *Apteryx australis* (Aves). Left pes in dorsal view: J) *Euparkeria capensis**, K) *Lagosuchus talampayensis**, L) *Herrerasaurus ischigualastensis** (Herrerasauridae*), M) *Lesothosaurus diagnosticus* (Ornithischia), N) *Anchisaurus polyzelus** (Sauropodomorpha), O) based on *Procompsognathus triassicus** (Theropoda incertae sedis), and *Segisaurus halli** and *Dilophosaurus wetherilli* (Ceratosauria), P) *Archaeopteryx lithographica** (Avialae). Medial view of articulation between digit I and metatarsal II: Q) *Compsognathus longipes* (Coelurosauria). Drawing A, G after Madsen (1976), B after Ostrom (1976b), C after Osmolska et al. (1972), D after Martin et al. (1980), E after Galton (1974), F after Welles (1984), G after Gilmore (1920), H after Ostrom (1969b), J after Cruickshank (1979), K after Bonaparte (1975a), L after Reig (1963), M after Bakker and Galton (1974), N after Marsh (1896), P after Ostrom (1976a), Q after Tarsitano and Hecht (1980).



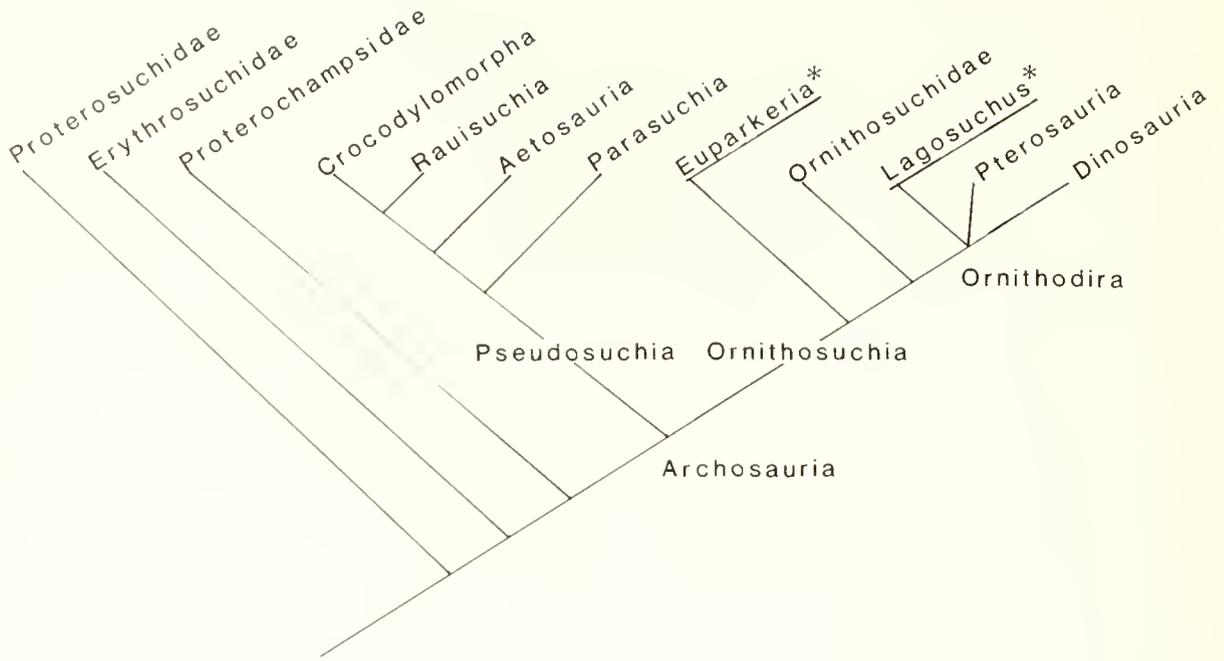


FIGURE 7. Cladogram depicting phylogenetic relationships among Archosauria.

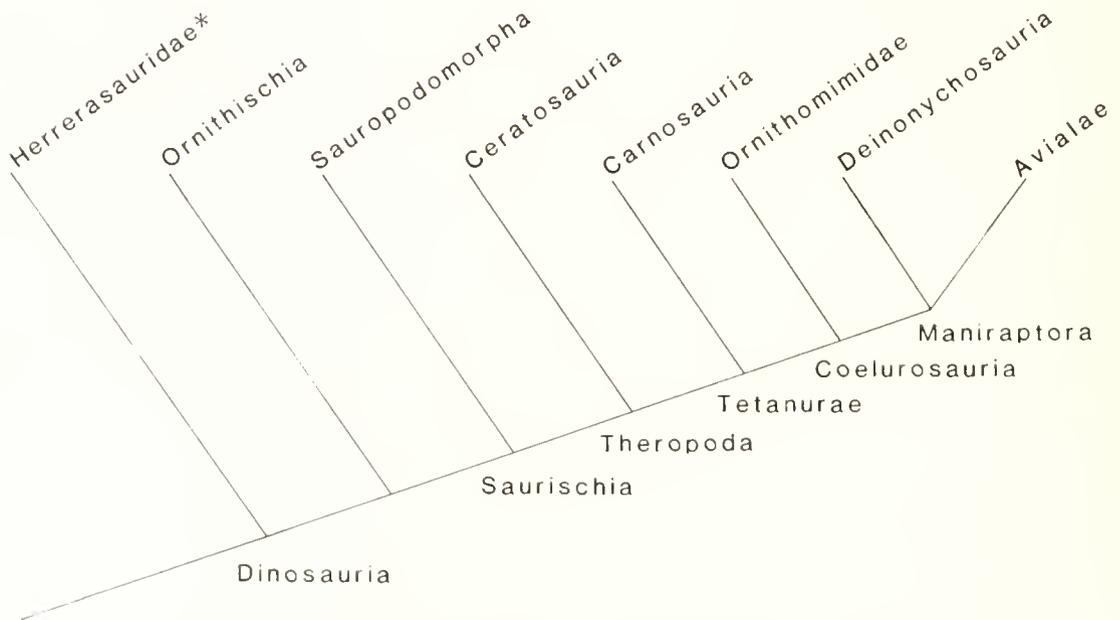


FIGURE 8. Cladogram depicting phylogenetic relationships among comparatively well known theropods and other dinosaurs.

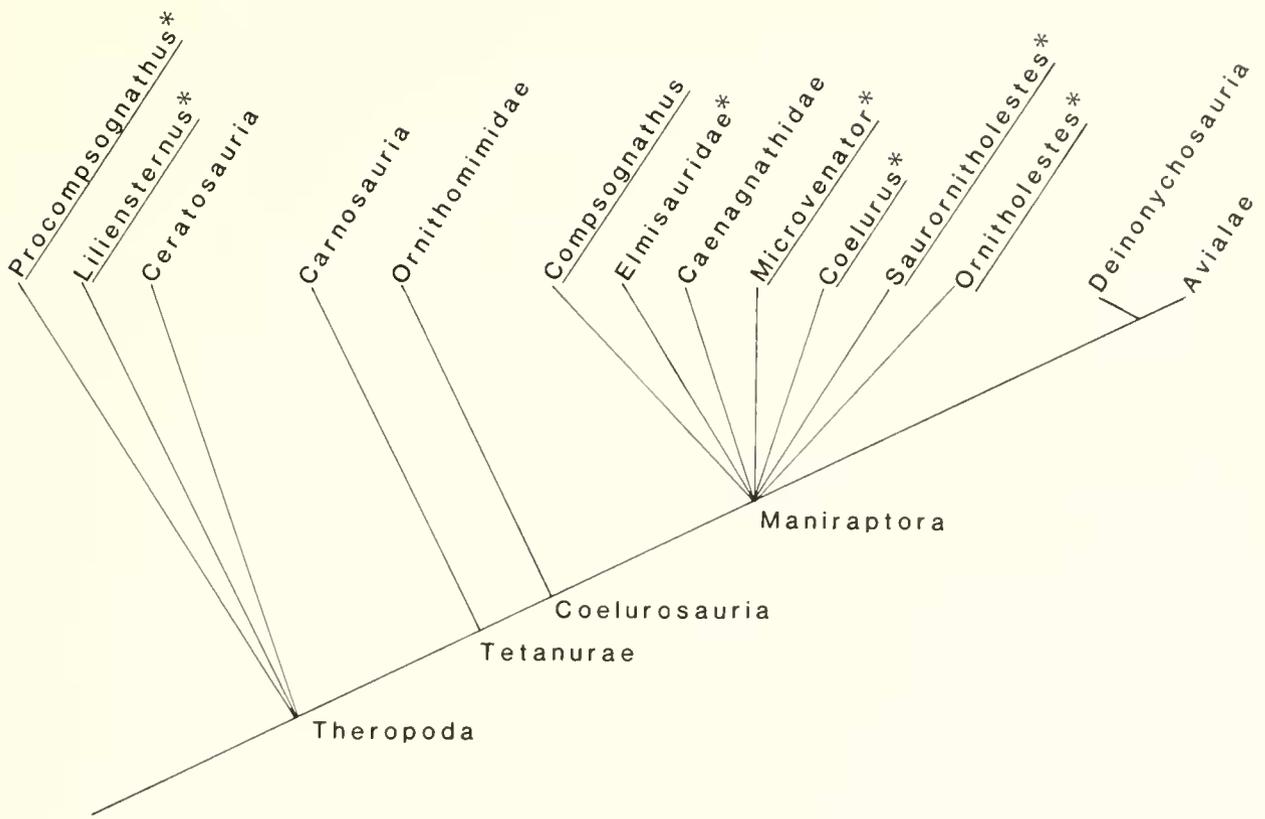


FIGURE 9. Cladogram depicting phylogenetic relationships among all theropods considered in this analysis.