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Origin and Interrelationships of Dinosaurs

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The Dinosauria form a well-defined group within the Archosauria and, with birds included within Dinosauria (as they must be on cladistic grounds), the group is clearly one of great significance among terrestrial vertebrates. Here, I shall review current evidence on the relationships of the Dinosauria as a whole within the Archosauria and then attempt to extract a pattern of relationships of the major taxa within the Dinosauria. The advent of cladistic analyses of archosaurs in the past ten years has revolutionized our views of their relationships, and attention will be focused on such studies.

CLADISTIC ANALYSES OF DINOSAURIA

Until recently, dinosaurian systematists were not always clear in distinguishing derived from nonderived characters, and this led to a great deal of confusion in trying to establish phylogenetic schemes that could be compared directly with one another. The work in the 1980s has established a large number of conclusions that were either suspected by only a few experts or were directly denied. Below are a few of the major conclusions and an indication of how attitudes have changed in the past few years by reference to some standard publications that represent generally held views. This is not meant as a direct criticism of the quoted authors, since they represent the views of most experts of their day.

1. The Archosauria is monophyletic. This view has been held generally for a long time, although the Archosauria have been regarded as hard to define anatomically (e.g., Romer 1956, 1966).

2. The Archosauria splits into two main evolutionary lines, one leading ultimately to crocodilians and the other to birds. This split was hinted at by Bonaparte (1975a), Krebs (1976), Cruickshank

(1979), and Chatterjee (1982), but the basal archosaurs were still generally left in a broad grouping, termed the Pseudosuchia, which included unstated ancestors of crocodilians, pterosaurs, dinosaurs, and birds.

3. The dinosaurs are closely related to ornithosuchids, *Lagosuchus*, and Pterosauria. These relationships along the bird-dinosaur line of archosaurs were not suspected by earlier authors (e.g., Romer 1956, 1966; Bonaparte 1975*a*, 1982*b*; Krebs 1976; Cruickshank 1979; Chatterjee 1982) until the work of Bakker and Galton (1974) and Gauthier (1984, 1986; Gauthier and Padian 1985).

4. The Dinosauria is monophyletic. Formerly, the origins of dinosaurs were usually seen as polyphyletic with as few as three or as many as six ancestors (Romer 1966; Reig 1970; Charig 1976; Krebs 1976; Cruickshank 1979; Thulborn 1980; Chatterjee 1982). Bakker and Galton (1974) and Bonaparte (1976) argued for dinosaurian monophyly before such views became generally accepted.

5. The Dinosauria falls into three main monophyletic groups: Theropoda, Sauropodomorpha, and Ornithischia. This view has been generally held for some time (Charig 1976, p. 87), although Cruickshank (1979) split up the Sauropodomorpha, and he and Chatterjee (1982) split up the Theropoda.

6. The Theropoda includes the ancestors of birds, which were small theropods similar to dromaeosaurids or troodontids. This view, dating from the nineteenth century, was generally denied (e.g., Romer 1956, 1966; Walker 1972; Tarsitano and Hecht 1980; Gardiner 1982). John Ostrom's work in the 1970s (e.g., 1976*b*), in which he detailed the anatomical similarities between theropods and birds, formed the basis for the present cladistic analyses, but such views were initially slow to gain acceptance and are still controversial (see papers in Hecht et al. 1985).

7. Within Sauropodomorpha, the Prosauropoda is a paraphyletic grade group that divides into outgroups of the Sauropoda. This view was hinted at by Colbert (1964*a*), Charig et al. (1965), and others but denied by Cruickshank (1979), although the precise relationships of sauropodomorph subgroups have not yet been worked out.

8. Within Ornithischia, there are two major groups, consisting of Ornithopoda (plus Ceratopsia plus Pachycephalosauria), and Thyreophora (principally Stegosauria plus Ankylosauria). This major split has been denied by some authors, (e.g., Thulborn 1971*b*), suspected by others, and ignored by most (e.g., Romer 1966) in the absence of strong evidence either way.

These major conclusions, and many others, are detailed below and in subsequent chapters of this volume.

THE ARCHOSAURIA

Among living vertebrates, birds and crocodilians are linked as sister groups within the Archosauria by most authors. Although seemingly very different kinds of animals, these two groups share numerous derived characters of the skull, postcranial skeleton, and soft parts (reviewed by Gauthier 1986; Benton and Clark 1988) that are absent in other living vertebrates. It should be noted, however, that Gardiner (1982) and Løvtrup (1985) have denied the existence of the Archosauria by pairing Aves with Mammalia and then those two with Crocodylia. Their postulated synapomorphies have been rejected by several authors (Benton 1985*b*; Kemp 1988; Gauthier, Kluge, and Rowe 1988*a*, *b*), and they have not gained general acceptance.

Molecular data on tetrapod phylogeny are equivocal regarding the relationships of birds and crocodilians. Some analyses do pair these two groups (e.g., Goodman et al. 1982; Stapel et al. 1984), but many tend to link birds and mammals more closely (e.g., Maeda and Fitch 1981; Bishop and Friday 1988). However, other protein sequence analyses give every other imaginable pairing of tetrapod groups, and their significance is debatable (Benton 1985*b*; Bishop and Friday 1988). The hard-part autapomorphies of Archosauria include:

1. possession of an antorbital fenestra

2. reduced postfrontal

3. fused or absent postparietals

4. laterosphenoid ossification in the braincase

5. laterally compressed serrated teeth

6. loss of trunk intercentra

7. ectepicondylar foramen absent on humerus

8. fourth trochanter on the femur

Archosaurs as Diapsids

The archosaurs, although formerly regarded as an independent reptilian subclass by Romer (1966), are now placed by nearly all biologists and paleontologists in the Diapsida (which also includes *Sphenodon*, lizards, snakes, and various extinct forms). The archosaurs form part of the Archosauromorpha, a branch of the diapsid reptiles, which includes *Trilophosaurus*, the Rhynchosauria, and the Prolacertiformes as successive outgroups to the Archosauria (Gow 1975; Brinkman 1981; Benton 1983*b*, 1984*a*, 1985*b*; Evans 1984, 1988; Gauthier 1984).

A few other recent theories of archosaur origins have suggested rather different, nondiapsid origins for the Archosauria, but these theories were based on noncladistic analyses of relationships. Romer (1966) suggested that they arose directly from captorhinomorphs, while Reig (1970) derived them from varanopsid pelycosaurs. Other authors (e.g., Hughes 1963; Cruickshank 1972; Gow 1975; Carroll 1976) suggested that the ancestor of the archosaurs was a Permian diapsid like *Youngina*, but that reptile is now recognized as be-

longing to the lepidosauromorph branch of diapsids (Currie 1982; Benton 1983*b*, 1984*a*, 1985*b*; Evans 1984; Gauthier 1984).

Limits of the Archosauria

There is a semantic question regarding the composition of Archosauria. That is, at which node should the name be applied? The "traditional" Archosauria (Benton 1984*c*, 1985*b*; Paul 1984*a*; Benton and Clark 1988) consists of *Proterosuchus* and more recently evolved relatives (fig. 1.1). The "crown-group" Archosauria (Gauthier 1986) consists of all the descendants of the closest common ancestor of the living forms (i.e., the Crocodylia and Aves). This latter arrangement corresponds to the Ornithosuchia and Crocodylotarsi but excludes a number of basal forms (fig. 1.1). There is no firm way of deciding which view is advisable. The traditionalists argue the need for stability in taxonomy and the convenience of having all taxa, including plesiomorphous ones, within a well-established taxon. The "crown-groupers" can support their case by pointing out that all archosaurs in their interpretation, even the fossil ones, can be said to have all the hard- and soft-part synapomorphies of the living forms. I use the traditional interpretation of the bounds of Archosauria rather than the crown-group Archosauria.
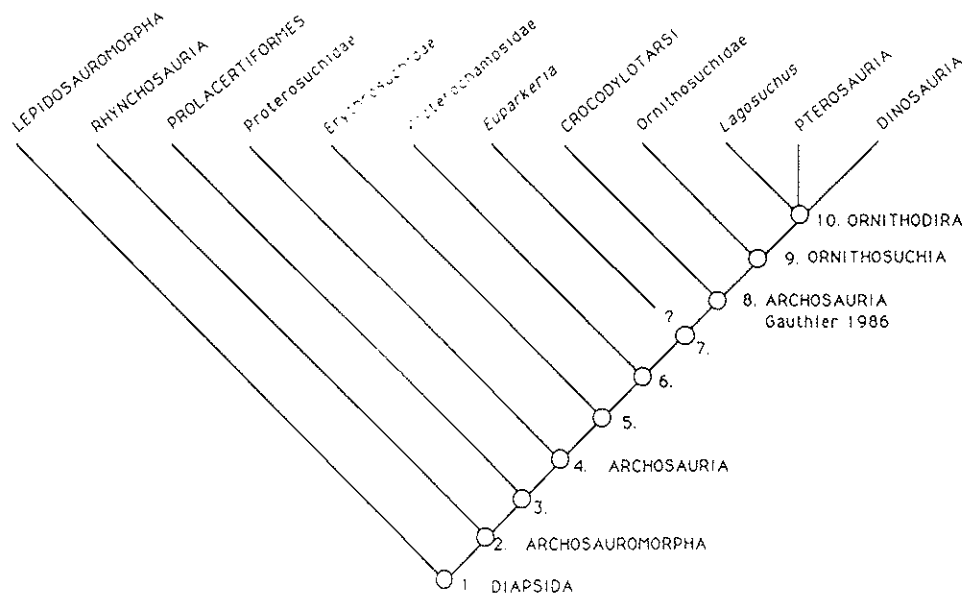

Fig. 1.1. Cladogram illustrating postulated relationships among the major archosauromorph and archosaur groups. Based on cladistic analyses by Benton (1984*a*, 1985*b*) and Benton and Clark (1988), with information from Gauthier (1986) and Evans (1988).

1. DIAPSIDA (Benton 1985*b*; Evans 1988): Supratem-

Figure 1.1, continued

poral fenestra; suborbital fenestra; cervical vertebrae longer than mid-dorsals.

2. ARCHOSAUROMORPHA (Benton 1985b; Evans 1988): Premaxilla extends up behind the naris; nares elongate and close to the midline; quadratojugal mainly behind the infratemporal fenestra rather than below it; tall quadrate; pineal foramen reduced or absent; tabulars absent; paroccipital process touches suspensorium; slender stapes without a foramen; vertebrae not notochordal; transverse processes on dorsal vertebrae project as distinctive narrow elongate processes; cleithrum absent; no entepicondylar foramen in the humerus; no foramen in carpus between ulnare and intermedium; lateral tuber on calcaneum; complex concave-convex articulation between the astragalus and calcaneum; fifth distal tarsal lost; pedal centrale displaced laterally; metatarsal V hooked in one plane only; elongate metatarsal IV.

3. UNNAMED GROUP: Long snout and narrow skull; nasals longer than frontals; posttemporal fenestrae small or absent; recurved teeth; extensive participation of the parasphenoid/basisphenoid in the side wall of the braincase; long, thin, tapering cervical ribs with two or three heads and a cranial dorsal process.

4. ARCHOSAURIA: Possession of antorbital fenestra; postfrontal reduced; postparietals fused or absent; caudal border of infratemporal fenestra bowed; marginal teeth laterally compressed; presence of an ossified laterosphenoid; no ectepicondylar groove or foramen on humerus; possession of a fourth trochanter on femur.

5. UNNAMED GROUP: Loss of the supratemporal; possession of a lateral mandibular fenestra; coronoid reduced or absent; presacral intercentra absent behind the axis; ossified portion of the scapula very tall and narrow (at least twice as tall as width of base); coracoid small, and glenoid faces largely backward; deltopectoral crest extends at least one-fourth of the way down the shaft of the humerus; distal end of the humerus is narrower than the proximal end; pelvis markedly three-rayed with a long, downturned pubis and ischium; iliac blade has a small cranial process; pubis has a strongly downturned cranial tuber in lateral view; ischium has a large caudoventral process (the ischium is longer than the iliac blade); tarsus contains only four elements; metatarsals II, III, and IV subequal in length, with III the longest; loss of cranioproximal "hook" on metatarsal V; fewer than four phalanges in pedal digit V.

6. UNNAMED GROUP: Parietal foramen absent; otic notch well developed; possession of thecodont dentition; ribs all one- or two-headed; hindlimbs under the body (semierect or erect gait); possession of "crocodiloid"

tarsus (foramen lost, and rotation between astragalus and calcaneum possible); possession of dermal armor with two osteoderms per vertebra.

7. UNNAMED GROUP: Antorbital fenestra large and lying in a depression; nasals run forward between the nares; diapophysis placed fairly high on the neural arch of cervical vertebrae; parapophysis transfers to the neural arch in cranial dorsal vertebrae; diapophysis and parapophysis fuse in the caudal dorsal vertebrae and the ribs become single-headed.

8. UNNAMED GROUP (= Archosauria of Gauthier 1986): Parietals send caudal processes onto the occiput; discrete postparietal and exoccipitals absent beyond juvenile stages of development; pterygoids meet medially in the palate; palatal teeth absent.

9. ORNITHOSUCHIA (Gauthier 1986): Septomaxilla absent (parallelism in Suchia); squamosal reduced and descending ramus gracile (also in *Euparkeria*); manual digit I short and equipped with a diverging claw; no puboischiadic plate, and much reduced contact between pubis and ischium (parallelism in Suchia); pubis long, narrow, and subvertically oriented (parallelism in Suchia); pubis longer than the ischium (parallelism in Suchia); possession of a lesser trochanter; fourth trochanter a sharp flange; shaft of femur bowed dorsally; prominent cnemial crest on tibia (also in *Gracilisuchus*); ventral flange of astragalus is absent (also in *Euparkeria*); digit V of the foot is reduced (shorter than I) (parallelism in Suchia).

10. ORNITHODIRA (Gauthier 1986): Presacral vertebral column is divided into three regions (cervical, cervical-thoracic, lumbar); centra steeply inclined in at least cervicals 3−6; zygapophyses of the middle and distal caudals inclined caudoventrally; loss of the interclavicle (possibly also in *Postosuchus*); acetabulum perforated to some extent (parallelism in *Postosuchus* and Crocodylomorpha); supraacetabular crest on ilium (parallelism in *Saurosuchus*, *Postosuchus*, Crocodylomorpha); pubis more than three times the width of the acetabulum (parallelism in *Saurosuchus*, *Postosuchus*, Crocodylomorpha); fourth trochanter a winglike process; fourth trochanter runs down one-third to one-half the length of the femur shaft (parallelism in *Erythrosuchus* and *Chanaresuchus*); distal end of femur forms two subterminal condyles; knee articulates at 90°; stance digitigrade (parallelism in *Gracilisuchus*, *Postosuchus*, Crocodylomorpha); mesotarsal ankle joint with astragalus and calcaneum fused to the tibia; calcaneum with no tuber at all; ascending process of astragalus fits between the tibia and fibula; metatarsals II−IV closely bunched as a unit; metatarsals II−IV elongate and the foot functionally tridactyl.

THE RELATIONSHIPS OF THE TRIASSIC ARCHOSAURIA

"Thecodontians"

The archosaurs radiated extensively during the Triassic period, and several distinctive lineages arose. It has been widely accepted that all of the later archosaur groups arose from within the Thecodontia, a paraphyletic group that excludes three or four descendant clades: crocodilians, pterosaurs, dinosaurs, and birds. The informal term *thecodontian* will be used here to refer to all Late Permian and Triassic archosaurs that do not fall into these last three named groups.

There is no currently accepted classification of the thecodontians. Most authors have favored a basic tripartite division: the Proterosuchia (for the Proterosuchidae and Erythrosuchidae and, at times, the Rauisuchidae and Proterochampsidae), the Parasuchia (for the Phytosauridae), and the Pseudosuchia (for everything else, including some early crocodylomorphs) (e.g., Romer 1956; Reig 1970; Krebs 1976). Others have separated the aetosaurs as the Aetosauria (Romer 1966, 1972b; Sill 1974; Bonaparte 1975a; Charig 1976; Thulborn 1980), some of the early crocodylomorphs as the Sphenosuchia (Bonaparte 1982b), ornithosuchids as the Ornithosuchia (Chatterjee 1982), and rauisuchids and poposaurids as the Rauisuchia (Chatterjee 1982). These divisions are abandoned here, except for the Rauisuchia and a revised Pseudosuchia.

Recent cladistic analyses of the Triassic archosaurs (e.g., Benton 1983b, 1984a, 1984c, 1985b; Gauthier 1984, 1986; Paul 1984a; Gauthier and Padian 1985; Benton and Clark 1988; Benton and Norman, in prep.) have produced similar cladograms that broadly resemble that shown in fig. 1.1. The controversial points are noted briefly below.

The Basal Archosaurs

The oldest known archosaur is *Archosaurus* from the latest Permian of the U.S.S.R. It is known from only fragmentary remains, but these show at least one diagnostic archosaurian character (the presence of an antorbital fenestra). *Archosaurus* is generally classed as a proterosuchid, a group best represented by *Proterosuchus* from the Early Triassic of South Africa, a 1.5-m long-snouted aquatic form (fig. 1.2a). *Proterosuchus* possesses all eight archosaur autapomorphies noted above.

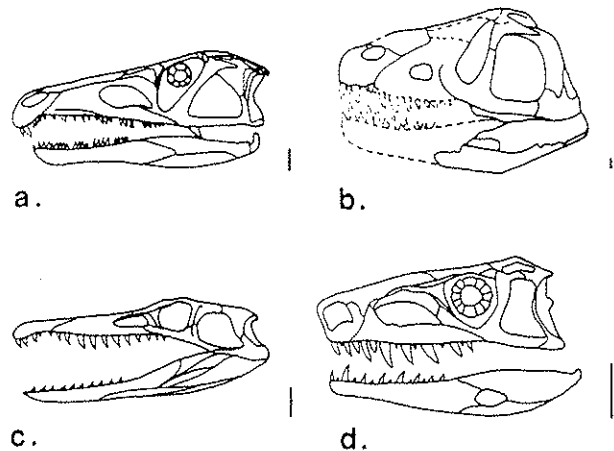Next on the cladogram is *Erythrosuchus* (fig.

Fig. 1.2. Skulls of primitive archosaurs: a. *Proterosuchus;* b. *Erythrosuchus;* c. *Chanaresuchus;* d. *Euparkeria.* The skulls are drawn to uniform length; scale = 20 mm. Based on several sources.

1.2b), another thecodontian from the Early Triassic of South Africa. *Erythrosuchus* and its relatives were up to 5 m long, and they were clearly the top carnivores of their day. Their synapomorphies compared to *Proterosuchus* include loss of the supratemporal, presence of an external mandibular fenestra, absence of most presacral intercentra, triradiate pelvis, four tarsal elements, and metatarsals II–IV subequal in length, among other synapomorphies with later archosaurs (Benton and Clark 1988).

The Proterochampsidae of the Middle Triassic of Argentina, typified by *Chanaresuchus* (fig. 1.2c), a superficially crocodilelike fish-eater, share numerous derived characters of skull and postcranial skeleton with later forms. These include the first appearance of true thecodont dentition, the loss of the parietal foramen, and the crocodiloid tarsus, which allowed rotation between the astragalus and calcaneum.

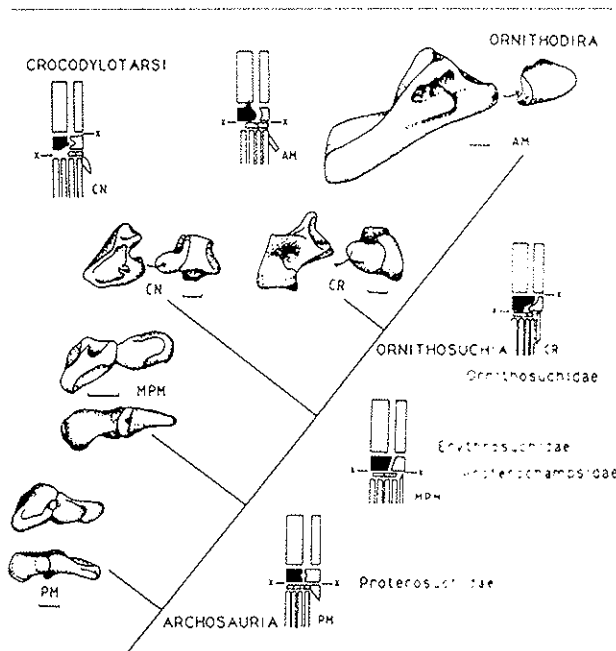## *Euparkeria* and Ankle Structure

Euparkeria, a small animal from the Early Triassic of South Africa, is close to a major split in archosaur evolution that gave rise to crocodiles, on the one hand, and birds and dinosaurs, on the other. The detailed relationships of *Euparkeria* are uncertain, however. Some authors (e.g., Ewer 1965; Cruickshank 1979) place it among the basal archosaurs in association with *Erythrosuchus,* while others (Thulborn 1980; Brinkman 1981; Chatterjee 1982) regard it as more derived. Currently,

Euparkeria is regarded either as the sister taxon of all later archosaurs (= crown-group Archosauria) or as a member of the line leading to dinosaurs (fig. 1.2d).

This dichotomy of opinions hinges around the ankle structure (fig. 1.3), which has been used by several authors (e.g., Bonaparte, 1975a, 1982b; Cruickshank 1979; Thulborn 1980; Chatterjee 1982) as a general guide to archosaur relationships. Early archosaurs have a primitive mesotarsal (PM) ankle in which bending is along a simple hinge between the astragalus-calcaneum unit and the rest of the foot. Later forms have a crocodiloid ankle in which part of the line of bending runs between the astragalus and the calcaneum. However, there are two types of crocodiloid ankle, the crocodile-normal (CN) ankle found in crocodilians, phytosaurs, aetosaurs, and rauisuchians

Fig. 1.3. Ankle structures of the archosaurs illustrated on a cladogram depicting broad relationships. For each ankle pattern, a cranial view of the astragalus (left) and calcaneum (right) complex is shown. An additional proximal view is shown for the PM and MPM types (upper drawing). For each ankle type, a diagram of the lower leg, ankle, and foot is shown (astragalus shaded black) with the main hinge line (x – x). The ankles are PM (primitive mesotarsal) of *Proterosuchus*, MPM (modified primitive mesotarsal) of *Chanaresuchus*, CN (crocodile-normal) of *Neoaetosauroides*, CR (crocodile-reversed) of *Riojasuchus*, and AM (advanced mesotarsal) of a prosauropod dinosaur. Based, in part, on Cruickshank and Benton (1985).

and the crocodile-reversed (CR) ankle of ornithosuchids, an outgroup to the Dinosauria. In the CN ankle, a peg on the astragalus fits into a socket on the calcaneum, while in the CR ankle, the reverse is the case. Dinosaurs, pterosaurs, and birds have a fourth, modified ankle called advanced mesotarsal (AM) in which the astragalus and calcaneum are firmly attached to the tibia and fibula and the line of bending is between the astragalus-calcaneum and the rest of the foot. The AM ankle differs fundamentally from the PM in that the astragalus is a broad element, the calcaneum is much reduced, and both elements are virtually fused to each other and to the tibia.

Some authors (Gauthier 1986; Parrish 1986) regard the ankle of *Euparkeria* as CR and thus close to ornithosuchids and dinosaurs, while others (Cruickshank and Benton 1985) see it as merely a generalized crocodiloid type, or modified primitive mesotarsal (MPM) type, with no special CR features. Other characters of the skull and postcranial skeleton are roughly equally balanced between rival placements of *Euparkeria*. In addition to its supposed CR ankle, *Euparkeria* shares a reduced gracile squamosal and the absence of a ventral flange on the astragalus with ornithosuchians (Gauthier 1986). In addition, it lacks occipital processes of the parietal, discrete postparietal and exoccipitals, and palatal teeth and possesses medial contact of pterygoids, characters of Archosauria (Benton and Clark 1988).

The Crocodylotarsi

The crocodilian line of archosaurs, characterized by the possession of the CN ankle and other synapomorphies (viz. Gauthier and Padian 1985; Gauthier 1986; Benton and Clark 1988), includes phytosaurs as the basal group and aetosaurs, rauisuchians, and crocodylomorphs (crocodilians and crocodilianlike forms) as successively higher taxa within the lineage (fig. 1.1).

Phytosaurs are a well-defined group of long-snouted, 2- to 4-m-long animals from the Late Triassic of Europe, North America, and parts of Asia. Although superficially crocodilelike (fig. 1.4a), their aquatic and fish-eating adaptations evolved convergently.

The remaining Crocodylotarsi form a group termed the Suchia (Krebs 1976), which appears to divide into the Pseudosuchia (aetosaurs and rauisuchians) and the Crocodylomorpha. Aetosaurs were 1- to 3-m-long herbivores of the Late Triassic. They had characteristic blunt snouts, peglike teeth (fig. 1.4b), and heavily armored bodies. Rauisuchians, from the Middle and Late Triassic, include large quadrupedal
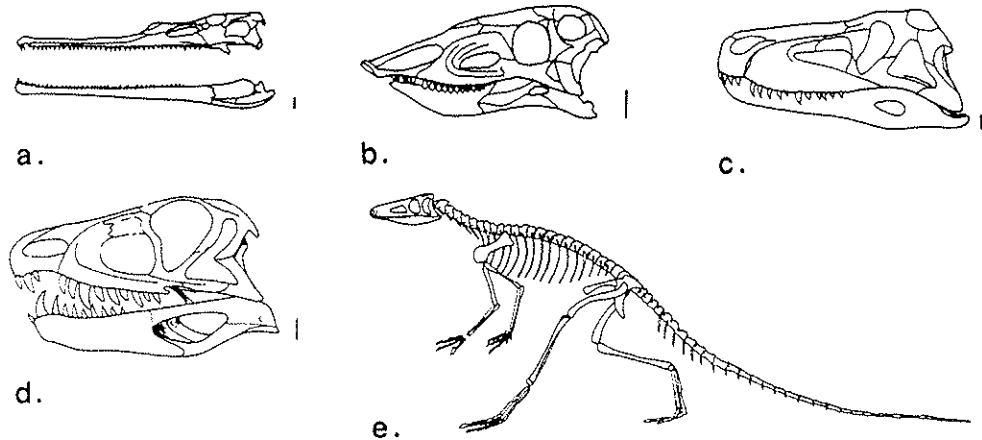
Fig. 1.4. Skulls of Triassic archosaurs: a. *Parasuchus;* b. *Stagonolepis;* c. *Saurosuchus;* and d. *Ornithosuchus.* Skeleton of e. *Lagosuchus.* Scale = 20 mm. Based on several sources.

carnivorous forms (fig. 1.4c), up to 5 m long, which had a specialized erect gait where the pelvis was tipped almost horizontally, and the femur fitted into the acetabulum like a vertical pillar. Poposaurids were bipedal carnivores whose relationships are still unclear. They might be rauisuchians, but they also seem to share some characters with crocodylomorphs (Gauthier 1986; Benton and Clark 1988). The crocodylomorphs arose in the Late Triassic initially as small bipedal terrestrial forms. Only later, in the Jurassic, did they adopt more "crocodilian" habits of life in fresh and salt water.

The Ornithosuchia

The dinosaur-bird line, the Ornithosuchia (Gauthier 1986), consists of those archosaurs with CR and AM ankles (figs. 1.1, 1.3). The group is characterized by numerous synapomorphies that relate largely to the acquisition of erect gait (long narrow pubis and ischium with reduced contacts, lesser trochanter and sharp fourth trochanter on femur, prominent cnemial crest on tibia, digit V of foot reduced) and includes the Ornithosuchidae, *Lagosuchus*, and the Pterosauria as relatively more intimate outgroups of the Dinosauria (including Aves).

The Ornithosuchidae, from the Late Triassic of Scotland (*Ornithosuchus*) and Argentina (*Riojasuchus, Venaticosuchus*) were 1- to 3-m-long facultatively bipedal carnivores. The skull (fig. 1.4d) shows a characteristic bulbous snout and a gap in the tooth row between the premaxilla and maxilla. The CR ankle is another synapomorphy of the family. Superficially, the

ornithosuchids are very dinosaurlike, and they demonstrate the ornithosuchian synapomorphies of the hindlimb just noted as well as some features of the skull (septomaxilla absent; squamosal reduced) and hand (manual digit I short and equipped with a diverging claw).

The remaining ornithosuchians, *Lagosuchus*, the Pterosauria, and the Dinosauria have been termed the Ornithodira (Gauthier 1986), and they possess a large number of synapomorphies of the vertebral column (distinctive cervical, cervical-thoracic, and lumbar regions), shoulder girdle (loss of interclavicle), pelvis (partially to fully perforated acetabulum, supraacetabular crest on the ilium, elongate pubis), hindlimb (femur is shorter than tibia; fourth trochanter is a winglike process very low on the femur, proximal head of the femur is inturned, distal end of the femur is split into two condyles, and knee articulates as a straight hinge), and foot (digitigrade stance, AM ankle joint with ascending tibial process on astragalus, metatarsals II–IV are elongate and closely bunched as a unit, and the foot is functionally tridactyl).

Lagosuchus, a slender, long-limbed animal from the Middle Triassic of Argentina (fig. 1.4e) shares all of these synapomorphies with the Dinosauria as well as with the Pterosauria. It is known from half a dozen skeletons that show postcranial features well, but the skull is incompletely known. *Lagosuchus* may be primitive to the pterosaur-dinosaur split since it appears to lack several of their synapomorphies (loss of postfrontal, caudal zygapophyses nearly vertical, no more than four phalanges in manual digit IV, proximal head of

femur fully offset; Benton and Norman in prep.). However, *Lagosuchus* shares some apparent synapomorphies with the Dinosauria which are absent in the Pterosauria, such as the caudoventrally facing glenoid facet on the scapulocoracoid, the reduced subcircular coracoid, the shortened forelimbs, and the brevis shelf on the caudal portion of the ilium (Gauthier 1986). Most of these relate to the flight specializations of pterosaurs, but it is still hard to sort out the relationships of the three ornithodiran taxa. The earlier view of Wild (1978b) and Benton (1982, 1984a, 1985b), that Pterosauria was the sister group of Archosauria, was proposed because they lacked seven archosauromorph synapomorphies as well as archosaurian and ornithosuchian characters such as the external mandibular fenestra, the nasals extending between the external nares, the pterygoids meeting medially, the loss of palatal teeth (*Eudimorphodon* has teeth on the pterygoid: Wild 1978b), the open acetabulum, the elongate pubis and ischium, the fourth trochanter on the femur, and the reduced pedal digit V (not in early pterosaurs). The view of Gauthier and Padian (1985), however, is accepted here since it is more parsimonious.

THE RELATIONSHIPS OF THE MAJOR DINOSAURIAN GROUPS

Monophyly of the Dinosauria

Until recently, nearly all authors assumed that dinosaurs were a polyphyletic group with at least two, and more probably three or four, separate origins from different thecodontian groups (Romer 1966, 1968, 1972b; Reig 1970; Charig 1976; Thulborn 1980; Bonaparte 1982b; Chatterjee 1982). Exceptions were Bakker and Galton (1974) and Bonaparte (1976), who speculated that the Dinosauria is a true clade. Recent cladistic analyses (Benton 1984b, 1984c, 1986; Gauthier 1984, 1986; Paul 1984a, 1984b; Benton and Cruickshank 1985; Cooper 1985; Gauthier and Padian 1985; Benton and Clark 1988), however, all agree that the Dinosauria is monophyletic on the basis of numerous autapomorphies:

1. elongate vomers that reach caudally at least to the level of the antorbital fenestra (Gauthier 1986).

2. three or more sacral vertebrae (paralleled in the crocodylotarsan *Postosuchus* and the Ornithosuchidae; this character is uncertain in basal dino-

saurs, and may apply to a higher node in the cladogram; *Lagosuchus* and *Lagerpeton* have only two sacrals: Arcucci 1986).

3. scapulocoracoidal glenoid facing fully backward

4. low deltopectoral crest that runs one-third or one-half of the way down the shaft of the humerus.

5. three or fewer phalanges in the fourth digit of the hand (Gauthier 1986)

6. largely to fully open acetabulum

7. fully offset proximal head of femur with a distinct neck and ball

8. greatly reduced fibula

9. well-developed ascending process of astragalus

It is worth noting that many of the characters that seem fully dinosaurian, but which are omitted here (e.g., the supraacetabular crest, elongate pubis, enlarged fourth trochanter, AM tarsus, digitigrade stance, etc.), were already present in the lineage since the origin of all ornithodirans.

The Basal Dinosaurs

There are a number of Late Triassic dinosaurs that do not fit into any of the major clades within the Dinosauria, and they are assumed here to be primitive outgroups to the main dinosaurian clade. These include *Herrerasaurus, Staurikosaurus,* and possibly a number of other poorly represented taxa (e.g., *Aliwalia, Ischisaurus, Spondylosoma*). In the past, attempts have been made (Colbert 1970; Cooper 1981a; Galton 1977a, 1985a) to place *Herrerasaurus* and *Staurikosaurus* in the Saurischia (prosauropod, theropod, or something in between: see Sues, this vol.).

It seems likely that *Herrerasaurus* and *Staurikosaurus* are successively closer outgroups of the main dinosaurian assemblage (fig. 1.5; Brinkman and Sues 1987). Galton (1985a) erected the Infraorder Herrerasauria for *Herrerasaurus* and *Staurikosaurus* and *Aliwalia,* while Gauthier (1986) included *Herrerasaurus, Staurikosaurus,* and *Ischisaurus* in the Herrerasauridae, but the authors just cited could find no potential synapomorphies of such a grouping. *Herrerasaurus* has all the dinosaurian characters noted above, although characters 1, and 3 through 5 cannot be determined from published accounts. It lacks an ornithodiran character, however, since its femur is apparently longer than its tibia (Galton 1977a). *Staurikosaurus* also shares the dinosaurian autapomorphies (1 and 5 cannot be deter-
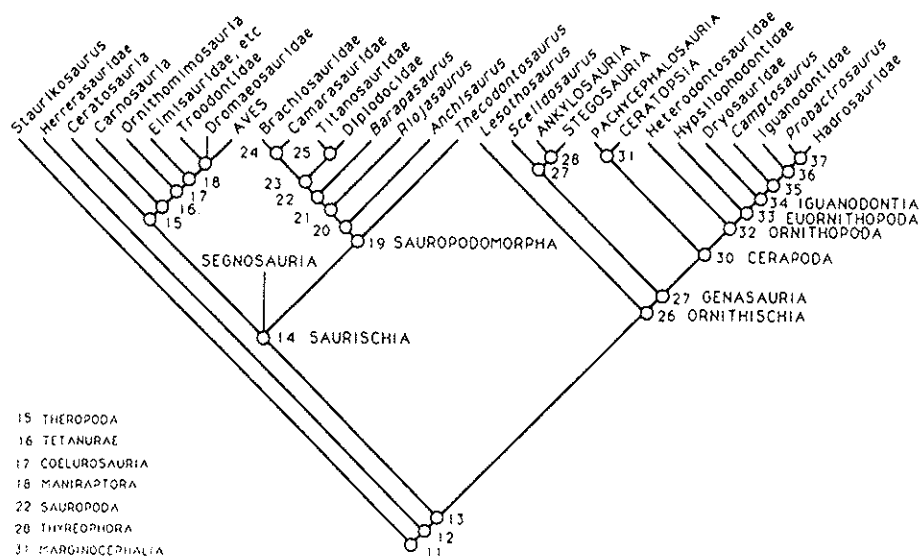
Fig. 1.5. Cladogram depicting phylogenetic relationships of the major groups of the Dinosauria, with particular focus on the early forms. Based on Gauthier (1986), Sereno (1986), and other sources (see text). Character information for nodes 15–18, 20–25, 27–37 is omitted since it is given in the text. Additional character information for certain nodes is given in other chapters of this volume: 28, 29 (Thyreophora; Weishampel, this vol.); 31 (Marginocephalia; Dodson, this vol.) 32–37 (Ornithopoda; Weishampel, this vol.).

11. DINOSAURIA: Elongate vomers that reach caudally at least to the level of the antorbital fenestra; three or more sacral vertebrae (paralleled in the crocodylotarsan *Postosuchus* and the Ornithosuchidae; this character is uncertain in basal dinosaurs); glenoid facing fully backward; low deltopectoral crest that runs one-third or one-half the way down the shaft of the humerus; three or fewer phalanges in the fourth digit of the hand; largely to fully open acetabulum; fully offset proximal head of femur with a distinct neck and ball; greatly reduced fibula; well-developed ascending process of astragalus.

12. UNNAMED GROUP: Elongate S-shaped neck; reduced contact between the pubis and the ischium.

13. UNNAMED GROUP: Presence of three or more sacral vertebrae (may move lower in cladogram); lesser trochanter on the femur is a spike or a crest; transversely expanded distal end of the tibia.

14. SAURISCHIA: Temporal musculature extending on to frontal; lateral overlap of quadratojugal on to the caudal process of the jugal; elongate caudal cervicals giving a relatively long neck; axial postzygapophyses set lateral to the prezygapophyses; epipophyses present on the cranial cervical postzygapophyses; presence of accessory intervertebral articulations (hyposphene-hypantrum) in dorsal vertebrae; manus more than 45%

of the length of the humerus + radius; distinctly asymmetrical manus, with digit II the longest; proximal ends of metacarpals IV and V lie on the palmar surfaces of digits III and IV in the hand, respectively; heavy pollex with a very broad metacarpal.

15. THEROPODA

16. TETANURAE

17. COELUROSAURIA (*sensu* Gauthier 1986)

18. MANIRAPTORA

19. SAUROPODOMORPHA: Relatively small skull (approx. 5% of body length); dentary curved down at the front; lanceolate teeth with coarsely serrated crowns; at least ten cervicals (each about twice as long as high), forming a very long neck; one to three extra sacral vertebrae, all modified from caudals; enormous pollex with an enlarged claw; absence of claws on manual digits IV and V; iliac blade with a reduced caudal process and a short cranial process (the brachyiliac condition); fused, deep, apron-like pubes that are twisted proximally; very large obturator foramen in pubis; femur longer than tibia; ascending process of astragalus keys into tibia, which has a matching descending process.

20. UNNAMED GROUP

21. UNNAMED GROUP

22. SAUROPODA

23. UNNAMED GROUP

24. CAMARASAURS

25. TITANOSAURS

26. ORNITHISCHIA: Rostral tip of the premaxilla toothless and roughened; horizontal or broadly arched palatal process of premaxilla; maxilla excluded from the margin of the external naris by a large lateral process of the premaxilla which meets the nasal; reduced antorbital fenestra; ventral margin of the antorbital fenestra parallels the maxillary tooth row; palpebral in the orbit; pre-

Figure 1.5, continued

frontal with a long caudal ramus that overlaps the frontal; subrectangular quadratojugal lying behind the infratemporal fenestra; elongate and massive quadrate; predentary bone at the front of the mandible; dorsal border of the coronoid eminence formed by the dentary; mandibular condyle set below the tooth rows (paralleled in most sauropodomorphs); buccal emargination of the jaws, suggesting the possession of cheeks in life; cheek teeth with low triangular crowns with a well-developed cingulum; crowns of cheek teeth with low and bulbous base; enlarged denticles on the margins; adjacent crowns of both maxillary and dentary teeth overlap (paralleled in part in some sauropodomorphs); recurvature absent in maxillary and dentary teeth; maximum tooth size near the middle of the maxillary and dentary tooth rows; at least five sacral vertebrae; gastralia absent (paralleled in Sauropoda); ossified tendons at least above the sacral region; opisthopubic pelvis, with small cranial process; ilium with lateral swelling of the ischial tuberosity; iliac blade with a long and thin cranial process and a deep caudal pro-

cess; pubic symphysis restricted to its distal end; ischial symphysis restricted to its distal end; pubis with an obturator notch rather than a foramen; obturator foramen formed between the pubis and ischium; distal puboischial symphysis; pendent fourth trochanter on the femur; fringe-like lesser trochanter on the femur; fifth digit of the foot reduced to a small metatarsal with no phalanges.

27. CERAPODA: Spout-shaped mandibular symphysis; entire margin of the antorbital fossa is sharply defined or extends as a lateral wall enclosing the fossa.
28. THYREOPHORA
29. EURYPODA
30. CERAPODA
31. MARGINOCEPHALIA
32. ORNITHOPODA
33. EUORNITHOPODA
34. IGUANODONTIA
35. ANKYLOPOLLEXIA
36. STYRACOSTERNA
37. UNNAMED GROUP

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mined), although it is not clear whether it had three sacral vertebrae (Colbert 1970) or two (Galton 1977a). In comparison with *Herrerasaurus, Staurikosaurus* has possibly acquired two further synapomorphies of later dinosaurs—an elongate S-shaped neck and a reduced contact between the pubis and the ischium. Brinkman and Sues (1987) and Sues (this vol.) place *Herrerasaurus* above *Staurikosaurus* in the cladogram since it has indications of a "twisted tibia" seen in later dinosaurs, but the twist is only about 60° (Galton 1977a: 238), compared to a dinosaurian 90°.

The "True" Dinosaurs

All other dinosaurs appear to form a clade that may be characterized by at least three synapomorphies: the presence of three or more sacral vertebrae (? two in *Staurikosaurus*, see above), unknown in *Herrerasaurus* (? three; Benedetto 1973); a spike or crestlike lesser trochanter on the femur (only a bump in the forms so described), and the transversely expanded distal end of the tibia. The sacral vertebral character may shift down the cladogram, as noted above, depending on new studies of the early dinosaurs.

The "true" dinosaurs are divided into three monophyletic groups: Ornithischia, Theropoda, and Sauropodomorpha. There are three possible arrangements of these three taxa. The generally accepted view seems

to be that the Theropoda and Sauropodomorpha pair off as sister groups (together these make a monophyletic Saurischia), and this is defended here. Alternative views are discussed later.

The Saurischia

The evidence for monophyly of the Saurischia includes the following autapomorphies (Gauthier 1986):

1. temporal musculature extending on to the frontal

2. lateral overlap of the quadratojugal on to the caudal process of the jugal

3. elongate caudal cervicals giving a relatively long neck

4. axial postzygapophyses set lateral to the prezygapophyses

5. epipophyses present on the cranial cervical postzygapophyses

6. presence of accessory intervertebral articulations (hyposphene-hypantrum) in dorsal vertebrae

7. manus more than 45 percent of the length of the humerus and radius together

8. distinctly asymmetrical manus, with digit II the longest

9. proximal ends of metacarpals IV and V lying on the palmar surfaces of digits III and IV in the hand, respectively

10. heavy pollex with a very broad metacarpal

Within the Saurischia (*sensu* Gauthier 1986), most authors would accept the major division into the Theropoda and Sauropodomorpha.

The Theropoda

Several cladograms of Theropoda are now available (Padian 1982; Paul 1984*a;* Thulborn 1984*a;* Gauthier 1986) which hinge around the key recognition by Ostrom (1976*b*) that birds are derived from theropods close to dromaeosaurids. The Theropoda is characterized (Osmólska, this vol.; Gauthier 1986) on the basis of a number of synapomorphies of the skull and postcranial skeleton (Gauthier 1986):

1. reduced overlap of dentary onto postdentary bases and reduced mandibular symphysis

2. lacrimal exposed on the skull roof

3. extra fenestra in the maxilla

4. vomers fused rostrally

5. expanded ectopterygoid with a ventral fossa

6. first intercentrum with large occipital fossa and small odontoid notch

7. second intercentrum with broad crescentic fossa for reception of first intercentrum

8. presacral vertebrae with pleurocoels (openings to hollow centrum)

9. at least five sacral vertebrae

10. transition point in tail, with marked changes in the form of the processes

11. enlarged distal carpal I overlapping the bases of metacarpals I and II

12. digit I of hand absent or reduced to a vestige

13. digit IV of hand absent or reduced

14. elongate penultimate phalanges in hand

15. digit III of hand with short first and second phalanges

16. unguals of hand enlarged, compressed, sharply pointed, strongly recurved, and with enlarged flexor tubercles

17. long preacetabular process on the ilium

18. pronounced brevis fossa on caudal part of the ilium

19. femur convex cranially

20. fibula closely appressed to tibia and attached to a tibial crest

21. narrow, elongate metatarsus

22. digit IV of foot reduced

23. digit V of foot represented by a very reduced metatarsal

24. metatarsal I reduced, and does not contact tarsus, being attached halfway, or further, down the side of metatarsal II

25. thin-walled, hollow, long bones

The theropod clade is very well characterized, and few authors have ever doubted its validity. The inclusion of birds has, however, been controversial, but current evidence now strongly supports this view (e.g., Ostrom 1976*b;* papers in Hecht et al. 1985; Gauthier 1986). The problems arise when attempts are made to subdivide the Theropoda. Some subgroups seem to be clearly set off as monophyletic taxa, among them, ornithomimosaurs, deinonychosaurs (but see below), and carnosaurs. Others are much less clearly supported by synapomorphies. A number of the standard theropod subgroups, such as Romer's (1966) Coelurosauria, Procompsognathidae, and Coeluridae, for example, are clearly paraphyletic or polyphyletic collections of superficially similar taxa (Paul 1984*a;* Thulborn 1984*a;* Gauthier 1986). Norman (this vol.) discusses many of the problematic taxa of theropods that are hard to fit into a cladistic scheme.

Gauthier (1986) presented a cladogram of the Theropoda in which he recognized five main clades of theropods: Ceratosauria, Carnosauria, Ornithomimidae, Deinonychosauria, and Aves (his Avialae), with a number of unplaced taxa (fig. 1.5).

The Ceratosauria, including a range of small to medium-sized Late Triassic to Late Jurassic taxa, such as *Ceratosaurus, Coelophysis, Dilophosaurus,* and *Syntarsus,* are characterized by loose attachment of the premaxilla to the maxilla, a thyroid fenestra in the pubis, a narrow boned pubis, a trochanteric shelf on the femur, and other features (Rowe and Gauthier, this vol.). They appear to form the sister-group to all other theropods, termed the Tetanurae (Gauthier 1986).

The Tetanurae, including carnosaurs, ornithomimosaurs, deinonychosaurs, and birds (fig. 1.5), is

defined by a number of skull and skeletal characters, including a greatly enlarged supplementary maxillary fenestra, termination of the maxillary tooth row in front of the orbit, a straplike scapula, a coracoid that tapers behind, a hand that is more than two-thirds the length of the arm (humerus and radius), absence of manual digit IV in adults, an obturator process on the ischium, a winglike lesser trochanter on the femur, a tall and broad ascending process of the astragalus, and numerous others.

The Carnosauria, the often very large carnivorous dinosaurs of the Jurassic and Cretaceous, are distinguished from other dinosaurs by their deep orbits, narrow frontals and parietals, greatly reduced hand, and other features (Molnar et al., this vol.).

The sister group to the Carnosauria is the Coelurosauria (*sensu* Gauthier 1986), including all other theropods and birds, which shows a number of autapomorphies: a subsidiary fenestra between the pterygoid and palatine, cervical ribs fused to the centra, sternal plates fused together, elongate forelimb, fourth trochanter reduced or absent, and a much enlarged ascending process of the astragalus, among others.

The basal coelurosaurs are the Ornithomimosauria, characterized by toothless jaws, a beaklike snout, all digits of the manus about equal in length, and slender hindlimbs with a very elongate metatarsus with metatarsal III strongly pinched between metatarsals II and IV (Gauthier 1986; Barsbold and Osmólska, this vol.). Ornithomimosaurians are the sister group of all remaining theropods and birds, the latter termed the Maniraptora by Gauthier (1986). The Maniraptora are characterized by reduction or loss of the prefrontal, prominent axial epipophyses, specialized ventral processes (hypapophyses) on cervicothoracic vertebrae, proximal position of transition point in tail subrectangular coracoid, elongate forelimb, ulna bowed posteriorly, semilunate carpals, very thin metacarpal III that bows laterally, very low pubic process of the ilium, reversed pubis, shortened ischium, lesser trochanter nearly confluent with proximal head of the femur, absence of a fourth trochanter, and digit IV of the foot longer than digit II as well as other synapomorphies (Ostrom 1976b; Gauthier 1986). The Maniraptora includes the Dromaeosauridae, Troodontidae, and Aves (*Archaeopteryx* and all other birds [= Avialae of Gauthier 1986, who used a crown-group interpretation of Aves]), and probably also a number of other poorly known taxa such as *Coelurus, Ornitholestes, Microvenator, Saurornitholestes, Hulsanpes,* the Caenagnathidae, the Elmisauridae, and *Compsognathus,* as basal outgroups (Gauthier 1986), but their exact order is uncertain be-

cause of incompleteness of the specimens (see also Norman, this vol.; Currie, this vol.). The Oviraptoridae is united with the Caenagnathidae to form the Oviraptorosauria, which itself is treated here as a basal maniraptoran taxon (Barsbold et al., this vol.).

The relationships of the Dromaeosauridae, Troodontidae, and Aves are much debated at present, and a resolution may be difficult because of incomplete material. One view is that the Dromaeosauridae and Troodontidae form a taxon Deinonychosauria, which is the sister group of Aves (Gauthier 1986), and other authors (Osmólska, this vol.) have also suggested that the Oviraptorosauria and Ornithomimosauria might be related as well. The dromaeosaurids and troodontids share a number of modifications to the foot, in particular an enlarged second digit with a very large sicklelike claw presumably used to slash prey animals. Of the seventeen maniraptoran characters listed by Gauthier (1986), dromaeosaurids share five uniquely with Aves, but the status of three of these, the vertebral features, is uncertain in troodontids. Troodontids share one of the others (absence of fourth trochanter), but, significantly, lack the fifth (reversed pubis: Barsbold 1983b; Gauthier 1986: 47), which suggests that they may be a more distant outgroup to Aves than the Dromaeosauridae. Paul (1984a) and Currie (1985, 1987a) have suggested, however, that troodontids might be the closest outgroup to Aves on the basis of a number of postulated synapomorphies (Currie 1987a)—periotic pneumatic cavities, pneumatic cavities associated with the internal carotid, a more medial position for the quadrate condyle than that seen in the larger theropods, a fenestra pseudorotunda, loss of interdental plates, and the presence of a constriction between the crown and root of the teeth. Dromaeosaurids apparently lack the last two features, but the status of the first three cannot be assessed until good dromaeosaurid braincases become available. The taxa Dromaeosauridae, Troodontidae, and Aves are left as an unresolved trichotomy (fig. 1.5) for the present.

Paul (1984a) and Thulborn (1984a) offered rather different cladistic analyses of Theropoda. Paul (1984a) made *Archaeopteryx* the outgroup of Deinonychosauria and birds, since it lacked ten shared characters of the latter two groups. Gauthier (1986) discounts these as inclusive at a lower level in the cladogram or as convergences. Thulborn (1984a) placed dromaeosaurids and *Archaeopteryx* below tyrannosaurids, troodontids, ornithomimids, and birds in his cladogram since they lack a tarsometatarsus with an intercotylar prominence and a hypotarsus (a spur on the tarsometatarsus), metatarsal III that is pinched proximally,

and a straplike coracoid. The distribution of these characters is uncertain in all the relevant taxa, and they appear to be greatly outweighed by the synapomorphies of *Archaeopteryx* and other birds given by Gauthier (1986).

The Sauropodomorpha

The moderate to large herbivores of the Late Triassic and Early Jurassic (the paraphyletic prosauropods) and the large to gigantic herbivores of the Early Jurassic to Late Cretaceous (the sauropods) form a well-defined second major saurischian clade called the Sauropodomorpha. The Sauropodomorpha is characterized (Dodson, this vol.) by a number of synapomorphies (Benton and Norman in prep.):

1. relatively small skull (about 5% of body length)

2. ventrally deflected front of the dentary (Paul 1984a)

3. lanceolate teeth with coarsely serrated crowns (Gauthier 1986)

4. at least ten cervicals (each about twice as long as high), forming a very long neck

5. one to three extra sacral vertebrae, modified from dorsals and caudals

6. enormous pollex with an enlarged claw

7. absence of claws on manual digits IV and V

8. iliac blade with a reduced postacetabular process and a short preacetabular process (the brachyiliac condition: Colbert 1964)

9. fused, deep, apronlike pubes that are twisted proximally

10. very large obturator foramen in the pubis

11. elongate femur (longer than tibia)

12. ascending process of astragalus that keys into tibia, the latter having a matching descending process (Charig et al. 1965)

Various prosauropods form successive outgroups to the Sauropoda (fig. 1.5), roughly in a sequence from *Efraasia* and *Thecodontosaurus* at the base, through *Anchisaurus, Plateosaurus, Massospondylus, Melanorosaurus, Riojasaurus, Vulcanodon,* and *Barapasaurus* (Gauthier 1986; Galton, this vol.). *Anchisaurus* is advanced over *Efraasia* and *Thecodontosaurus* in the possession of an even more robust manual digit I, wide-based neural spines on proximal caudals, an arched dorsal margin of the ilium, and a completely open acetabulum (Gauthier 1986). *Riojasaurus* and higher sauropodomorphs share a compressed internarial process of the premaxilla and large nares, a mandibular condyle placed below the level of the tooth row, robust forelimbs, a broad pes, and numerous other synapomorphies (Gauthier 1986).

The placement of the Sauropoda as the most derived relatives of a paraphyletic Prosauropoda is questioned by Dodson (this vol.) and by McIntosh (this vol.). They suggest that the sauropodomorphs may have branched into two major lineages in the Late Triassic, the Prosauropoda and the Sauropoda. This solution could imply that the sauropods were primitively quadrupedal (e.g., Charig et al. 1965). It would also solve some problems with the scheme presented in figure 3.5. For example, the prosauropods share serrated leaf-shaped teeth and other dental, cranial, and skeletal characters seemingly like those of ornithischians (see below) but quite unlike those of sauropods. Of the twelve synapomorphies of the Sauropodomorpha listed above, three (nos. 2, 4, 8) do not apply to the earliest sauropods.

The Sauropoda (McIntosh, this vol.) are defined by about forty synapomorphies (Gauthier 1986) if the line is drawn below *Vulcanodon* and *Barapasaurus.* These features include the shortening of the caudal portion of the skull, deeply excavated nasals, reduced postorbital, lower temporal fenestra partly beneath the orbit, absence of an epipterygoid, absence of an external mandibular fenestra, twelve or more cervicals, cavernous vertebrae, five or six sacrals, stout metacarpals, a manus with reduced digits, a massive pubis, massive and vertical limbs, solid long bones, and a stout and broad pes.

Sauropods fall into two major lineages, according to Gauthier (1986): the camarasaurs (Camarasauridae, Brachiosauridae) and the titanosaurs (Titanosauridae, Diplodocidae). The camarasaurs are distinguished by a strongly arched internarial bar of the premaxilla, a snout that is sharply demarcated from the rest of the skull, an ischium that extends well posteriorly and twists to become more horizontal distally, and a relatively deep puboischial contact (Gauthier 1986). The Camarasauridae has as possible autapomorphies the slender ascending process of the maxilla and a jugal that is excluded from the lower rim of the skull (McIntosh, this vol.). The Brachiosauridae shares elevated nasals, a relatively elongate forelimb (humerus : femur ratio = 0.90–1.05), and an ilium with a broad anterior lobe (McIntosh, this vol.).

The titanosaurs, if they include *Euhelopus* as a basal outgroup, have as synapomorphies a quadrate that slopes up and back from the mandibular condyle, neural spines that are slightly to deeply bifurcate (also in *Camarasaurus*), and the incorporation of three or more trunk vertebrae into the cervical series (Gauthier 1986). If *Euhelopus* is excluded (McIntosh, this vol.), the titanosaur synapomorphies also include the long broad snout, premaxilla and maxilla extending dorsally to the level of the orbit, internasal processes of premaxilla and nasal reduced or absent, and external nares confluent high on the skull, reduced lacrimal, reduced dorsal process of the quadratojugal and the rostral process contacts the maxilla beneath the orbit, very long basipterygoid processes, elongate pencillike teeth at the very front of the jaws, very tall sacral neural spines, very long tail with long series of cylindrical distal caudals, relatively short forelimbs, and metatarsal IV longer than metatarsal III (Gauthier 1986). The Titanosauridae have as synapomorphies the possession of body armor (also in other sauropods?) and the biconvex first caudal centrum with the others procoelous (Gauthier 1986). The Diplodocidae show modified haemal arches with fore and aft processes, deeply cleft V-shaped neural spines in the shoulder region, and distally expanded ischia (Gauthier 1986).

These synapomorphies are tentative and may be heavily modified when a full cladistic analysis of sauropodomorphs is carried out. McIntosh (this vol.), for example, does not support Gauthier's (1986) analysis of sauropod relationships, preferring a division into two different lineages, camarasaurids plus diplodocids, and titanosaurids plus brachiosaurids. The first lineage has as potential synapomorphies the presence of bifid neural spines, forked chevrons, short metacarpals, absence of the calcaneum, and complete loss of the internal trochanter on the femur, while the titanosaurids and brachiosaurids have low sacral spines, a relatively short radius and ulna, and ischia that meet one another edge to edge distally. Within Sauropoda, then, many taxa are hard to place, and resolution of the cladogram must await fuller information on certain Asian and Gondwanan taxa and a successful splitting up of the basal paraphyletic Cetiosauridae.

The Segnosauria

Segnosaurus and its allies were initially classified (Perle 1979) as aberrant, probably herbivorous, saurischians (Barsbold and Maryańska, this vol.). Paul (1984a, 1984b) placed the Segnosauria midway be-

tween prosauropods and ornithischians on the basis of a cladistic analysis, with the assumption of a nonmonophyletic Saurischia. *Segnosaurus* shares with the Ornithischia a toothless beak, a diastema, cheeks, an opisthopubic pelvis, and a tibia that partly articulates with the pes behind the astragalus. In view of the stronger evidence for a monophyletic Saurischia (see above), *Segnosaurus* might occupy a rather different position on a reanalyzed cladogram of dinosaurs. Indeed, Gauthier (1986) suggests relationship with the sauropodomorphs, and thus interprets the "ornithischianlike" features as convergences, while Dodson (this vol.) and Barsbold and Maryańska (this vol.) regard the Segnosauria as part of an unresolved trichotomy with the Theropoda and Sauropodomorpha.

The Ornithischia

The monophyly of the Ornithischia has been accepted for over a century (Seeley 1888a), and recent cladistic analyses (Maryańska and Osmólska 1984a, 1985; Norman 1984a, 1984b; Sereno 1984, 1986; Cooper 1985; Gauthier 1986) have identified a large number of autapomorphies:

1. rostral tip of the premaxilla toothless and roughened (but not in *Technosaurus*)

2. horizontal or broadly arched palatal process of premaxilla

3. maxilla excluded from the margin of the external naris by a large lateral process of the premaxilla which meets the nasal

4. reduced antorbital fenestra

5. ventral margin of the antorbital fenestra that parallels the maxillary tooth row

6. palpebral in the orbit

7. prefrontal with a long caudal ramus that overlaps the frontal

8. subrectangular quadratojugal lying behind the infratemporal fenestra

9. elongate, massive quadrate

10. predentary bone at the front of the mandible

11. dorsal border of the coronoid eminence formed by the dentary

12. mandibular condyle set below the tooth row (paralleled in most sauropodomorphs)

13. buccal emargination of both upper and lower jaws, suggesting the possession of cheeks

14. cheek teeth with low triangular crowns with a well-developed cingulum beneath

15. crowns of cheek teeth with low and bulbous base; enlarged denticles on the margins

16. adjacent crowns of both maxillary and dentary teeth overlapping (paralleled in part in some sauropodomorphs)

17. recurvature absent in maxillary and dentary teeth

18. maximum tooth size near the middle of the maxillary and dentary tooth rows

19. at least five sacral vertebrae

20. gastralia absent

21. ossified tendons at least above the sacral region

22. opisthopubic pelvis; pubis with small prepubic process

23. ilium with lateral swelling of the ischial tuberosity

24. iliac blade with a long and thin preacetabular process and a deep caudal process

25. pubis with an obturator notch, rather than a foramen; obturator foramen formed between the pubis and ischium

26. distal pubic and ischial symphyses

27. pubic symphysis restricted to its distal end

28. ischial symphysis restricted to its distal end

29. pendant fourth trochanter on the femur

30. fringelike lesser trochanter on the femur

31. digit V of the foot reduced to a small metatarsal with no phalanges

The basal ornithischian *Pisanosaurus*, which is based on incomplete material (Bonaparte 1976, Weishampel and Witmer, this vol.), shows the dinosaurian characters 2, 8, and 9, with 6 doubtfully present (see above). The two additional features seen in *Staurikosaurus* may also be present, and it shares the possession of tibial torsion of "about 90°" (Bonaparte 1976) with all later dinosaurs. *Pisanosaurus* has generally been regarded as the first ornithischian, whether as a basal ornithopod, a fabrosaur, a hypsilophodontid, or a heterodontosaurid. The arguments have centered largely on the nature of the teeth, which display ornithischian attributes 11 through 14 and 17, 18, and possibly 19 (Weishampel and Witmer, this vol.). Other ornithischian autapomorphies cannot be assessed in *Pisanosaurus*: the diagnostic predentary element and opisthopubic pelvis are only assumed by Bonaparte (1976). *Pisanosaurus* is presently regarded as a basal ornithischian.

CLADES WITHIN THE ORNITHISCHIA

Certain groups within the Ornithischia are apparently well supported by synapomorphies, and these will be noted briefly before a review of current views of their overall relationships.

The earliest ornithischians, the Fabrosauridae, are generally regarded as phylogenetically the most primitive (Weishampel and Witmer, this vol.), but they are hard to define cladistically as a family, since only *Lesothosaurus* is reasonably complete. The characters for the family noted by Galton (1978) and Cooper (1985) are primitive.

The Stegosauria (Galton, this vol.) also appear to be a monophyletic clade, all members sharing a large oval fossa in the pterygoquadrate wing, tall neural arches in middle and caudal dorsal vertebrae, a broad cup-shaped laterally facing acetabular surface on the pubis, loss of pedal digit I, prominent upright midline plates on the neck and back grading backward into spines, a lateral spine over each shoulder, and lack of ossified epaxial tendons (Sereno 1986).

The Ankylosauria (Coombs and Maryańska, this vol.) are similarly well defined as a monophyletic group by as many as twenty-six synapomorphies (Sereno 1986), including the rectangular occiput, closed antorbital and supratemporal fenestrae, contact of the quadratojugal and postorbital, fusion and dermal sculpturing of the dorsal skull roof, at least three dorsal vertebrae incorporated into the sacrum, fused scapula and coracoid, closed acetabulum, and dorsal and lateral armor of bone plates.

The Heterodontosauridae (*Abrictosaurus, Heterodontosaurus, Lycorhinus*) are distinguished from other ornithischians by the presence of three premaxillary teeth with no distinction between the root and the crown, reduced mesial two dentary teeth with no tubercles, wedge-shaped predentary, proximal head of humerus offset medially, relatively long manus, metacarpals with blocklike proximal ends, slender fibula, and extensor pits at the distal ends of proximal phalanges of pes digits II-IV (Sereno 1986; Weishampel and Witmer, this vol.).

The Hypsilophodontidae (*Hypsilophodon, Othnielia, Yandusaurus, Zephyrosaurus*) are also regarded as a monophyletic taxon by most authors (Sues and Norman, this vol.) on the basis of their shared narrow interorbital position of the frontal, premaxillary diverticulum, and steeply sloping ventral braincase region (Sereno 1986). If *Thescelosaurus* is also included in this clade, they all share a short scapula, partial ossification of sternal segments of the ribs, a rod-shaped prepubic process, and ossified hypaxial tendons in the tail (Sereno 1986).

Among other ornithopods, the Dryosauridae and Iguanodontidae are problematic. These are regarded as monophyletic groups by Norman (1984*a*) and Milner and Norman (1984) but less confidently by Norman (1984*b*). In this latter account, and Norman and Weishampel (this vol.), the two families are placed in an "iguanodontoid" clade, characterized by a large, median vertical ridge on the crowns of maxillary teeth, contact between the premaxilla and lacrimal, a distinct notch in the jugal wing of the quadrate, and a rodlike decurved ischium with a distal foot. The genera *Camptosaurus, Iguanodon,* and *Ouranosaurus* are grouped on the basis of multiple ridging of their dentary tooth crowns, and their shared robust manus, with fused carpals, metacarpal I fused to the radiale, and development of a spurlike manual digit I. The last two genera are further paired (Iguanodontidae) on the basis of the spiked pollex, the platelike first phalanx of manual digit I, the short postpubic ramus, and the reduced pedal digit I. Most authors now accept that the families Dryosauridae and Iguanodontidae, as commonly understood, are paraphyletic, forming a sequence of outgroups to Hadrosauridae, in a sequence from *Tenontosaurus,* through *Dryosaurus, Camptosaurus, Iguanodon,* and *Ouranosaurus,* as closest outgroup (Sereno 1984, 1986), or *Probactrosaurus* as closest outgroup (Sues and Norman, this vol.; Norman and Weishampel, this vol.).

The Hadrosauridae have been regarded as monophyletic by most authors (e.g., Norman 1984*a*, 1984*b*; Sereno 1984, 1986; Cooper 1985) on the basis of their well-developed dental magazines, lozenge-shaped teeth, displacement of the antorbital fenestra, loss or fusion of the palpebral, loss of the paraquadrate foramen, loss of manual digit I, loss of metatarsals I and V, and a large antitrochanter on the ilium (Milner and Norman 1984; Weishampel and Horner, this vol.). In addition, a large number of synapomorphies are shared with the successive dryosaur and iguanodont outgroups (Sereno 1986; Weishampel and Norman, this vol.). Horner (1985, in press), however, has questioned this view, arguing for close relationships of the lambeosaurine hadrosaurs with *Ouranosaurus.* His fourteen postulated synapomorphies (chap. 2) are fewer than those supporting Sereno's (1986) scheme, and some are probably plesiomorphous (e.g., high neural spines and massive ischium in lambeosaurines and *Ouranosaurus,* versus low neural spines and slender ischium in hadrosaurines and *Iguanodon*).

The Pachycephalosauria (Maryańska, this vol.) are defined by the thickened frontoparietal skull roof, broad expansion of the squamosal on the skull roof, tubercular ornamentation of the skull, elongate sacral ribs, very long ribs on proximal caudal vertebrae, relatively short forelimb, slender scapula, reduced deltopectoral crest, pubis nearly excluded from the acetabulum, and sixteen more postulated synapomorphies (Sereno 1986).

Finally, the Ceratopsia (Dodson, this vol.) all share a triangular skull in dorsal view, a median rostral bone, a tall snout with external nares highly placed, broad parietals, and other cranial features. The characteristic horns and frills are, of course, absent in psittacosaurs and are thus synapomorphous higher in the cladogram, defining the Neoceratopsia (Dodson and Currie, this vol.). Within the Neoceratopsia, two families, the Protoceratopsidae and Ceratopsidae, have generally been recognized. However, the diagnostic characters of Protoceratopsidae are primitive, or common to all neoceratopsians, and Sereno (1986) has argued that the Protoceratopsidae is a paraphyletic group.

RELATIONSHIPS WITHIN THE ORNITHISCHIA.

Although the monophyly of the Ornithischia is not questioned, relationships of the taxa within that clade are controversial. So far, five cladograms of the Ornithischia have been published, by Maryańska and Osmólska (1984*a*, 1985), by Cooper (1985), by Norman (1984*a*, 1984*b*; Milner and Norman 1984; Norman and Weishampel 1985), by Sereno (1984, 1986), and by Weishampel and Witmer (this vol.). Additional comments along these lines have also been made by Gauthier (1986, 44). These cladograms agree generally in some features—the grouping of Ankylosauria, Stegosauria, and possibly *Scelidosaurus* and *Scutellosaurus* as Thyreophora (see Coombs et al., this vol.) and the grouping of most ornithopods in the sequence of the Hypsilophodontidae, to the Dryosauridae, to the Iguanodontidae, and finally to the Hadrosauridae (see above). However, the placement of the Fabrosauridae, Heterodontosauridae, Pachycephalosauridae, and Ceratopsia is disputed. The four main proposals for ornithischian phylogeny by Maryańska and Osmólska (1985), Cooper (1985), Norman (1984*a*), and Sereno (1986) are compared in figure 1.6.
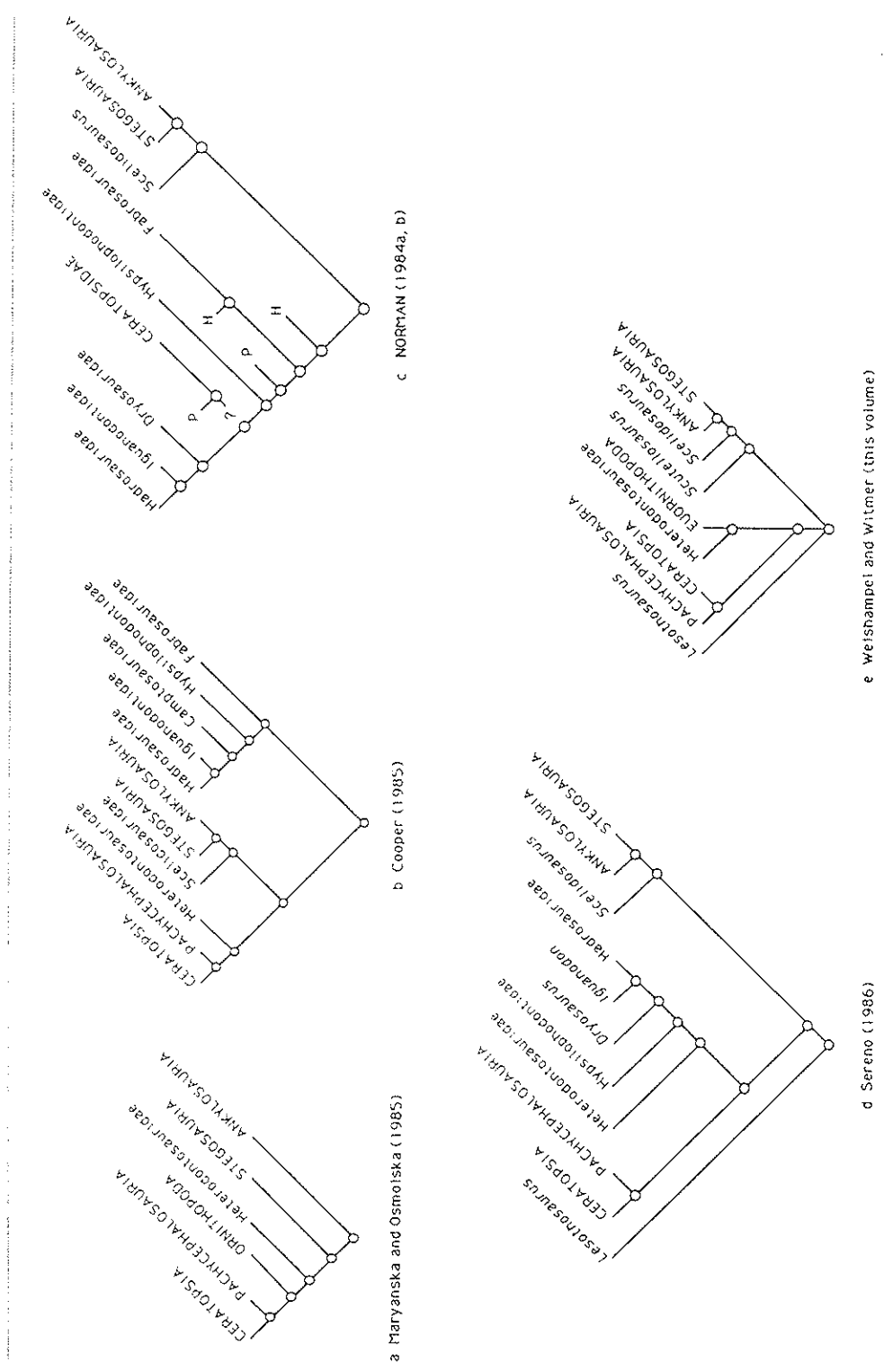
Fig. 1.6. Five cladograms depicting alternative hypotheses of the phylogenetic relationships of the Ornithischia: a. after Maryańska and Osmólska (1985); b. after Cooper (1985); c. after Norman (1984a, 1984b); d. after Sereno (1986); e. after Weishampel and Witmer (this vol.). In c, H = Heterodontosauridae; P = Pachycephalosauria.

The ankylosaurs, stegosaurs, *Scelidosaurus*, and possibly *Scutellosaurus*, all appear to fall into a clade termed the Thyreophora (Norman 1984a; Sereno 1984, 1986; Coombs et al., this vol.). If *Scutellosaurus* is omitted, this clade has as synapomorphies the sinuous curve of the dentary tooth row, the incorporation of a supraorbital bone into the skull roof between the frontal, postfrontal, and postorbital, the relative robustness of the medial portion of the quadrate condyle, a much shortened basisphenoid, and a tall midpalatal keel formed from the pterygoid and vomer. With the addition of *Scutellosaurus* (Thyreophora *sensu* Sereno 1986), the synapomorphies are transversely broad jugal-orbital bar, and parasagittal row of low-keeled scutes on the dorsal body surface with additional rows of lateral low-keeled scutes. Note that Maryańska and Osmólska (1984a, 1985) did not support Thyreophora but made Ankylosauria the sister group of the Stegosauria and all other ornithischians that share a perforate acetabulum. They noted that acceptance of this postulated synapomorphy was contingent on the acceptance of a nonmonophyletic Dinosauria. Since dinosaurian monophyly is now generally accepted, polarity of the acetabulum reverses and the imperforate acetabulum of the Ankylosauria becomes the derived state. This shift has the effect of falsifying the basal dichotomies in figure 1.6a.

The composition of the Ornithopoda is disputed. Santa Luca (1980) recognized the problem of including basal taxa such as fabrosaurs and heterodontosaurs. He suggested that there were two main ornithopod clades, one consisting of hypsilophodonts and fabrosaurs and one of iguanodonts and hadrosaurs. This view has not been accepted by later authors. Norman accepts the Fabrosauridae as the basal taxon of the Ornithopoda + Ceratopsia, while Sereno (1984, 1986) and Gauthier (1986) see this as a paraphyletic group. They regard *Lesothosaurus* as the only adequately known relatively complete fabrosaur and place it as the sister group of all later ornithischians, the Genasauria. The latter was ascribed a number of synapomorphies by Sereno (1986), which Weishampel and Witmer (this vol.) accept. In contrast, Maryańska and Osmólska and Cooper include *Lesothosaurus* in their Ornithopoda. The Heterodontosauridae have been interpreted as the sister group to the Cerapoda (Norman 1984a, 1984b; Maryańska and Osmólska 1985), to the Marginocephalia (Cooper 1985), or to the Ornithopoda (Sereno 1986; Weishampel and Witmer, this vol.).

All of the above authors, except for Cooper, group the Ornithopoda and Ceratopsia together, although their interpretations of Ornithopoda differ, and some also include Pachycephalosauria. This clade has been termed Cerapoda by Sereno (1986), who notes several synapomorphies: premaxillary/maxillary diastema, asymmetrical enamel on the cheek teeth, no more than five premaxillary teeth, a fingerlike lesser trochanter, a fully open acetabulum with no supraacetabular crest, and other features. Cooper (1985) places Ceratopsia in a line with heterodontosaurs and Thyreophora, separate from his Ornithopoda.

The placement of the Pachycephalosauria and Ceratopsia is still rather uncertain. Maryańska and Osmólska (1984a, 1985), Sereno (1984, 1986), Cooper (1985), and Gauthier (1986) all pair the Ceratopsia with the Pachycephalosauria, in a clade that Sereno (1986) names the Marginocephalia. The basis for this relationship includes the narrow parietal shelf that extends over the occipital elements, involvement of the squamosal in this shelf, a reduced premaxillary contribution to the palate, and a relatively short pubis (Sereno 1986). Norman (1984a) notes an alternative position for the Pachycephalosauria in association with basal ornithopods (fig. 1.6b), but this is based only on the primitive nature of their respective dentitions. He includes the Ceratopsia within his Ornithopoda, possibly grouped with the Hadrosauridae, Iguanodontidae, and Dryosauridae (fig. 1.6b), since they all share a reduced antorbital fenestra, maxillary teeth with sharp median ridges, distal dentary teeth lying medial to the coronoid process, and a strengthened predentary-dentary joint. Later, Norman (1984b) excluded the Ceratopsia and Pachycephalosauria from the Ornithopoda because they lack an obturator process on the ischium.

Alternative Arrangements within Dinosauria

The monophyly of Saurischia has been defined above, but a number of authors have presented a radical alternative in which the Sauropodomorpha is paired with the Ornithischia and the Theropoda are separated as the sister group of this new taxon. The third possible hypothesis of relationships, a sister group relationship between theropods and ornithischians, has not been seriously proposed and is very hard to support (Gauthier 1986). The pairing of sauropodomorphs and ornithischians was hinted at by Bakker and Galton (1974) and Bonaparte (1976), while Paul (1984a, 1984b) and Cooper (1985) have presented this view cladistically. Cooper (1981a, 1985), Paul (1984a, 1984b), and Sereno (1984) noted several apparent synapomorphies shared by the Sauropodomorpha (or Prosauropoda alone) and the Ornithischia:

1. tooth crown a transversely flattened blade with denticulate margins; a leaf-shaped spatulate tooth

2. differentiation of the tooth crown shape from the front backward, the mesial teeth being peglike and the distal ones more leaf-shaped

3. teeth set at an angle to the longitudinal axis of the jaws, and the distal edge of each tooth overlapping the anterior edge of the tooth behind

4. depressed jaw joint

5. reduced parietal

6. low occiput

7. elongate vomer

8. elongate preacetabular process on ilium

The dental similarities between sauropodomorphs and ornithischians (characters 1–3), in particular those in primitive forms, are striking. There are differences in the cheek teeth in both groups: the crowns are elongate in sauropodomorphs, but low in ornithischians, and the serrations are fewer and larger in ornithischians than in sauropodomorphs (Charig 1976), but this does not demonstrate that both forms were independently derived (Gauthier 1986). Characters 4–7 are less clear-cut (Gauthier 1986). The depressed jaw joint (character 4) is typical of many herbivores, and it is not seen clearly in basal sauropodomorphs like *Anchisaurus* and *Thecodontosaurus*. The parietals are reduced (character 5) in basal theropods. The occiput is not markedly lower (character 6) in sauropodomorphs or ornithischians than it is in theropods. The vomer is just as long (character 7) in theropods as it is in sauropodomorphs or ornithischians. Last, the elongate iliac prong (character 8) is seen only in *Anchisaurus* and *Ammosaurus* among sauropodomorphs and not in the basal forms· *Efraasia* and *Thecodontosaurus*. The three dental characters (1–3) stand as the only potential synapomorphies in favor of a clade consisting only of the Sauropodomorpha and the Ornithischia, and they are far outweighed by the autapomorphies of the Saurischia.

THE FUTURE

The cladistic revolution in classification of the Dinosauria has only just begun, with publications dating essentially only from 1984. Already, however, a number of areas of stability have seemingly become clear: the monophyly of Archosauria; the split of Archosauria into a "bird line" and a "crocodilian line"; the close association of Ornithosuchidae, *Lagosuchus*, Pterosauria, and Dinosauria; the monophyly of Dinosauria, Sauropodomorpha, Theropoda, and Ornithischia; the positioning of Aves within Theropoda; and some general features of the relationships of major groups within Ornithischia (Ornithopoda, Thyreophora).

A great deal of work is still required, however, to address a broad range of key problems at the base of cladogram—the position of *Euparkeria*, the exact relationships of *Lagosuchus*, Pterosauria, and Dinosauria, and the arrangement of basal dinosaurian taxa. All of these problems are presently hard to solve because of poorly preserved material (many key taxa lack crucial evidence of distinguishing characters) and because of the great subsequent modifications of pterosaurs, and many dinosaurian groups, which may conceal potential synapomorphies.

Within Dinosauria, the controversy over the origin of birds has finally resolved itself in favor of Theropoda, but the relationships of theropod groups to birds, and to each other, are still unresolved. Key questions include the definitions of Dromaeosauridae and Troodontidae, and their relationships to Aves, the relative position of maniraptoran taxa that vie for positions on the cladogram close to Aves, whether below or within that taxon. Basal theropods, such as Ceratosauria and Carnosauria may be easier to resolve because the material is often of better quality. The arguments over the relationship of birds to terminal theropods will continue for some time since the material is often poor, and the characters (largely braincase and vertebral features) require exquisitely preserved specimens for determination.

The Sauropodomorpha still require a phylogenetic analysis. Some general outlines toward a cladogram are noted by Gauthier (1986: 44–45) and by Dodson, Galton, and McIntosh (this vol.). The idea of a paraphyletic Prosauropoda forming outgroups to a monophyletic Sauropoda seems clear, but the exact sequencing of prosauropod taxa and the relationships within Sauropoda have not yet been analyzed in detail. Crucial in the latter will be the breakup of the basal Cetiosauridae into several lineages.

The Ornithischia have so far, among dinosaurs, been favored with the greatest number of cladistic analyses, involving as many as ten authors to date. These studies have shown general agreement over the division of the Ornithischia broadly into an ornithopod clade and a thyreophoran clade. Basal taxa, such as fabrosaurs and scelidosaurs, have historically been hard to place, partly because of limited fossil material and partly because of incomplete descriptions of what

exists. The relationships of ceratopsians and pachycephalosaurs, whether within the ornithopod clade or as an outgroup to it, are still to be decided. Other problems concern the genetic-level phylogeny within Ornithopoda (the relationships of dryosaurs, iguanodonts, and hadrosaurids) and within the armored ornithischian clades.

Dinosaur systematists have made significant advances in recent years as a result of the application of cladistic methods. For the first time, paraphyletic basal taxa have been widely abandoned, problems in phylogenetic placement have been explicitly stated, new characters have been analyzed, and some novel, but convincing, patterns of relationship have emerged. The revolution we are currently witnessing marks the beginning of an exciting new era of clarity and precision in attempts to unravel the patterns of dinosaurian evolution. Whether the conclusions shown here are right or wrong, it is now possible to specify problems and conflicts, to sort out significant character transformations, and to erect a firm baseline for robust and innovative evolutionary discussion, which is, after all, why we are in the business of paleobiology.

References not included, since they are gathered in a single reference list in the book(pp. 619-681).

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