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Paul C. Sereno

Phylogeny of the Bird-hipped Dinosaurs (Order Ornithischia)

Approximately half of existing dinosaur species belong to the Order Ornithischia, or the "bird-hipped" dinosaurs, which include such familiar forms as the stegosaurs (plated dinosaurs), ankylosaurs (armored dinosaurs), hadrosaurs (duck-billed dinosaurs), and ceratopsids (horned dinosaurs). Although ornithischians are generally conceded to have descended from a common ancestor, little is known about the pattern of descent. Comparison of more recently discovered ornithischian fossils from China and Mongolia to better-known North American forms has shed light on the pattern of evolutionary diversification among ornithischians, a pattern that began approximately 200 million years ago and ended abruptly nearly 140 million years later at the end of the Cretaceous.

More than any other fossil group, with the possible exception of hominids, dinosaurs stir the popular imagination. Despite significant popular interest, paleontologists have not established with any surety the evolutionary relationships among the many kinds of dinosaurs. In fact a satisfactory scientific definition that would encompass all animals collectively referred to as "dinosaurs" has yet to be formulated. An effective definition would specify the unique, or derived, characteristics shared by the entire group — characteristics that presumably arose in the common dinosaur ancestor and were inherited by the descendants.

Traditionally dinosaurs have been divided on the basis of hip morphology into two groups of approximately equal size: the Order Saurischia, in which the pelvic elements are arranged in a triradiate configuration, and the Order Ornithischia, in which the pubic bone has rotated posteriorly to lie alongside the ischium in a birdlike configuration (Figure 1). Ornithischian dinosaurs include such familiar forms as the stegosaurs (plated dinosaurs), ankylosaurs (armored dinosaurs), hadrosaurs (duck-billed dinosaurs), pachycephalosaurs (thick-headed dinosaurs), and ceratopsids (horned dinosaurs) (Figure 2).

Since the earliest classifications of dinosaurs over a century ago (e.g., Cope 1866), the overriding consensus has been that ornithischians have descended from a common ancestor and thus represent a monophyletic, or natural, group. Despite acknowledgment of common ornithischian ancestry, the unique aspects of ornithischian morphology — upon which the argument for common ancestry is based — have not been clarified, and the phylogenetic relationships among major subgroups of ornithischians remain largely unsolved.

Recently deposits in Mongolia and China have added significantly to

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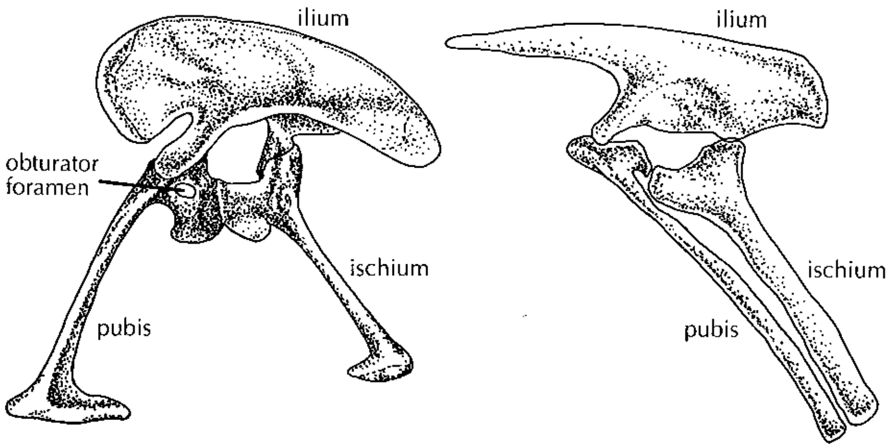


Figure 1. Dinosaur pelvis in lateral view: left, *saurischian pelvis* (Ceratosaurus, *after Gilmore 1920);* right, *ornithischian pelvis* (Scelidosaurus, *after Charig 1972).*

the understanding of ornithischians (Dong 1973; Dong, Li, et al. 1977; Dong, Tang, & Zhou 1982; Dong, Zhou, & Zhang 1983; He & Cai 1983, 1984; Hou 1977; Hu 1973; Maryańska 1977; Maryańska & Osmólska 1974, 1975, 1981; Tumanova 1977, 1981; Zhou 1983, 1984). Basing the assessment of phylogenetic affinity on the pattern of derived morphologic characters, the present study advances a testable hypothesis for the phylogenetic relationships within the Order Ornithischia.

The Order Ornithischia

Before attempting to resolve ornithischian phylogeny, evidence must first be secured that the Order Ornithischia does indeed constitute a monophyletic taxon. Coined by Seeley in 1887, the Order Ornithischia has persisted to the present day as a valid taxonomic unit principally because historic definitions of the order specify characteristics unique to ornithischians. Over a century ago Cope (1870) recognized the unusually elongate and narrow preacetabular process of the ilium. Shortly thereafter, Seeley (1887) observed the characteristic biramus pubis; Baur (1891), the predentary bone and strong posterodorsal process of the premaxilla; and Marsh (1895), the ossified palpebral. More recently Romer (1956:624–626) noted additional derived ornithischian characters including the "leaf-shaped" tooth crown, relatively smaller antorbital fenestra, ossified tendons along the vertebral column, and absence of gastralia. These derived characters establish the Order Ornithischia as a natural taxonomic grouping. Unfortunately previous diagnoses of the Ornithischia mix these defining characters with numerous primitive characters common to saurischians or other tetrapods.

The present study clarifies the derived morphologic traits common to ornithischians (Figure 2, node 1; Table 1). In all ornithischians a horny bill encased at least the anterior margin of both lower and upper jaws, as indicated by the rough external surface of the predentary and anterior portion of the premaxilla, respectively. At the anterior end of the upper jaw, all ornithischians have a toothless border that spans the width of at least one alveolus, in contrast to the tooth row in saurischians, which continues anteriorly to the midline. The toothless border is well preserved in one of the earliest ornithischians, *Lesothosaurus* (British Museum [Natural History], London, R8501; University College, London, B.17; Thulborn 1970:Figure 6A), but has been incorrectly shown as dentigerous in the palatal reconstruction of Thulborn (1970:Figure 8F).

The antorbital fossa, a smooth-walled depression surrounding the

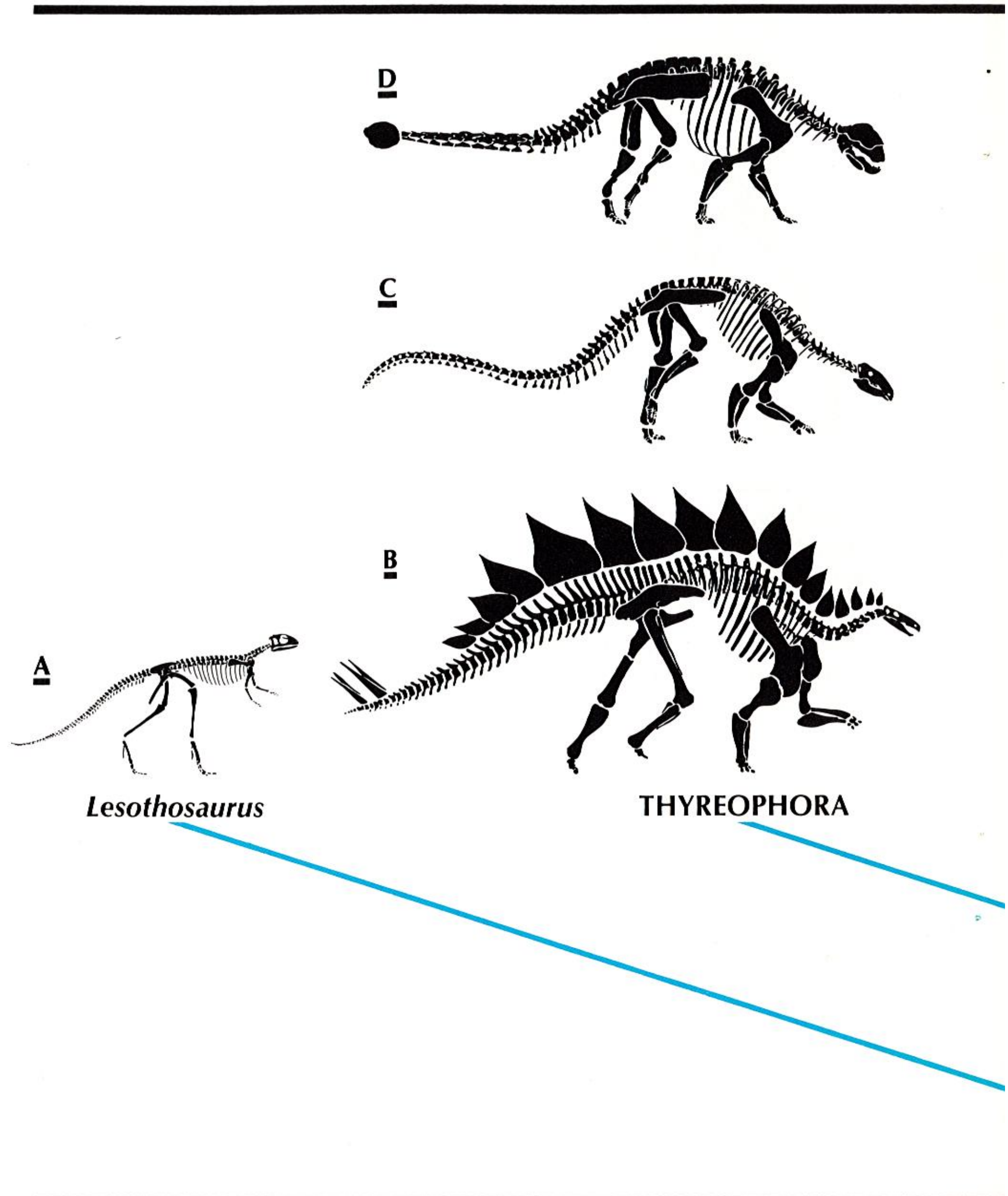
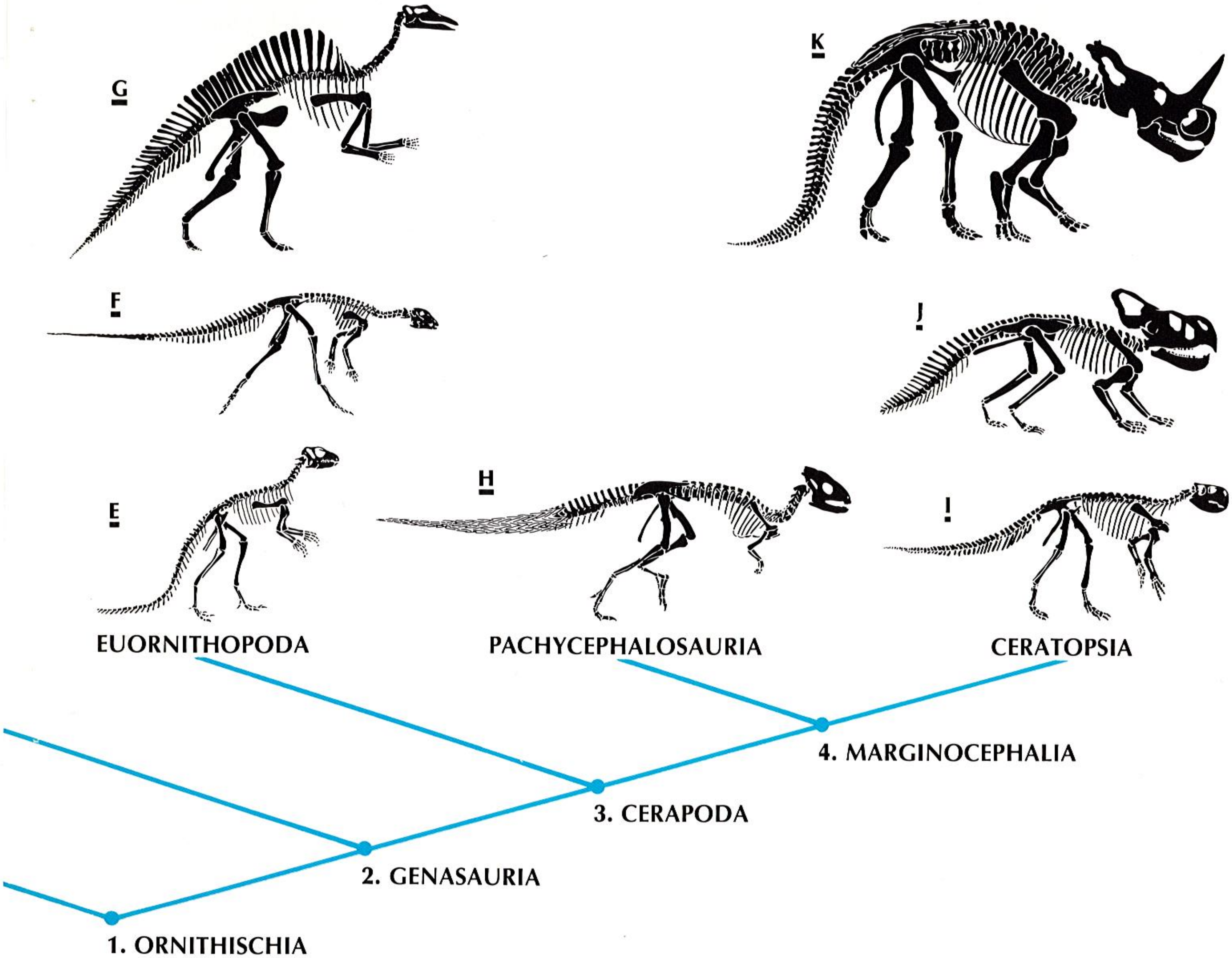


Figure **2.** *Phylogenetic relationships of the major subgroups of ornithischians. Characters in support of nodes 1 through 4 are listed in Table 1.* **A,** Lesothosaurus *(after Thulborn 1972);* **B,** Stegosaurus; **C,** Sauropelta *(after Carpenter 1984);* **D,** Euoplocephalus *(after Carpenter 1982);* **E,** Heterodontosaurus *(after Santa Luca 1980);* **F,** Hypsilophodon *(after Galton 1974);* **G,** Ouranosaurus *(after Taquet 1976);* **H,** Homalocephale *(after Paul unpublished);* **I,** Psittacosaurus *(after Osborn 1924);* **J,** Protoceratops; **K,** Centrosaurus *(after Brown 1917).*

antorbital fenestra, is reduced in size in all ornithischians as compared with most saurischians and more primitive archosaurs; the anterodorsal margin of the fossa does not extend to the maxilla–nasal suture, and the ventral margin of the fossa runs horizontally, parallel to the maxillary alveolar border, rather than angling posteroventrally to intersect the border posteriorly.

In the ornithischian postcranium, the most remarkable modification involves the pubis (Figure 1). The pubic shaft, which projects anteroventrally primitively, has rotated to a posteroventral orientation, which has occurred independently in segnosaurs and some advanced theropods including birds (Barsbold 1979). In ornithischians the pubic shaft is slender and rod-shaped, the pubic symphysis restricted to the distal end. Beneath the acetabulum, the proximal base of the pubis joins the ischium to form the puboischial plate. Primitively the puboischial plate is broad with an obturator foramen piercing the base of the pubis. In ornithischians, in contrast, the puboischial plate is markedly reduced in dorsoventral height, and the obturator foramen is located between the pubis and the ischium.



Joan A. Wolbier

Ornithischian Phylogeny

The Problem

In considerations of ornithischian phylogeny, the analysis of morphology has taken second seat to the construction of the phylogenetic tree. Based on little, if any, evidence, a general concept of ornithischian evolution has emerged; it proposes that the major subgroups diverged along many independent lineages from either a hypsilophodont (Romer 1968, Thulborn 1971) or fabrosaur stem group (Galton 1972), with separate and perhaps more remote origins for stegosaurs and ankylosaurs. Current classifications reflect the absence of phylogenetic resolution by listing ornithischian subgroups serially (Romer 1956, 1966; Steel 1969).

Recent work has rephrased the problem of ornithischian relations in cladistic terms, in which derived characters are listed in support of a particular branching pattern (Cooper 1985; Gauthier in press; Maryańska & Osmólska in press; Milner & Norman 1984; Norman 1984a, b; Sereno 1984). These hypotheses differ profoundly in the supporting morphologic data and nature of the terminal taxonomic units.

The General Pattern

The diagram in Figure 2 and accompanying data in Table 1 outline a scheme of relationships for the major subgroups of ornithischians. *Lesothosaurus,* a small-bodied ornithischian from the Lower Jurassic of South Africa, appears to be the most primitive ornithischian described to date. All other ornithischians share a more recent common ancestry as evidenced by several derived characters that are present primitively in all ornithischian subgroups but are absent in *Lesothosaurus* (Figure 2, node 2; Table 1).

An outstanding characteristic of ornithischians more advanced than *Lesothosaurus* is the development of a buccal emargination along the maxilla such that the maxillary tooth row is inset medially from the lateral surface of the face (Figures 4, 7, 8). This emargination — the ornithischian cheek (Galton 1972, Romer 1956) — is absent or extremely weakly developed in *Lesothosaurus* and saurischians, but is present in virtually all other ornithischians, including the primitive thyreophoran *Scutellosaurus* (Museum of Northern Arizona, Flagstaff, Pl.175; Museum of Comparative Zoology, Cambridge, 8797; contra Colbert 1981:10).

A rounded, spout-shaped mandibular symphysis and at least a moderate coronoid process also characterize all ornithischians except *Lesothosaurus,* in which the mandibular rami join at an acute angle and the coronoid process is very low as in saurischians. Ankylosaurids are alone among more advanced ornithischians to have secondarily reduced the coronoid process.

Postcranially all ornithischians more advanced than *Lesothosaurus* have reduced the relative size of the pubic peduncle of the ilium and have shifted the fourth trochanter to a relatively more distal position on the shaft of the femur.

Separating *Lesothosaurus* as the most primitive ornithischian, what phylogenetic pattern is most consistent with morphologic data from the remaining ornithischians? The great diversity of remaining ornithischians can be divided into two major groups: the armored thyreophorans, consisting of the stegosaurs, ankylosaurs, and near relatives; and a more diverse group of ornithopods, pachycephalosaurs, and ceratopsians.

Thyreophora

The taxon Thyreophora, erected by Nopcsa (1915), is restricted here to include only the stegosaurs, ankylosaurs, and Lower Jurassic *Scelidosaurus* and *Scutellosaurus* (Figure 2) (Gauthier in press). Body armor, to which the group name refers, is the most striking character of these dinosaurs. Primitive thyreophoran armor appears to have consisted of parasagittal and lateral rows of low, keeled scutes, which have been greatly modified in proportion in later stegosaurs and ankylosaurs. The most primitive thyreophoran, *Scutellosaurus,* is of great interest but, unfortunately, remains poorly known. Recently discovered material of *Scutellosaurus* reveals that, unlike more advanced thyreophorans, the frontal forms the dorsal rim of the orbit without any accessory supraorbital elements. Importantly, the ischium lacks an obturator process (Museum of Comparative Zoology, Cambridge, 8801), the presence of which was suggested by Colbert (1981:Figure 23A, B).

Although an articulated skeleton of *Scelidosaurus* has been known for over a century (Owen 1861, 1863), its phylogenetic affinity has remained problematic. *Scelidosaurus* has been referred on various occa-

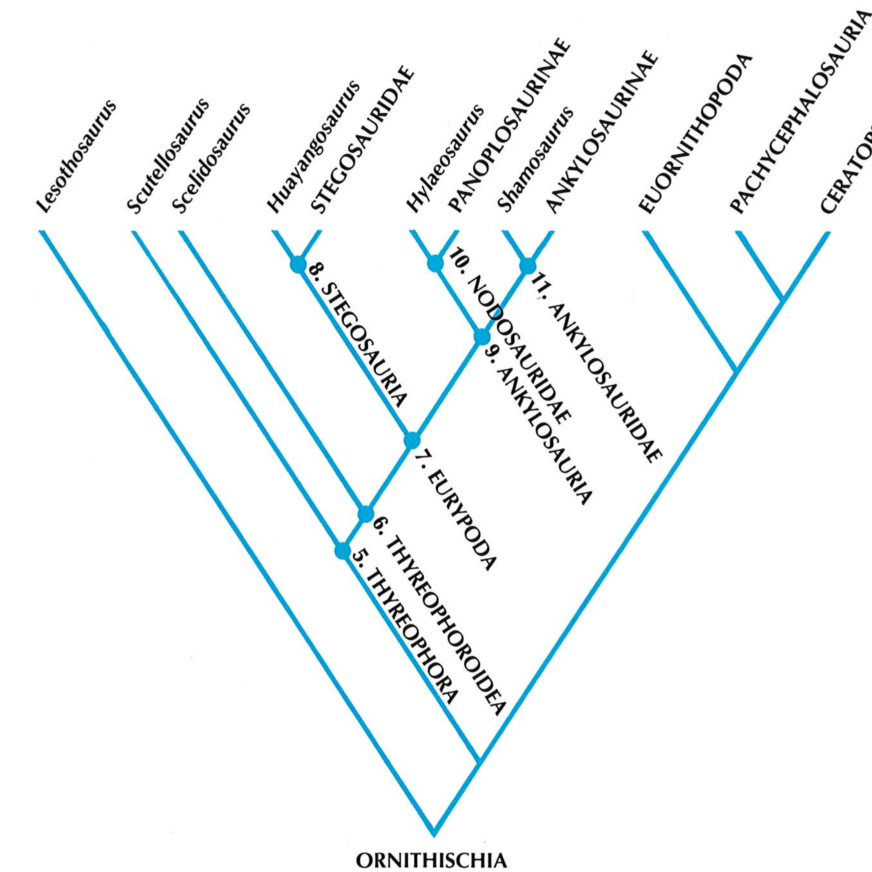


Figure 3. Phylogenetic relationships within the Thyreophora. Characters in support of nodes 5 through 11 are listed in Table 1.

sions to the Stegosauria, Ankylosauria, and Ornithopoda, but is more appropriately regarded as the sister taxon to the stegosaurs and ankylosaurs within the Thyreophora (Figure 3, node 6). In the skull of *Scelidosaurus*, an ovate supraorbital bone forms the lateral portion of the orbital roof (Owen 1861:Plate 6, Figure 1). In this position, it excludes the frontal from the orbital margin and separates the prefrontal and postorbital. A supraorbital element (misidentified as the prefrontal), very similar in shape and position to that of *Scelidosaurus*, is incorporated into the orbital roof of *Huayangosaurus* (Zhou 1984:Figure 2), *Stegosaurus* (Gilmore 1914:Plate 6), and the ankylosaurid *Pinacosaurus* (Maryańska 1977:Figure 2A1). No other ornithischian has a supraorbital with these sutural relations, and it thus appears to be a derived character uniting *Scelidosaurus*, stegosaurs, and ankylosaurs. Two additional derived cranial characters for this group include the asymmetrical quadrate condyle and the proportions of the ventral braincase elements. The medial portion of the quadrate condyle is broadened relative to the lateral side; in the braincase, the basisphenoid is noticeably shorter in anteroposterior length than the basioccipital.

The current research introduces substantial evidence in favor of common ancestry for the stegosaurs and ankylosaurs within the Thyreophora (Figure 3, node 7; Table 1) (Sereno 1984). Cranially two additional supraorbital elements have been added to the orbital roof (Figure 4). The quadrate of a stegosaur or ankylosaur is quickly identified by the absence of the primitive lateral ramus; the shaft and pterygoid ramus of the quadrate lie in a single plane. Postcranially the ilium is unmistakable, the preacetabular process greatly lengthened and directed

Table 1. Characters in Support of the Phylogenetic Arrangements Shown in Figures 2, 3, and 6*

1. ORNITHISCHIA

Dental

- Low, triangular-shaped tooth crowns in lateral view
- Recurvature absent in M and D teeth
- Well-developed neck separating crown from root
- Overlap of adjacent crowns in M and D teeth
- Maximum tooth size attained near the central, or posterior central, portion of the M and D tooth rows

Cranial

- Ossified palpebral
- Anterior tip of the PM roughened and edentulous
- Horizontal or broadly arched PM palate
- Strong PM posterodorsal pr. on the lateral aspect of the face, excluding the M from the margin of the external nares
- QJ anterior pr. relatively shorter; tall straplike shape
- QJ anterior ramus broader than the dorsal ramus
- Ventral margin of antorbital fossa parallels M tooth row
- Antorbital fossa relatively smaller; separated from M–N suture
- Antorbital fenestra relatively smaller
- PF with long posterior ramus overlapping the dorsal surface of the F
- Predentary
- Anterior coronoid margin formed by the posterodorsal pr. of the D

Postcranial

- At least five sacral vertebrae
- Iliac preacetabular pr. elongate and dorsoventrally narrow
- Pubis directed posteroventrally (= postpubic pr.)
- Shaft of pubis consisting of an elongate, slender rod
- Pubic symphysis restricted to the distal end
- Distal puboischial symphysis
- Proximal puboischial plate relatively narrower dorsoventrally
- Pubis with obturator notch, rather than foramen; obturator foramen formed between pubis and ischium
- Pubis with transversely flattened prepubic pr.
- Ischial symphysis restricted to the distal end
- Distally expanding, ventromedially angling, bladelike ischial shaft
- Flat lateral surface of the greater trochanter broader anteroposteriorly
- Pendant fourth trochanter
- Pes digit V consisting of a metatarsal splint; phalanges absent
- Ossified epaxial tendons

2. GENASAURIA

Cranial

- Cheeks; M dentition offset medially
- Spout-shaped mandibular symphysis
- Moderate coronoid process
- Edentulous anterior portion of the PM
- Entire margin of the antorbital fossa sharply defined or extended as a secondary lateral wall enclosing the fossa
- External mandibular foramen relatively smaller

Postcranial

- Pubic peduncle of ilium relatively less robust than ischial peduncle

3. CERAPODA

Cranial

- Significant diastema between PM and M teeth
- Asymmetrical enamel in cheek teeth: thicker on medial side of D teeth and lateral side of M teeth
- No more than five PM teeth
- PD equals length of opposing PM surface; PM teeth articulate only with PD

Postcranial

- Fingerlike lesser trochanter closely applied to the greater trochanter
- Fully open acetabulum; iliac ventral acetabular flange absent
- Iliac supraacetabular rim absent
- Laterally protruding ischial peduncle of the ilium

4. MARGINOCEPHALIA

- Anteroposteriorly narrow P shelf, extending over the occiput, filling the posteromedian embayment of the skull roof, and obscuring the occipital elements in dorsal view
- Lateral portion of the posterior shelf of the skull roof formed by the SQ
- Posterior PM palate relatively short; M exclude PM from the border of the internal nares
- Postpubic pr. relatively very short; pubic symphysis absent

5. THYREOPHORA

- J orbital bar with transversely broad orbital rim; transversely broader than dorsoventrally tall
- Parasagittal row of keeled scutes on dorsal body surface
- Lateral rows of low keeled scutes on dorsal body surface

6. THYREOPHOROIDEA

- Sinuous curve to D tooth row in lateral view
- One SORB completely incorporated into the orbital roof, contacting the F, separating the F from the margin of the orbit, and intervening between the PF and PO
- Medial portion of Q condyle much more robust than lateral portion
- BS markedly shortened in length relative to the BO
- Median palatal keel in mid-palate; PT, and especially V, vertically tall

7. EURYPODA

Cranial

- Two lateral SORB form the dorsal margin of the orbit
- Q condyle angled strongly ventromedially
- Q shaft not laterally distinct from the pterygoid ramus
- Otic notch between the Q and paroccipital pr. absent
- Vertical median portion of the PT palatal ramus developed posteriorly; median palatal keel extends to the posterior end of the palate
- EO border of the foramen magnum with short recessed section on each side; SO and dorsal portion of the EO border overhang the recess from above, and the occipital condyle floors the recess from below
- Symphyseal portion of the D very slender relative to the D ramus at midlength

Postcranial

- Fusion of the neural arches of the atlas to the atlar intercentrum
- Scapular blade with parallel dorsal and ventral borders; distal expansion of the blade minor or absent
- Fourth trochanter present as a muscle scar or absent altogether
- Lesser trochanter completely fused to the greater trochanter in the adult
- Hypertrophied preacetabular pr. of the ilium
- Iliac preacetabular pr. directed approximately 40° lateral to the axial column
- Postacetabular pr. of the ilium relatively shorter
- Distal expansion of the ischial blade absent
- Ventromedial slant of the distal ischial blade absent
- Pes digit IV with no more than four phalanges (loss of one phalanx)
- Spreading metatarsals; no sigmoid curve in shaft of metatarsal 4
- Metacarpals relatively short
- Metatarsals relatively short

8. STEGOSAURIA

Cranial

- Large oval fossa or fenestra in pterygoquadrate wing

Postcranial

- Tall neural arches in mid and posterior dorsal vertebrae and high-angled transverse processes at least in posterior dorsal vertebrae
- Anterior dorsal vertebrae with relatively large neural canal

- Acromial region of scapula broad proximodistally
- Prominence on the dorsal margin of the ischial blade at midshaft
- Broad, cup-shaped, laterally facing acetabular surface on pubis
- Postpubic pr. with distal expansion
- Pes digit III with no more than three phalanges (loss of one phalanx)
- Pes digit I absent
- Prominent parasagittal osteoderms: moderate-sized anterior plates grading posteriorly into longer, posterodorsally angling spines
- Parasacral spine with expanded base
- Ossified epaxial tendons absent

9. ANKYLOSAURIA

Cranial

- Rectangular skull in occipital view; long axis horizontal
- Closure of supratemporal and antorbital fenestrae by the SQ–PO–P and M–L–J, respectively
- Very deep, dorsally arched M cheek emargination
- Hook-shaped QJ extending almost directly laterally from the Q suture and arching anteriorly
- QJ–PO contact
- Moderate J–PO shelf extending medially into the orbit
- Dorsoventrally narrow pterygoid ramus of the Q
- Median palatal keel, composed of the V and PT, extending ventrally to the level of the M crowns
- Fused, median N septum extending from the ventral surface of the skull roof to join the V ventrally; divides the respiratory passage into two separate bony canals
- Vertical orientation of the PT closing the passage between the space above the palate and that below the braincase
- Accessory antorbital ossification(s) partially or completely separating orbit and antorbital space
- Fusion and dermal sculpturing of the outer surface of the entire dermal skull roof except the posterior portion of the QJ and the ventral margin of the M and PM
- Oval osteoderm, with ventrally offset keel, fused to the ventrolateral side of the lower jaw
- Ventral predentary pr. relatively very short

Postcranial

- Atlar neural arches join dorsally above the neural canal
- Atlar intercentrum nearly surrounded by the odontoid
- At least three posterior dorsal vertebrae added to the sacrum with long ribs contacting the preacetabular pr.
- Anteroposteriorly broad posterior caudal hemal spines that contact adjacent hemal spines: inverted T-shaped chevrons
- Anteroposteriorly broad neural spines and long pre- and postzygapophyses in posterior caudal vertebrae
- Narrow sternal ventrolateral pr.
- Scapula and coracoid fused
- Acetabulum closed and composed almost entirely of the ischium and ilium
- Anteroventrally projecting, prominent pubic peduncle of the ilium absent
- Postpubic pr. relatively very short; pubic symphysis absent
- Two cervical plate rows each consisting of a transverse, arched band of contiguous plates without intervening ossicles
- Mosaic of small scutes forms transverse bands between successive cervical plate rows and surrounds larger keeled plates on all sides in the trunk region

10. NODOSAURIDAE

Cranial

- Dorsoventrally low skull
- Hourglass-shaped palate with the constriction occurring at the junction of PM and M tooth rows
- Basipterygoid prs. consisting of a pair of rounded, rugose stubs
- Hemispherical occipital condyle set off from the ventral braincase by a distinct neck and angled approximately 50° from the level of the M tooth row; oval to subcircular (not crescentic) occipital condyle in posterior view
- Occipital condyle formed exclusively by the BO
- Q shaft angled strongly anteroventrally
- Scute pattern on the skull roof as indicated by grooves and sculpturing:
  — large subcircular scute covering most of the skull roof between the orbits
  — anteroposteriorly narrow scute along the posterior border of the skull roof
  — series of three scutes on orbital roof on each side, one directly above and one anterior and posterior to the orbit
- Sinuous ventral margin of lower jaw which parallels the sinuosity of the dorsal margin in lateral view

Postcranial

- Coracoid anteroposteriorly long relative to dorsoventral width
- Postpubic pr. flattened dorsoventrally
- Pectoral dermal plate row similar in form, and positioned posterior, to the pair of cervical dermal plate rows

11. ANKYLOSAURIDAE

Cranial

- PM teeth absent
- Maximum skull width equal to, or greater than, maximum skull length
- Snout arches above the level of the postorbit skull roof
- External nares divided by a horizontal PM septum with the lower opening leading to a M sinus above the cheek emargination
- PM with short posterior prs. along the bill margin which lie lateral to the anteriormost M teeth
- PM palate wider transversely than long anteroposteriorly
- Continuous surface formed by the PM palate and M cheek; continuous edge formed by the PM bill margin and lateral edge of the M cheek
- Anterior portion of the M tooth row obscured in lateral view by the lateral edge of anterior M cheek, which extends ventrally to join the PM bill margin
- Secondary palate developed posteriorly as far as the orbits; S-shaped respiratory route, i.e., proximal portion of the respiratory tract passes posteriorly beneath the skull roof and doubles back above the posterior palate before passing through the choanae
- Paired PM sinus
- Paired N sinus
- Paired M sinus positioned above the cheek emargination
- PO–J postocular shelf well-developed, bounding the orbit posteriorly and ventrally, and tapering medially to the braincase
- EPT obtaining a near-horizontal orientation, establishing contact with the PT anteriorly and POT posteriorly
- QJ dermal ossification prominent and wedge-shaped, projecting ventrolaterally
- Prominent wedge-shaped SQ dermal ossification present, projecting posterolaterally; joins the QJ ossification along the side of the skull hiding the laterotemporal fenestra, QJ, paroccipital pr., and all but the ventral tip of the Q in lateral view of the skull
- Sharp lateral rim and low dorsal prominence for each lateral SORB element; flat lateral SORB margin above the orbit
- Scute pattern on the skull roof as indicated by grooves and sculpturing:
  — anterior paired PM scutes that meet in the midline
  — median N scute just posterior to the PM scutes
  — two lateral snout scutes posi-

Table 1. continued

tioned between the external naris orbit
— scutes covering each lateral SORB element
— scute covering SQ dermal horn
— rugose, slightly depressed, rectangular supratemporal region with poorly defined scute boundaries

- Coronoid pr. very low and rounded; projects only slightly above the level of the D tooth row

Postcranial

- Partial or complete fusion of caudal centra in the posterior half of the tail
- Elongate pre- and postzygapophyses in the posterior half of the tail; prezygapophyses broad dorsoventrally; posteromedian notch between postzygapophyses absent resulting in a single dorsoventrally flattened, tonguelike median pr.
- Elongate interlocking hemal arches that articulate as in zygapophyses with the anterior pr. overlapping laterally; bases are also very long anteroposteriorly and contact adjacent hemal bases to form an enclosed, bony, hemal canal
- Acromion projects laterally; does not project above the dorsal margin of the scapular blade
- Fused sternal plates
- Deltopectoral crest and the transverse axis through the distal condyles of the humerus occupy the same plane
- Iliac postacetabular pr. relatively very short
- Ischium with convex proximal margin within the acetabulum
- Ischium with near vertical orientation beneath the acetabulum
- Pubis consisting of a nubbin fused to the other pelvic elements
- Fourth trochanter located on the distal half of the femur
- Dermal tail club: two large, wedge-shaped lateral plates; two smaller terminal plates that meet in the midline; more variable, small, dorsal and ventral plates positioned at the junction of the four larger plates; often fused
- Ossified tendon sheath surrounding the caudal vertebrae of the posterior half of the tail

12. EUORNITHOPODA

- PM tooth row offset ventral to the M tooth row
- Crescent-shaped paroccipital pr.
- Ventral extension of the Q lowering the jaw articulation well below the tooth row; skull rectangular in occipital view with the long axis vertical
- Posterior elongation of the PM posterolateral pr.; PM–L contact excludes M–N contact

13. HETERODONTOSAURIA

Cranial

- Three PM teeth
- PM teeth without distinction between root and crown
- Anterior two D teeth without denticles; first D tooth relatively very small and subcylindrical
- PD wedge-shaped; lateral and median prs. absent; smooth, dorsoventrally concave articular surface for each D ramus

Postcranial

- The head of the humerus is positioned to the lateral side of the proximal end
- Relatively long manus
- Metacarpals with blocklike proximal ends
- Fibula very slender relative to the tibia; distal end only very slightly expanded
- Proximal phalanges of pes digits II through IV with extensor pits on the distal heads

14. XIPHOSAURIDAE

- Caniniform anterior D tooth; relatively larger than PM caniniform tooth and fitted to a PM–M arched diastema
- Caniniform posterior PM tooth

15. ORNITHOPODA

- External opening of the antorbital fossa of moderate size or smaller
- External mandibular foramen absent
- Elongate prepubic pr. extending farther anteriorly than the preacetabular pr. of the ilium
- Tabular obturator pr. on ischium

16. HYPSILOPHODONTIA

- Length of the scapula equal to or shorter than the length of the humerus
- Partial ossification of sternal segments of anterior dorsal ribs
- Prepubic pr. rod-shaped; wider transversely than tall dorsoventrally
- Ossified hypaxial tendons in the tail

17. HYPSILOPHODONTIDAE

- Skull roof with narrow interorbital width; F relatively narrow transversely
- PM diverticulum
- Ventral margin of the occipital condyle, basal tubera and basipterygoid prs. lie in a plane sloping about 35° anteroventrally

18. IGUANODONTIA

Cranial

- PM teeth absent
- Leaf-shaped denticles
- Strong primary ridge on the medial side of the D crowns
- Enamel restricted to the distal half of the crown on the medial side of the M teeth and lateral side of the D teeth
- Eversion of the ventral PM margin
- External opening of the antorbital fossa is relatively small or entirely absent
- External nares enlarged relative to the orbit
- M with paired anterior prs.: primitive anteromedial pr. and new anteroventral pr. which laps the PM palate ventrally
- QJ reduced in size relative to the Q
- D with parallel dorsal and ventral borders
- PD with paired ventral prs.
- Denticulate PD bill margin

Postcranial

- Manus digit III with only three phalanges (one phalanx absent)
- Femur with weak anterior intercondylar groove and deep posterior intercondylar groove

19. DRYOMORPHA

Cranial

- M crown narrower anteroposteriorly than the opposing D crown
- Lateral M primary ridge stronger than the medial D primary ridge
- Diamond-shaped M and D tooth crowns; M crowns with rounded anterior and posterior corners
- Enamel absent from the medial side of the M teeth and the lateral side of the D teeth
- Space separating the ventral margin of the QJ from the jaw articulation

Postcranial

- Ischial shaft round in cross section; transversely compressed distally (dorsoventrally compressed distal blade absent)
- Distal ischial shaft with a moderate foot
- More proximally positioned obturator pr.

20. ANKYLOPOLLEXIA

Cranial

- Close packing along the tooth row and in the replacement series eliminating spaces between the bases of the crowns of adjacent functional teeth
- Prominent primary ridge on the lateral side of the M crown
- Ornamentation of the apical margin of individual denticles
- External opening of antorbital fossa relatively very small or absent

Postcranial

- Cervical neural spines very weak or absent

- Robust, arching cervical postzygapophyses posterior to the axis
- Moderate opisthocoely in cervical vertebrae 4 to 9; slight opisthocoely in dorsal vertebrae 1 to 2
- Partial fusion of carpals into two blocks: block 1 consisting of the radiale, intermedium, distal carpals 1 and 3, and metacarpal 1; block 2 consisting of the ulnare and distal carpals 4 and 5
- Metacarpal 1 inset into the carpus and fused to distal carpal 1 and the radiale
- Metacarpal 1 shorter relative to the other metacarpals
- 40 to 50° angle of divergence of manus digit I from axis of the forearm
- Subconical manus digit I ungual
- Stout phalanx 1 of manus digit I; wider transversely than long anteroposteriorly
- Pes digit I relatively shorter and less robust
- Metatarsal 1 markedly less robust relative to the other metatarsals

21. STYRACOSTERNA

- At least 25 vertical columns in the M and D tooth rows
- Lanceolate-shaped M crowns
- Postdentary elements of the lower jaw are positioned posterior to the vertical midline of the coronoid pr.
- Strong opisthocoely in cervical vertebrae, beginning with the third cervical
- Sternal ventrolateral pr.
- Humerus with a proximally and posteriorly prominent head
- Shafts of metacarpals 2 to 4 closely appressed
- Metacarpal 4 subequal in length to metacarpal 3
- Distal end of the prepubic pr. moderately expanded dorsoventrally
- Pubis with distinct, stout iliac peduncle
- Postpubic pr. consisting of a tapering rod approximately half the length of the ischium
- Femur with deep anterior intercondylar groove

22. IGUANODONTOIDEA

Cranial

- Space between the first D tooth and the PD
- External nares enlarged
- At least a slight transverse narrowing of the cranium from the postorbital region posteriorly in dorsal view
- Paroccipital pr. relatively broader proximally and narrower distally
- Postpalatine foramen absent

Postcranial

- Complete fusion of the radiale, distal carpal 1, and metacarpal 1
- Metacarpal 1 relatively very short or absent
- Phalanx 1 of manus digit I represented by a flattened disk or absent altogether
- Phalanx 2 of manus digits II to IV very short relative to phalanx 1 of the respective digit
- Ungual of manus digit II with transversely narrower proportions than the ungual of manus digit III
- Manus digit V with at least three phalanges (one phalanx added)
- Hoof-shaped unguals on manus digits II and III
- Metatarsal 1 represented by a transversely thin, short splint
- Hoof-shaped unguals on pes digits II to IV
- Pes digit V absent
- Double-layered lattice of ossified tendons from the posterior cervical–anterior dorsal region to the midcaudal region of the vertebral column; tendons of both deep and superficial layers insert high on the lateral side of the neural spines, the former coursing anteroventrally and the latter posteroventrally across adjacent neural spines

23. HADROSAUROIDEA

Cranial

- Relatively greater space between the first D tooth and the PD
- Anterior end of the premaxillary snout expanded transversely; narial fossa lengthened anteroposteriorly and defined laterally by a reflected rim
- Anterior end of the jugal expanded dorsoventrally in front of the orbit
- Distinct transverse narrowing of the cranium from the postorbital region posteriorly in dorsal view
- SQ approach the midline of the posterior skull roof, separated by only a narrow band of the P
- Distal end of the paroccipital pr. and accompanying SQ pr. curve anteriorly

Postcranial

- Caudal neural spines exceed their respective chevrons in length
- Scapular blade with convex dorsal margin
- Phalanx 1 of manus digit I absent
- Pubic peduncle of ilium relatively small; articulates against the prominent dorsally directed iliac peduncle of the pubis
- Iliac antitrochanter present
- Iliac preacetabular pr. relatively longer
- Marked dorsoventral expansion of the distal prepubic blade
- Proximally positioned obturator pr.
- Deep obturator notch between the obturator pr. and pubic peduncle of the ischium
- Distal tarsals 2 and 3 absent
- Pes digit I absent

24. PACHYCEPHALOSAURIA

Cranial

- Thickened F–P skull roof
- PO–SQ temporal bar with flat and transversely broad dorsal surface
- Broad expansion of the SQ on the occiput; P posterolateral wings absent
- Free ventral margin of the QJ eliminated by the proximity of J and Q
- Orbital roof with two SORB which exclude the F and PF from that orbital margin; contact between SORB 1 and the N excludes PF–L contact
- Pterygoquadrate wings curve ventromedially, approaching the midline above the palatal rami of the PT
- Broad, thin, platelike basal tubera, composed of the BS laterally and joined dorsally by a flange of the EO, establishing BS–EO contact
- POT–BS plate present which extends laterally from the braincase, contacting the pterygoquadrate wing and effectively separating subtemporal and occipital regions; POT–Q and POT–PT sutures established
- Tubercular ornamentation on the dorsal surface of the skull roof
- Prominent tubercles on the posterolateral corner of the SQ, which continue as smaller tubercles around the corner of the skull roof and onto the PO

Postcranial

- Double groove and ridge present on the articular surfaces of the pre- and postzygapophyses, respectively, in the dorsal vertebrae
- Elongate sacral ribs broaden the pelvis transversely
- Two anterior chevrons absent (first chevron located between the fifth and sixth caudal vertebrae)
- Elongate, transversely narrow sternals with articular surfaces restricted to the proximal and distal ends
- Relatively short distal forelimb elements; forelimb shortened relative to the hindlimb
- Slender scapular blade much longer than the humerus
- Bowed humeral shaft which is laterally convex
- Deltopectoral crest rudimentary
- Rotation in the humeral shaft only approximately 20°
- Tabular pr. extending medially from the dorsal margin of the proximal portion of the postacetabular pr.
- Gentle sigmoid curve to the iliac blade in dorsal view
- Pubic peduncle of the ischium narrow dorsoventrally but broad transversely

Table 1. continued

- Pubic body relatively small and nearly excluded from the acetabulum
- Caudal "basket": multiple rows of fusiform ossified tendons, which narrow in width posteriorly, and are applied to the lateral sides of the vertebrae and chevrons of the posterior half of the tail

25. GOYOCEPHALIA
- PO–P contact excludes the F from the margin of the supratemporal fenestra
- Postorbital bar transversely broadened with an interdigitating PO–J suture
- Linear row of five to seven prominent tubercles on the posterior margin of the SQ
- ANG and posterior SANG ornamented with rugose tubercles; horizontal ridge of tubercles crosses the ventral portion of the ANG

26. HOMALOCEPHALOIDEA
- Supratemporal fenestra reduced in size: P broadened between, and anterior to, the supratemporal fenestrae
- Medial flange on the dorsal margin of the postacetabular pr. of the ilium relatively broader anteroposteriorly at its base, which tapers posteriorly along the postacetabular pr.

27. THOLOCEPHALIDAE
- Doming of the F, P, medial portion of the PO, and N; separate thickening of SORB 1 and 2; dome centered above the posterior orbital margin
- F–F and F–P sutures fused in the adult
- Supratemporal fenestra very small or closed in the adult
- Further posterior projection of the P and SQ over the occiput and occipital condyle

28. DOMOCEPHALINAE
- Supratemporal fenestra closed in the adult
- Pronounced doming of the skull cap, incorporating nearly all of the PF, SQ, and PO into the dome, eliminating the posterior and lateral shelves
- Q–J contact

29. CERATOPSIA

Cranial
- Triangular-shaped head in dorsal view: very narrow beak anteriorly and J that flare well beyond the skull roof
- Median rostral bone on anterior snout
- Tall snout with relatively tall PM
- External nares high on snout
- Biplanar lateral surface of the J better developed
- M is proportionately tall, at least two thirds as tall as long
- J orbital bar broader dorsoventrally than the posterior ramus below the laterotemporal fenestra
- Transversely broad P overhang extending across most of the occipital margin
- Vaulted PM palate (deep and transversely arched)
- Immobile mandibular symphysis: symphysis broad; strong union between the D rami and PD

30. NEOCERATOPSIA

Cranial
- Ovate shape to M and D crowns in lateral view
- Prominent primary ridge on the lateral side of the M teeth
- Close packing along the tooth row and in the replacement series eliminating spaces between the alveolar border and crowns of adjacent functional teeth; groove present on the anterior and posterior sides of the root, fitted against the edge of the crown of the adjacent replacement tooth
- Head very large relative to body size
- Anterior keel on R which curves ventrally to a point
- Frill oriented in a posterodorsal plane so that the dorsal frill surface passes smoothly into the supratemporal fossa, rather than forming a distinct posterior edge to that fossa
- P frill extending relatively farther posteriorly
- P relatively broader transversely, comprising the great majority of the posterior skull roof margin
- SQ–J contact above the laterotemporal fenestra
- EO exclude BO from the border of the foramen magnum
- Epijugal
- Sharp ventral keel on PD
- PD with ventrolaterally angling triturating surface on at least the posterior half of the dorsal margin
- PD dorsal margin curves dorsally to a sharp point at the anterior end
- PD with posteriorly bifurcated ventral pr.

Postcranial
- Centra of cervicals 1 to 3 fused
- Anteromedial pr. (prezygapophysis) of the atlar neural arch absent

31. CORONOSAURIA

Cranial
- Enamel absent on the lateral side of the D teeth and the medial side of the M teeth
- Paired P fenestrae
- Frontoparietal depression
- P–SQ frill relatively expanded
- Straight SQ–P frill suture; medial SQ flange absent
- PD with triturating surface along the entire dorsal margin

Postcranial
- At least a small, wedge-shaped anterior atlar intercentrum fused to the anterior surface of the atlas intercentrum
- Fusion of the atlar neural arches to the intercentrum
- Fusion of the atlar neural arches to the lateral sides of the axial neural arch
- Neural spine of the third cervical fused to the axial neural spine

32. CERATOPSOIDEA
- External nares relatively large
- Broad-based N horn core
- N horn core positioned anteriorly, nearly directly above the external nares and anterior to the dorsoventrally broad posterior portion of the N on the side of the face
- Anterior atlar intercentrum at least crescent-shaped in anterior view, extending dorsally around the anterior rim of the atlar intercentrum and fusing to the atlar neural arch
- Tall cervical neural spines
- Postpubic pr. relatively very short

***Skull element abbreviations**

ANG = angular(s)
BO = basioccipital
BS = basisphenoid
D = dentary(ies)
EO = exoccipital(s)
EPT = epiterygoid(s)
F = frontal(s)
J = jugal(s)
L = lacrimal(s)
M = maxilla(e), maxillary
N = nasal(s)
OP = opisthotic(s)
P = parietal
PD = predentary
PF = prefrontal(s)
PM = premaxilla(e), premaxillary
PO = postorbital(s)
pr(s). = process(es)
POT = prootic(s)
PT = pterygoid(s)
Q = quadrate(s)
QJ = quadrotojugal(s)
R = rostral
SANG = surangular(s)
SO = supraoccipital
SORB = supraorbital(s)
SP = splenial(s)
SQ = squamosal(s)
V = vomers(s)

anterolaterally at approximately 40° from the axis of the vertebral column. Stegosaurs and ankylosaurs are also unique among ornithischians in the reduction of the pendant fourth trochanter to a muscle scar, at best, and in the spreading, rather than compact, arrangement of the metatarsals of the pes.

Cerapoda

Opposing the thyreophorans, the Cerapoda include the heterodontosaurs, ornithopods (sensu stricto), pachycephalosaurs, and ceratopsians. The common ancestry of this group is inferred from derived characters that are absent in *Lesothosaurus* and thyreophorans (Figure 2, node 3; Table 1). In Cerapoda the enamel enveloping the crowns of the cheek teeth has an asymmetrical distribution such that the enamel on the medial side of the dentary teeth and on the lateral side of the maxillary teeth is several times thicker than on the opposite side. Previously recorded in some ornithopods and ceratopsians, asymmetrical enamel is here reported in the pachycephalosaurs and psittacosaurs. Two outstanding derived postcranial characters are the completely open acetabulum of the pelvic girdle and the laterally protruding ischial peduncle of the ilium (*Psittacosaurus sinensis* type skeleton, page 122 [Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, V738], a Lower Cretaceous psittacosaur from Shandong Province, China). In *Lesothosaurus* and thyreophorans, in contrast, the acetabulum is partially closed by a ventral acetabular flange of the ilium, and the ischial peduncle of the ilium does not protrude laterally.

Within this group, pachycephalosaurs and ceratopsians are more closely related, although evidence for their affinity is not overwhelming. The conformation of the posterior skull roof is the most striking characteristic: The fused parietal extends posteriorly as a shelf, which in advanced ceratopsians expands broadly to form the shield-like frill.

Stegosaurs

The monophyly of the stegosaurs has never been questioned once they had been distinguished from other armored forms (Brown 1908, Romer 1927). Two outstanding characteristics were recognized early: the prominent parasagittal osteoderms, and the heightened neural arches of the mid and posterior dorsals. Primitively the parasagittal osteoderms consist of moderate-sized plates over the cervicals grading into long, posterodorsally angling spines over the caudals. Other diagnostic features include the absence of digit I in the pes and the absence of ossified tendons along the vertebral column. The absence of ossified tendons in stegosaurs is quite clearly a reversal to the primitive condition, given the presence of ossified tendons in all other subgroups of ornithischians including other thyreophorans.

The recent discovery of well-preserved skeletal remains of *Huayangosaurus*, a Middle Jurassic stegosaur from the Sichuan Basin of China, has added a new dimension to the understanding of stegosaur phylogeny (Dong, Tang, et al. 1982; Zhou 1983, 1984). *Huayangosaurus* is clearly the most primitive stegosaur discovered to date (Figure 3, node 8; Table 1) and is the only stegosaur besides *Stegosaurus* for which relatively complete skull material is known. Derived characters of the skull of *Stegosaurus* relative to *Huayangosaurus* include the posterior position of the orbit (posterior to the maxillary tooth row); closure of the antorbital fenestra; and a very reduced, bluntly rounded retroarticular process (Gilmore 1914:Plate 5). In *Huayangosaurus* the relatively tall snout bears seven premaxillary teeth on each side (Figure 5) in contrast to the derived dorsoventrally narrow snout and edentulous premaxillae of *Paranthodon* and *Stegosaurus.*

Derived postcranial characters indicate that *Dacentrurus, Kentrosaurus, Lexovisaurus, Tuojiangosaurus, Wuherosaurus,* and *Stegosaurus* belong to a group more advanced than *Huayangosaurus.* They include: complete, or nearly complete, fusion of the dorsal portion of adjacent sacral ribs; relative lengthening of the prepubic process of the pubis; and an increase in the ratio of the lengths of the humerus and femur to at least 1:1.5 (*Huayangosaurus,* Zhou 1984; *Dacentrurus,* Owen 1875; *Kentrosaurus,* Hennig 1924; *Lexovisaurus,* Galton 1985; *Wuherosaurus,* Dong 1973; *Stegosaurus,* Gilmore 1914).

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Figure 4. Juvenile skull of Pinacosaurus grangeri *(Institute of Paleobiology, Warsaw, MgD-II/1), an Upper Cretaceous ankylosaurid from the central Gobi Desert of Mongolia.*

Ankylosaurs

A long list of derived characters strongly supports the monophyly of the armored dinosaurs (Figure 3, node 9; Table 1). The shape of the skull is unique among dinosaurs: The occiput is rectangular with the long axis horizontal. The closed ankylosaur acetabulum is interpreted here as a derived character for the group, rather than a retained primitive archosaur character. The ankylosaurs comprise two distinct subgroups, the nodosaurids and ankylosaurids (Coombs 1978), which can be explicitly defined on shared, derived characters (Figure 3, nodes 10, 11; Table 1). Among nodosaurs *Hylaeosaurus* appears to be the most primitive, although none of the skull is preserved. Other nodosaurs (e.g., *Panoplosaurus, Sauropelta,* and *Struthiosaurus*) have a prominent scapular spine, located in the middle of the proximal end of the scapular blade.

Among ankylosaurids, *Talarurus* and the recently discovered *Shamosaurus* stand out as the primitive sister taxa (Maleev 1954, Tumanova 1981). All remaining ankylosaurids — including *Ankylosaurus, Euplocephalus, Pinacosaurus, Saichania,* and *Tarchia* — share a more recent common ancestry as exemplified by the derived proportions of the cranium, which is wider transversely than long. Other features of these advanced ankylosaurids include broader continuity between the premaxillary palatal surface and the maxillary cheek, paroccipital processes that lie along a straight transverse axis, and more prominent quadratojugal and squamosal dermal ossifications.

Euornithopods

Traditionally the Suborder Ornithopoda has been defined on primitive characters alone and, as a result, has included more distantly related groups such as the pachycephalosaurs and psittacosaurs (Galton 1972; Romer 1956, 1966; Steel 1969). Recent attempts to rectify this situation have used the obturator process on the ischium as a defining character for the Ornithopoda. The process is presumed to be present in the supposed basal ornithopod *Lesothosaurus* (Cooper 1985; Maryańska & Osmólska in press; Milner & Norman 1984; Norman 1984a, b; Santa Luca 1980, 1984). Its absence, it follows, is reason to exclude heterodontosaurs, psittacosaurs, and pachycephalosaurs from the Ornithopoda.

The obturator process by itself, however, does not provide a sufficient definition for the Ornithopoda (Sereno 1984). Contrary to the original account (Thulborn 1972), a distinct obturator process is clearly absent

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Figure 5. Type skull of Huayangosaurus taibii *(Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, V6728), a Middle Jurassic stegosaur from the Sichuan Basin of China.*

in *Lesothosaurus* as shown by the appropriate portion of the right ischium of the type specimen (University College, London, B.17). The obturator process is present in an undescribed, primitive ornithischian from the Stormberg Series of South Africa of possible close affinity to *Lesothosaurus.* Given current knowledge of the occurrence of this process in ornithischians, the simplest hypothesis is one of parallel acquisition. That is, the obturator process appeared in a near relative of *Lesothosaurus* and also arose independently in the common ancestor of hypsilophodonts, iguanodonts, and hadrosaurs (Figure 6, node 15; Table 1).

The taxon Euornithopoda, or the true ornithopods, is proposed here for a group that includes the heterodontosaurs, hypsilophodonts, iguanodonts, and hadrosaurs but excludes *Lesothosaurus,* psittacosaurs, and pachycephalosaurs (Figure 6, node 12; Table 1). In the snout of these ornithischians, the premaxilla extends posterodorsally to establish contact with the lacrimal, which effectively eliminates contact between the maxilla and nasal. In posterior view, the euornithopod skull has a rectangular shape, the result of ventral extension of the quadrate with consequent lowering of the jaw articulation relative to the tooth rows.

The Euornithopoda can be divided into three major subgroups, each representing separate and distinct lineages: the heterodontosaurs, hypsilophodonts, and iguanodonts and hadrosaurs (Figure 6). Known only from the Lower Jurassic, the small-bodied heterodontosaurs are characterized by several unusual modifications in the cranium and postcranium (Figure 6, node 13; Table 1). The wedge-shaped predentary bone, for example, has smooth, rounded articular surfaces for the dentaries, without any development of lateral or ventral processes. In the postcranium the manus is relatively long and the fibula is very slender relative to the tibia. Until now the concept of the heterodontosaurs has been based in large part on the complete skeleton of *Heterodontosaurus* (Santa Luca 1980). Additional unpublished material from the Stormberg Series of South Africa and the Kayenta Formation of Arizona now confirms that many of the unusual features of *Heterodontosaurus* are common to other heterodontosaurs. Within the heterodontosaur radiation, the characteristic caniniform teeth of the posterior premaxilla and anterior dentary appear to be restricted to a subgroup of heterodontosaurs more advanced than *Abrictosaurus* (Figure 6, node 14; Table 1).

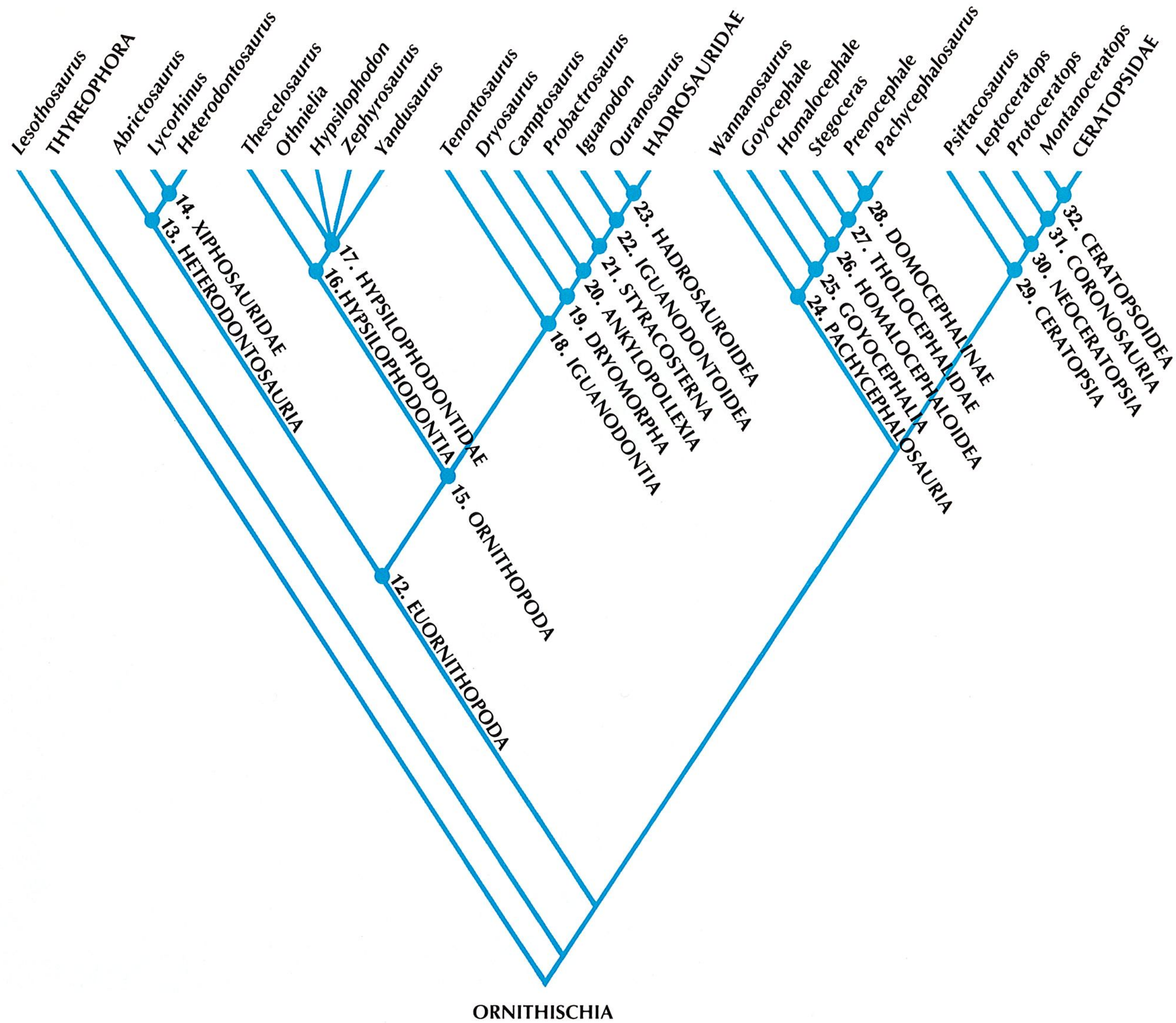
Of the three major subgroups of euornithopods, two are more closely related, the hypsilophodonts and the iguanodonts and hadrosaurs, which together constitute the Suborder Ornithopoda as it is here restricted (Figure 6, node 15; Table 1). In the lower jaw of ornithopods (sensu stricto), the external mandibular foramen is closed, and postcranially the elongate prepubic process of the pubis extends farther anteriorly than the preacetabular process of the ilium.

The hypsilophodonts are restricted to include, among better-known forms, *Hypsilophodon, Othnielia, Parksosaurus, Thescelosaurus, Yandusaurus,* and *Zephyrosaurus* (Figure 6, node 16; Table 1). Partially ossified sternal segments and a rod-shaped prepubic process are two derived features of the group. *Dryosaurus* and *Tenontosaurus,* however, are more closely related to iguanodonts and hadrosaurs than to hypsilophodonts. Milner & Norman (1984) and Norman (1984a, b) reached similar conclusions concerning *Dryosaurus.* The fragmentary *Mochlodon* from the Upper Cretaceous of Europe is also more closely related to iguanodonts and hadrosaurs but appears to be more primitive than *Dryosaurus.* Contrary to Norman (1984b) and Cooper (1985), no current evidence suggests that *Mochlodon* or other ornithopods, except *Valdosaurus,* share a very close relationship to *Dryosaurus.*

The present study introduces substantial evidence in favor of a monophyletic group including *Tenontosaurus, Dryosaurus,* and all other iguanodonts and hadrosaurs, but excluding heterodontosaurs and hypsilophodonts (Figure 6, node 18; Table 1). The absence of premaxillary teeth, the presence of leaf-shaped denticles in the cheek teeth, and the loss of one phalanx from manus digit III are derived features common to this group.

As previously demonstrated (Sereno 1984), the advanced ornithopods, termed iguanodonts, do not constitute a monophyletic group. Despite recent attempts that argue in favor of common iguanodont ancestry separate from the hadrosaurs (Dodson 1980, Milner & Norman 1984, Norman 1984a, b), the so-called iguanodonts represent a series of sister taxa to the Family Hadrosauridae. One well-defined subgroup within the iguanodont–hadrosaur group includes *Camptosaurus, Probactrosaurus, Iguanodon, Ouranosaurus,* and hadrosaurs (Figure 6, node 20; Table 1). In all members, coalescence of the individual teeth into a dental battery is at least in its initial stages with the elimination of space between the bases of adjacent crowns. A strong primary ridge dominates the lateral side of the maxillary crowns. Digit I of the manus exhibits several unique specializations; metacarpal 1 fuses to the radiale and distal carpal 1 of the carpus, and the ungual has a characteristic subconical shape, reported here for the first time in *Camptosaurus* (University of Utah Vertebrate Paleontology Collection, Salt Lake City, 6231, 6278, 10 964). Metacarpal 1 is relatively shorter in *Iguanodon* and *Ouranosaurus,* and the entire digit is lacking in hadrosaurs.

The count of at least 25 vertical columns in maxillary and dentary tooth rows, the presence of ventrolateral processes on the paired sternal



bones, and the distinct, stout iliac peduncle of the pubis identify *Probactrosaurus* as a member of a more select group within the iguanodont–hadrosaur lineage (Figure 6, node 21; Table 1). Contrary to previous suggestions of close affinity with the hadrosaurs (Rozhdestvensky 1966), *Probactrosaurus* appears to be more distantly related to hadrosaurs than either *Iguanodon* or *Ouranosaurus.* Evidence in favor of this reinterpretation resides in derived characters present in *Iguanodon, Ouranosaurus,* and hadrosaurs but absent in *Probactrosaurus* and more primitive ornithopods, such as the noticeable transverse narrowing of the skull roof from the postorbital region posteriorly, and the hoof-shaped unguals of the pes. However, additional articulated skeletal remains of *Probactrosaurus* are necessary to establish its phylogenetic position with greater confidence.

Ouranosaurus, from the Lower Cretaceous of Niger (Taquet 1976), is more closely related to hadrosaurs than to any other ornithopod (Figure 6, node 23; Table 1). The characteristic duck-like bill of the hadrosaurs is present in all essentials in *Ouranosaurus:* the expanded narial fossa, widened anterior premaxillary bill margin, and reflected rim. Other features that can be found only in *Ouranosaurus* and hadrosaurs include

*Figure **6**. Phylogenetic relationships of euornithopods, pachycephalosaurs, and ceratopsians. Characters in support of nodes 12 through 32 are listed in Table 1.*

the dorsoventrally expanded anterior tip of the jugal and the presence of an antitrochanter on the dorsal margin of the ilium. The monophyly of the Hadrosauridae has never been seriously disputed and is so thoroughly supported by morphological evidence that it shall not be considered further in this context.

Pachycephalosaurs

Gilmore's 1924 account of North American *Stegoceras* constituted virtually the entire knowledge of this interesting group until the pioneering work on Mongolian pachycephalosaurs by Maryańska & Osmólska (1975) and subsequent descriptions of Chinese and Mongolian forms by Hou (1977) and Perle et al. (1982).

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Figure 7. Type skull of Prenocephale prenes *(Institute of Paleobiology, Warsaw, MgD-I/104), a fully domed pachycephalosaur from the Upper Cretaceous of the Nemegt Basin in the central Gobi Desert of Mongolia.*

The pachycephalosaur cranium is easily recognized by the thickening of the frontal and parietal portions of the skull roof and the prominent tubercles on the squamosal and postorbital (Figure 7). The postcranium, equally distinct, is characterized by shortened forelimb proportions and unusual, interweaving ossified tendons surrounding the distal tail. Recently Dong (1978) proposed a division of pachycephalosaurs into two families based on the degree of thickening of the skull roof: the Homalocephalidae, for the flat-headed pachycephalosaurs, and the Pachycephalosauridae, for the dome-headed forms. The flat-headed forms, however, do not appear to constitute a monophyletic taxon but rather a sequence of increasingly advanced forms that diverged independently from the lineage leading to the domed forms (Figure 6).

The fragmentary *Wánnanosaurus,* from the Upper Cretaceous of China (Hou 1977), may represent the most primitive pachycephalosaur yet discovered. All pachycephalosaurs except *Wannanosaurus* have a postorbital, transversely broadened bar and a linear row of five to seven distinct tubercles projecting from the posterior margin of the squamosal (Figure 6, node 25; Figure 7; Table 1). Likewise, all except *Wannanosaurus* and *Goyocephale* have reduced the relative size of the supratemporal openings (Figure 6, node 26; Table 1).

Doming of the frontal and parietal, fusion of the interfrontal and frontal–parietal sutures, and further reduction of the supratemporal fenestrae occur in a smaller subset of the pachycephalosaurs, including *Stegoceras*, *Prenocephale*, and *Pachycephalosaurus* (Figure 8, node 27; Table 1). Finally, a small group of advanced pachycephalosaurs have completely closed the supratemporal fenestrae and intensified the doming of the skull roof to fully incorporate the prefrontal, squamosal, and postorbital (Figure 6, node 28; Figure 7; Table 1).

Ceratopsians

Traditionally the Suborder Ceratopsia included only the large-bodied, horned forms of the Family Ceratopsidae and their smaller-bodied progenitors in the Family Protoceratopsidae, both families restricted to the

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Figure 8. Type skull of Psittacosaurus youngi *(Beijing Natural History Museum, BPV.149), a Lower Cretaceous psittacosaur from Shandong Province, China.*

Upper Cretaceous. One hallmark of ceratopsian morphology is the median rostral bone at the anterior end of the snout. Initial descriptions of the Lower Cretaceous psittacosaurs misidentified the rostral bone as the premaxilla (Osborn 1923, Young 1958), and until quite recently the psittacosaurs were referred to the Suborder Ornithopoda (Coombs 1982, Maryańska & Osmólska 1975). Actually the psittacosaur skull exhibits a number of derived characters present in all ceratopsians, such as the triangular shape of the skull in dorsal view, tall snout, wide parietal frill margin, and immobile mandibular symphysis (Figure 6, node 29; Figure 8; page 122; Table 1) (Sereno 1984).

Setting the psittacosaurs aside, remaining ceratopsians display modifications that indicate a more recent common ancestry including the expanded frill, presence of an epijugal bone, and fusion of the first three cervical centra (Figure 6, node 30; Table 1). Contrary to previous opinion, the evolutionary history of this diverse group of advanced ceratopsians does not branch neatly along two lineages, the Protoceratopsidae and Ceratopsidae. Evidence abounds for the monophyly of the Ceratopsidae, the most obvious of which includes the absence of premaxillary teeth, double-rooted cheek teeth, enlarged external nares, postorbital horn cores, elongate prepubic processes, and increase in body size (Sereno 1984). Some protoceratopsids, however, are more closely related to

Classification of Ornithischia

Order ORNITHISCHIA Seeley 1888
Lesothosaurus
Parvorder GENASAURIA, new

Nanorder THYREOPHORA Nopcsa 1915, emended
Scutellosaurus
Hypoorder THYREOPHOROIDEA Nopcsa 1928, emended
Scelidosaurus
Minorder EURYPODA, new
Suborder STEGOSAURIA Marsh 1877
Huayangosaurus
Family STEGOSAURIDAE Marsh 1880
Dacentrurus
Kentrosaurus
Lexovisaurus
Paranthodon
Stegosaurus
Tuojiangosaurus
Wuerhosaurus
Suborder ANKYLOSAURIA Osborn 1923
Family NODOSAURIDAE Marsh 1890
Hylaeosaurus
Polacanthus
Subfamily PANOPLOSAURINAE Nopcsa 1929
Panoplosaurus
Sauropelta
Silvisaurus
Struthiosaurus
Family ANKYLOSAURIDAE Brown 1908
Shamosaurus
Talarurus
Subfamily ANKYLOSAURINAE Nopcsa 1918
Ankylosaurus
Euoplocephalus
Pinacosaurus
Saichania
Tarchia
Nanorder CERAPODA, new
Hypoorder EUORNITHOPODA, new
Suborder HETERODONTOSAURIA Cooper 1985, emended
Abrictosaurus
Family XIPHOSAURIDAE, new
Heterodontosaurus
Lanasaurus
Lycorhinus
Suborder ORNITHOPODA Marsh 1871
Infraorder HYPSILOPHODONTIA Cooper 1985, emended
Thescelosaurus
Family HYPSILOPHODONTIDAE Dollo 1882
Hypsilophodon
Othnielia
Parksosaurus
Yandusaurus
Zephyrosaurus
Infraorder IGUANODONTIA Dollo 1888, emended
Tenontosaurus
Gigafamily DYROMORPHA, new
Megafamily DRYOSAUROIDEA, new
Dryosaurus
Valdosaurus
Megafamily ANKYLOPOLLEXIA, new
Camptosaurus
Grandfamily STYRACOSTERNA, new
Probactrosaurus
Hyperfamily IGUANODONTOIDEA Hay 1902, emended
Iguanodon
Superfamily HADROSAUROIDEA, new
Ouranosaurus
Family HADROSAURIDAE Cope 1869
Hypoorder MARGINOCEPHALIA, new
Suborder PACHYCEPHALOSAURIA Maryańska and Osmólska 1975
Wannanosaurus
Infraorder GOYOCEPHALIA, new
Goyocephale
Superfamily HOMALOCEPHALOIDEA, new
Homalocephale
Family THOLOCEPHALIDAE, new
Stegoceras
Subfamily DOMOCEPHALINAE, new
Pachycephalosaurus
Prenocephale
Suborder CERATOPSIA Marsh 1890
Psittacosaurus
Infraorder NEOCERATOPSIA, new
Leptoceratops
Microorder CORONOSAURIA, new
Bagaceratops
Microceratops
Protoceratops
Superfamily CERATOPSOIDEA Hay 1902
Montanoceratops
Family CERATOPSIDAE Marsh 1888

ceratopsids than others. Thus *Leptoceratops* appears to be the most primitive protoceratopsid, lacking the frontoparietal depression, parietal fenestrae, and greatly expanded parietal–squamosal frill of other protoceratopsids and ceratopsids (Figure 6, node 30; Table 1). *Montanoceratops,* on the other hand, appears to be the most derived protoceratopsid, sharing with ceratopsids the enlargement of the external nares, a broad-based nasal horn core, and at least a crescent-shaped anterior atlar intercentrum (Figure 6, node 32; Table 1) (Sereno 1984). The Mongolian protoceratopsids — *Bagaceratops, Microceratops,* and *Protoceratops* — are more advanced than *Leptoceratops* but less advanced than *Montanoceratops.*

Summary

In view of the large array of morphologic specializations unique to ornithischians, it is possible to state with little reservation that all ornithischian dinosaurs descended from a common ancestor that existed no later than the Late Triassic, approximately 200 million years ago.

The phylogenetic relationships for the diverse group of dinosaurs in the Order Ornithischia can be summarized as follows:

• *Lesothosaurus,* from the Lower Jurassic upper Stormberg Group of South Africa, is the most primitive ornithischian described to date and represents the sister taxon to other ornithischians.

• The Thyreophora is a monophyletic taxon when restricted to include armored ornithischians such as *Scutellosaurus, Scelidosaurus,* stegosaurs, and ankylosaurs.

• Within the Thyreophora, *Scelidosaurus* and *Scutellosaurus* represent successively more remote outgroups to a monophyletic taxon comprising the stegosaurs and ankylosaurs. *Huayangosaurus* is the primitive sister taxon within the Stegosauria. The Ankylosauria can be divided into the monophyletic Families Nodosauridae and Ankylosauridae, with *Hylaeosaurus* and *Shamosaurus* representing primitive sister taxa, respectively.

• Ornithopods (sensu stricto), heterodontosaurs, pachycephalosaurs, and ceratopsians form a monophyletic group that includes the majority of ornithischian taxa. Within this large assemblage, limited evidence favors a close relationship between heterodontosaurs and ornithopods and between pachycephalosaurs and ceratopsians.

• *Abrictosaurus* is the primitive sister taxon among heterodontosaurs.

• The Suborder Ornithopoda — redefined to exclude *Lesothosaurus,* heterodontosaurs, pachycephalosaurs, and psittacosaurs — is composed of two monophyletic subgroups: hypsilophodonts, and iguanodonts and hadrosaurs. *Thescelosaurus* is the primitive sister taxon among hypsilophodonts. *Tenontosaurus* and *Dryosaurus* are primitive members of the iguanodont–hadrosaur subgroup. Iguanodonts, alone, do not constitute a monophyletic taxon and can be more simply arranged as a sequence of sister taxa to the Family Hadrosauridae.

• Within the Suborder Pachycephalosauria, the flat-headed pachycephalosaurs of the Family Homalocephalidae do not constitute a monophyletic group, but rather can be arranged as a series of sister taxa to the partially and fully domed forms.

• *Psittacosaurus* is the primitive sister taxon among ceratopsians. Although the Family Ceratopsidae is unquestionably monophyletic, protoceratopsids do not appear to constitute a monophyletic group. Among protoceratopsids, *Leptoceratops* is the most primitive and *Montanoceratops* the most derived.

The classification at left reflects the phylogenetic history of the Ornithischia as summarized above. Following Farris (1976), redundant (monotypic) taxa are avoided, and new categorical ranks are introduced to preserve the ranks of traditional monophyletic taxa.

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