

SYSTEMATICS OF HYSILOPHODONTIDAE AND BASAL IGUANODONTIA (DINOSAURIA: ORNITHOPODA)

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The phylogenetic relationships of species attributed to the ornithopod family Hypsilophodontidae are evaluated using morphological characters from the skull, dentition, and postcranium. Based on our analyses, Hypsilophodontidae constitutes a monophyletic taxon that comprises the sister taxon to Iguanodontia, together forming Euornithopoda. Three clades within the family are consistently demonstrated: *Zephyrosaurus schaffi*+*Orodromeus makelai*, *Parksosaurus warreni*+*Hypsilophodon foxii*, and *Yandusaurus hongheensis*+*Othnielia rex*. *Thescelosaurus neglectus* is the sister taxon to these six genera and constitutes the basal hypsilophodontid. *Tenontosaurus tilletti* is the basal member of Iguanodontia, with species of *Dryosaurus* and *Camptosaurus* as higher taxa within the clade. To understand the effects missing data may have on tree topology, tree length, and consistency indices, poorly represented characters were secondarily removed from the character matrix. In these analyses, all relationships remain stable, but tree length and consistency index decrease with increasingly more complete culled data sets. An average of 42.5 million years is accumulated as minimal divergence time for the hypsilophodontid and basal iguanodontian relationships described here. These figures underscore the large amount of hypsilophodontid evolution yet unaccounted for in the fossil record.

KEY WORDS: Systematics, Hypsilophodontidae, Iguanodontia, missing data, PAUP analysis, minimal divergence time.

INTRODUCTION

The past decade has witnessed a virtual explosion in dinosaur studies. This research reflects, in part, changing views on systematic approaches to phylogenetic reconstruction. Increasing interest in the phylogenetic systematics of dinosaurs dates principally to the publication of several short papers in conjunction with the Third Symposium on Mesozoic Terrestrial Ecosystems in Tübingen, Federal Republic of Germany, in 1984, and to 1986 with Gauthier's revision of Saurischia and Sereno's revision of Ornithischia (Milner and Norman, 1984; Norman, 1984a; Paul, 1984; Sereno, 1984, 1986; Gauthier, 1986).

Within the broad phylogenetic framework elaborated by these studies, a number of controversial relationships remain within Dinosauria. Among these are Maniraptora (a polytomy of derived theropods) and basal Sauropodomorpha within Saurischia (Gauthier, 1986; Sereno, 1989; Norman, 1990a; Galton, 1990), and Marginocephalia (Pachycephalosauria+Ceratopsia) and Hypsilophodontidae within Ornithischia (Sereno, 1986; Sues and Norman, 1990; Dodson, 1990; Norman, 1990b). The last, a plexus of ornithopod taxa, known from the Middle Jurassic through the Cretaceous (170–65 mybp), forms the basis of this study.

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Ornithopoda consists of three major clades, with a number of intercalated taxa (Figure 1; see Sereno, 1986; Cooper, 1985; Weishampel and Witmer, 1990; Sues and Norman, 1990; Weishampel and Horner, 1990). Hadrosauridae and a number of successive outgroup taxa constitute Iguanodontia, itself the sister taxon of Hypsilophodontidae. Together, Iguanodontia and Hypsilophodontidae together constitute a monophyletic clade, Euornithopoda. Finally, Euornithopoda and its sister taxon Heterodontosauridae comprise Ornithopoda. [This usage of Euornithopoda and Ornithopoda differs from that suggested by Sereno (1986). See Weishampel (1990a) for historical and logical justification for use advocated here.] Of these, hypsilophodontids and basal iguanodontians form the principal focus of this study.

Hypsilophodontidae was originally erected by Dollo (1882) to include those ornithopods with a single row of teeth, four functional pedal digits, and a rhomboid sternum. The sole hypsilophodontid known to Dollo was *Hypsilophodon foxii* itself. With the addition of new taxa, the family was revised by Sternberg (1940) to include a variety of small to medium-sized ornithopods with premaxillary teeth, sacra consisting of six vertebrae, and proximally expanded ischium, among other features. Included in Sternberg's hypsilophodontids were *H. foxii*, *Dryosaurus* (= *Dysalotosaurus*) *lettowvorbecki*, *Parksosaurus warreni*, and species of *Thescelosaurus*. Galton's (1972) Hypsilophodontidae comprised those ornithopods with tooth rows set in from the sides of the jaws, randomly-formed dental wear surfaces, and elongate tibiae. Included were *Dryosaurus*, *Parksosaurus*, and *Hypsilophodon*, among other less well known genera.

The application of cladistic analyses to dinosaur phylogeny resulted in a slightly different interpretation of hypsilophodontid relationships. Sereno's (1986) comprehensive study of Ornithischia is the only work to date that attempts to assess phylogenetic relationships among these animals. He established Hypsilophodontia in which *Thescelosaurus* stands as the sister taxon to Hypsilophodontidae. Hypsilophodontidae consists of an unresolved cluster of four genera (*Othnielia*, *Hypsilophodon*, *Zephyrosaurus*, *Yandusaurus*). Although they do not attempt a resolution of relationships, Sues and Norman (1990) apply the

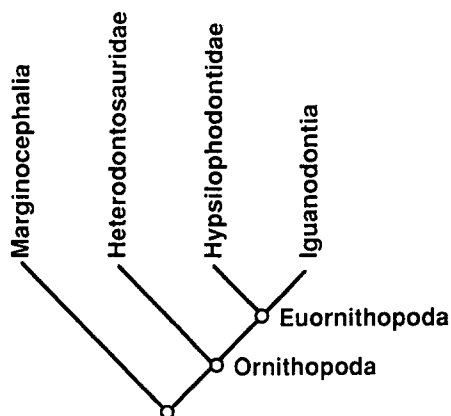


Figure 1 Relationships of Ornithopoda (after Sereno, 1986).

name Hypsilophodontidae to the entire clade, more or less along the lines of Sternberg's prior usage. We follow Sues and Norman (1990) here.

The numerical cladistic analyses presented here attempt to assess the affinities of forms that are generally regarded as hypsilophodontids. In doing so, we naturally are interested in the distribution of characters among basal iguanodontians. Particularly relevant to this distribution are the relationships of *Dryosaurus* and *Tenontosaurus* to remaining taxa.

Historically, *Dryosaurus* has been regarded as hypsilophodontid (Sternberg, 1940; Galton, 1977, 1981, 1983; Cooper, 1985), whereas *Tenontosaurus* was originally described as a member of Iguanodontidae (Ostrom, 1970). Only recently has *Dryosaurus* been separated from Hypsilophodontidae to form, along with *Valdosaurus*, a monophyletic Dryosauridae (Milner and Norman, 1984; Sues and Norman, 1990). Likewise, *Tenontosaurus* has been reclassified as a hypsilophodontid (Dodson, 1980; Weishampel and Weishampel, 1983; Weishampel, 1984; Norman, 1984a, b, 1986, 1990b). More recently, *Tenontosaurus* has been positioned closer to what Ostrom (1970) originally suggested, that is as the most primitive iguanodontian (Serenó, 1986; see also Sues and Norman, 1990; Forster, 1990).

In order to resolve the evolutionary relationships of hypsilophodontid and basal iguanodontian taxa (i.e., *Dryosaurus* and *Tenontosaurus*), we analyzed a broad array of skeletal characters. The distribution and polarity of these characters are evaluated using *Camptosaurus* and higher iguanodontians and heterodontosaurids as outgroups. Because of the vagaries of preservation, the character matrix used in our numerical phylogenetic analyses is incomplete. Hence, we follow up our initial analyses by an attempt to understand the effects of these missing data on tree topology. Finally, we discuss the minimal boundary for divergence times within the euornithopodan clade by comparing the stratigraphic distributions of the taxa under consideration.

MATERIALS AND METHODS

Thirteen hypsilophodontid and iguanodontian species distributed in twelve genera were selected for numerical phylogenetic analyses (Appendix 1) using 37 cranial, dental, and postcranial characters (Appendix 2). None of the characters analyzed are autapomorphic for taxa under consideration. All data were collected from specimens clearly referable to the taxa under consideration (including new information on *Orodromeus*, courtesy of J.R. Horner), with the exception of *Yandusaurus* and the HMN material of *Dryosaurus lettowvorbecki*, for which data were obtained from He (1979) and He and Cai (1983), and Janensch (1955) and Galton (1983), respectively. All characters are described in some detail in order to be as explicit as possible about the form of each (Appendix 3; Figures 2–7). Many of these characters are also illustrated. We also included some of the characters used by Sereno (1986) and Norman (1990b) as apomorphies for relevant nodes; only some of these are figured. Characters are binary, being scored as either primitive (0) or derived (1), and all are given equal weight although character 35, position of the obturator process, could not be polarized (see Appendix 3 for a discussion of this character) and was therefore run unordered. Using the branch-and-bound and accelerated transformation algorithms provided by Phylogenetic Analysis Using Parsimony (PAUP, version 2.4; Swofford, 1985), the most

parsimonious trees were generated from our data set. All trees were rooted to a hypothetical ancestor using the hypothetical-ancestor/root-to-ancestor option.

As noted earlier, *Camptosaurus dispar* was used to establish the character distribution for the iguanodontian clade. Additional higher iguanodontians (e.g., species of *Iguanodon*, *Ouranosaurus nigeriensis*) also were consulted at this level. A second outgroup consisted of *Heterodontosaurus tucki*, and to a lesser extent, *Abrictosaurus consors*. These outgroups provided the basis for establishing character polarity relative to hypsilophodontid taxa, *Tenontosaurus*, and *Dryosaurus*.

One of our characters (position of obturator process; character 35) presented a problem in terms of polarity. Since the obturator process is absent in Heterodontosauridae, basally in Marginocephalia (absent in Pachycephalosauria and *Psittacosaurus*), and possibly basally in Thyreophora (i.e., absent in *Scelidosaurus*), it is impossible to polarize the position of the obturator process in euornithopodans. Consequently, we ran character 35 as an unordered feature (using the UNORD option of PAUP), thereby letting tree topology independently assess polarity for obturator process position.

Not included in this analysis are a number of ornithopod taxa (*Leaellynasaura*, *Atlascoposaurus*, and *Fulgotherium*) from Australia referred by Rich and Rich (1989) to Hypsilophodontidae, *?Thescelosaurus garbanii* and *?Thescelosaurus* sp., both from South Dakota (Morris, 1976), and *Drinker nisti* from Wyoming (Bakker *et al.*, 1990). The Australian taxa and *?Thescelosaurus garbani* have been omitted from consideration because their preservation is limited and thus deemed insufficient for character analysis. Material pertaining to *?Thescelosaurus* sp. and *Drinker nisti* was not included because they were unavailable when these analyses were conducted. In addition, *Rhabdodon priscus* from Europe (Nopsca, 1902, 1904) is presently under study (Norman *et al.*, in prep.).

Two kinds of PAUP analyses were run. The first analyses was based on the entire 37-character data matrix. The second analysis attempted to evaluate the problems associated with missing data within the matrix. In this second approach, those characters poorly known across taxa were deleted prior to running PAUP. The resulting tree topologies therefore were based on fewer but potentially more informative characters. By comparing topologies, tree length, and consistency indices from Analysis 1 and Analysis 2, we have attempted to assess the effects of missing data on tree stability. In addition, we ran our analyses using the accelerated transformation optimization (ACCTRAN). This option maximizes the ratio of reversals to parallelisms within a given cladogram. In order to evaluate these impositions of synapomorphies low on the tree, we also used delayed transformation optimization (DELTRAN) to maximize parallelisms relative to reversals. These regions of ambiguity with respect to parallelism and reversal are identified where they occur and discussed in the context of their impact on the tree.

Because monophyletic clades imply sequential derivation of new taxa, it is possible to link the topology of a given clade with the stratigraphic distribution of taxa. This linkage implies that the common ancestor for each monophyletic taxon must have an age no younger than the oldest member within the two included derived taxa. The difference in age between sister taxa is the minimal divergence time within the clade. These minimal divergence times, as estimates of the lower boundary of the completeness of the fossil record, were calculated from the phylogenetic information based on the PAUP analyses of hypsilophodontids and basal iguanodontians.

ANALYSES

Analysis 1—Full Data Set

Analysis 1 employed the entire data set of 37 characters. A single most parsimonious tree topology was generated, summarized in Figure 7. The tree is 57 steps in length and has a consistency index of 0.649.

Euornithopoda Hypsilophodontidae and Iguanodontia are united at Node 0 to form *Euornithopoda* based on the following synapomorphies:

- 1) absence of a jugal boss [10; reversed at Node 6],
- 2) angle less than 100° between prepubic process and pubis [32; reversed in *Yandusaurus*].

Four additional characters are ambiguous with respect to apomorphies at Node 0: contact between the dorsal process of the premaxilla and the rostral process of the nasal [3], absence of contact between the caudolateral process of the premaxilla and the rostral portion of the lacrimal [4], relatively short palpebral [9], presence of ossified hypaxial tendons [27], and most caudal flexure of the humerus at the level of the deltopectoral crest [29]. Using the ACCTRAN option in PAUP, each of these features is imposed as synapomorphies for *Euornithopoda* and then reversed at Node 8. However, independent acquisition of these features by Hypsilophodontidae and *Tenontosaurus* may be equally likely (DELTRAN option of PAUP). Without prior knowledge of the probability of reversal and convergence among these features, these five features must remain ambiguous at the level of *Euornithopoda*.

Hypsilophodontidae Analysis 1 supports monophyly of Hypsilophodontidae, with inclusion of *Zephyrosaurus*, *Orodromeus*, *Parksosaurus*, *Hypsilophodon*, *Yandusaurus*, *Othnielia*, and *Thescelosaurus* (Node 1). The features that diagnose Hypsilophodontidae are few in number, but clearly separate these taxa from those of the iguanodontian clade. Hypsilophodontid synapomorphies include:

- 1) absence of ridges that culminate in marginal denticles on the heavily enamelled surface of cheek teeth [21; reversed in *Hypsilophodon*],
- 2) presence of a cingulum on dentary teeth [24],
- 3) ossification of the sternal segments of the cranial dorsal ribs [26],
- 4) rod-shaped prepubic process [31].

Among these taxa, *Thescelosaurus* represents the basal member within the hypsilophodontid clade. Features that diagnose hypsilophodontids above *Thescelosaurus* (Node 2) include: transverse width of the combined frontals less than their rostrocaudal length [12] and an angle of approximately 35° between the base and long axis of the braincase [16]. This basal hypsilophodontid position confirms Sereno's (1986) placement of *Thescelosaurus*.

The remaining six hypsilophodontids are paired to form three small clades, *Yandusaurus+Othnielia* (Node 4), *Parksosaurus+Hypsilophodon* (Node 5), and *Zephyrosaurus+Orodromeus* (Node 6). *Yandusaurus+Othnielia* is the most basal of these clades, diagnosed by the following synapomorphies: reduction of quadratojugal [15; found also at Node 8], dorsal curvature of the pubis [33], dorsal curvature of the ischial mid-shaft region [34; also found in *Parksosaurus*], and an

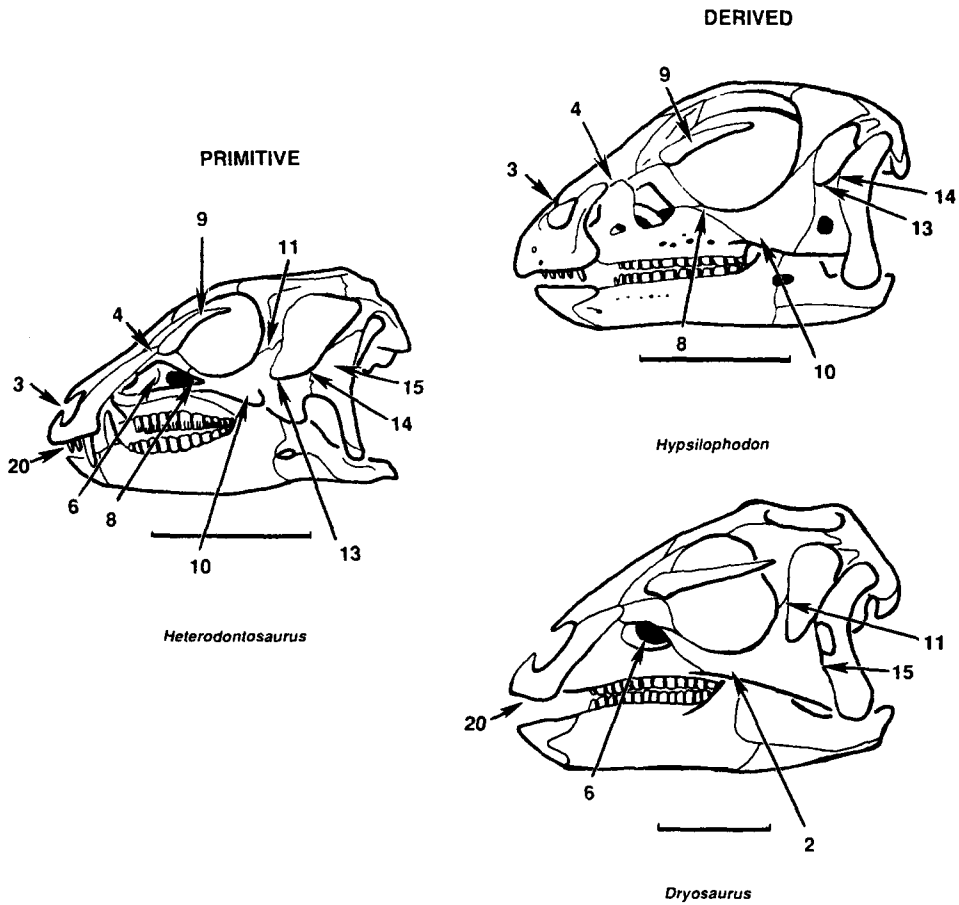


Figure 2 Skull in left lateral view. The primitive conditions are found at left (*Heterodontosaurus*) and the derived conditions are found at right (*Hypsilophodon*, *Dryosaurus*). Numbers refer to characters described in the text. Scale=5 cm.

angle greater than 100° between the femoral neck and shaft [36; also found in *Hyposilophodon*].

Taxa at Node 3 are united by reduction of the caudal process of the jugal to form only the ventral margin (and not part of the caudal margin) of the infratemporal fenestra [14; also found in *Tenontosaurus*]. Our unordered running of character 35 (position of the obturator process) suggests that a distal placement for this process may also be derived for Node 3. Within this clade of higher hypsilophodontids, the *Parksosaurus*+*Hypsilophodon* clade (Node 5) is united solely by the exclusion of the jugal from contact with the antorbital fenestra [8, also found in *Tenontosaurus*]. A single character also unites the *Zephyrosaurus* and *Orodromeus* clade (Node 6): development of a jugal boss [reversal of 10; also found in *Heterodontosaurus*].

Iguanodontia Using the entire matrix, the iguanodontian clade consists of *Tenontosaurus*, *Dryosaurus*, and *Camptosaurus* (plus higher iguanodontians not analyzed here). This clade (Node 7) can be diagnosed by the following characters:

- 1) eversion of the oral margin of the premaxilla [1],
- 2) enlarged external nares relative to the orbit [2],
- 3) circular or ovate antorbital fossa [6; also found in *Parksosaurus*],
- 4) relatively small external antorbital opening [7; also found in *Parksosaurus*],
- 5) denticulate oral margin of the prementary [17],
- 6) paired ventral process of prementary [18],
- 7) parallel dorsal and ventral margins of the dentary [19],
- 8) loss of premaxillary teeth [20],
- 9) humeral length less than scapular length [28],
- 10) loss of phalanx from manual digit II [30],
- 11) deep cranial intercondylar groove on the distal femur [37].

Within Iguanodontia, *Tenontosaurus* is the basal member of the clade, as

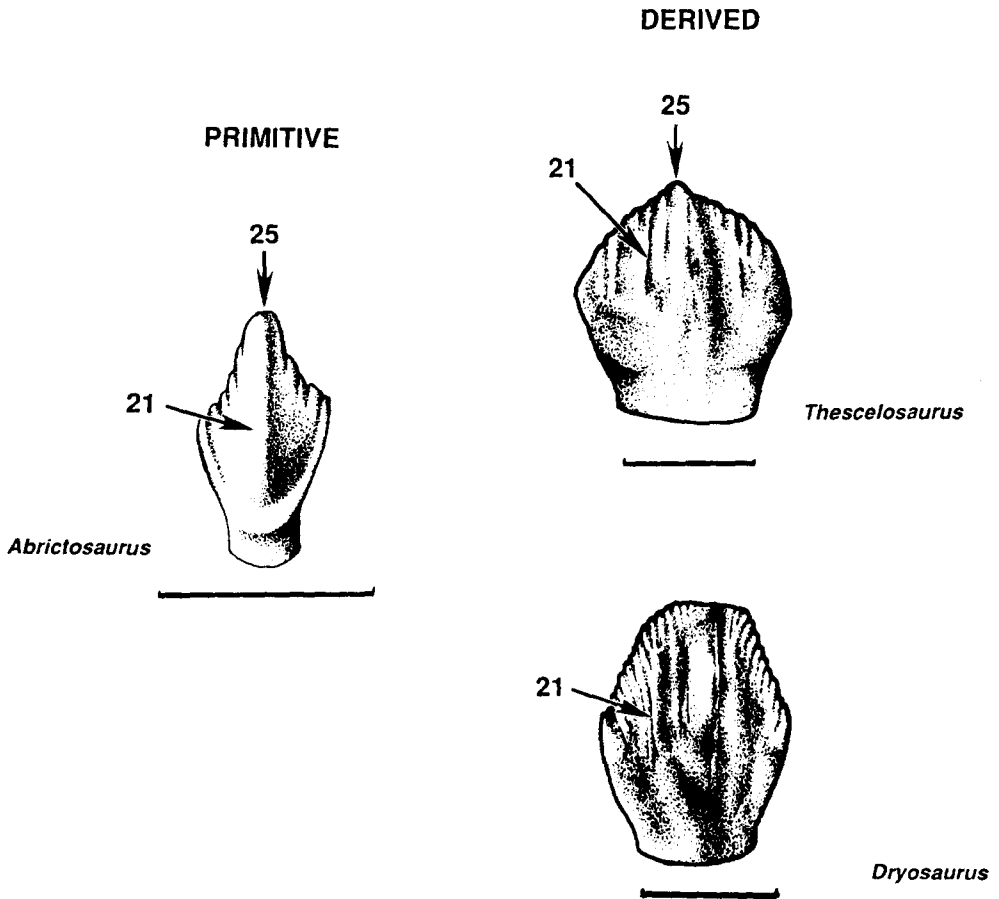


Figure 3 Lingual view of dentary tooth and buccal view of maxillary tooth. The primitive conditions are found at left (*Abrictosaurus*) and the derived conditions are found at right (*Thescelosaurus*, *Dryosaurus*). Numbers refer to characters described in the text. Scale=5 mm.

previously indicated by Sereno (1986) and Sues and Norman (1990). Characters allying *Dryosaurus* with higher iguanodontians (Node 8; *Dryomorpha sensu* Sereno, 1986) include presence of a second (rostromedial) maxillary process [5], a somewhat out-turned jugal-postorbital articulation [11; found also in *Zephyrosaurus*], reduction of the quadratojugal [15; also found at Node 4], and relatively high maxillary tooth crowns [22; also found in *Parksosaurus*]. Delayed transformation (DELTRAN option) also places characters 3, 4, 9, 27, and 29 at this node, as discussed above. Since the ACCTRAN option places these same characters as synapomorphies for Euornithopoda, they must be considered ambiguous for iguanodontian relationships as well.

In summary, Analysis 1 provides complete resolution of the relationships of all of the taxa under consideration. Hypsilophodontidae and Iguanodontidae together constitute a monophyletic Euornithopoda. Hypsilophodontidae is monophyletic. *Thescelosaurus* is the basal member of Hypsilophodontidae. Higher clades within this family include *Yandusaurus*+*Othnielia* (Node 4), *Parksosaurus*+*Hypsilophodon* (Node 5), and *Zephyrosaurus*+*Orodromeus* (Node 6). *Tenontosaurus* represents the basal iguanodontian and sister taxon to a clade formed by *Dryosaurus* and *Camptosaurus* (and with them, all higher iguanodontians).

Analysis 2—The Effects of Missing Data

Missing data are the result of several factors. One is that characters present in available material may not be accessible given the condition of the fossils. For example, a diverticulum within the body of the premaxilla (see Sereno, 1986) may be present, but verification of this feature across taxa requires special contexts, such as broken material or radiographic examination, which is not always available. The other major factor limiting the availability of character information is the differential preservation of material referred to a taxon. It is the latter that is of significance to this study.

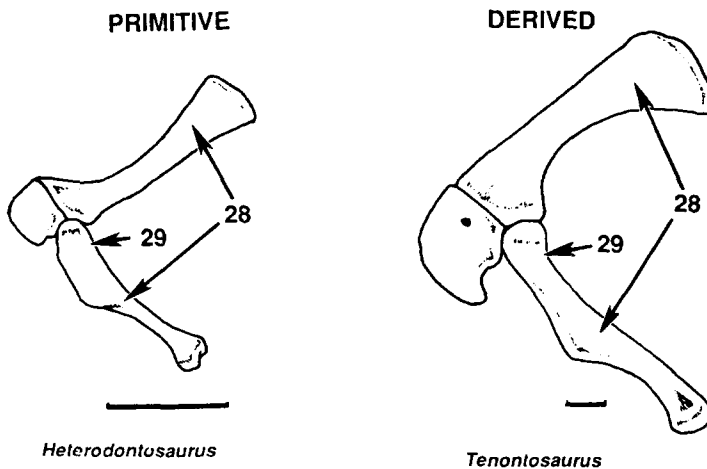


Figure 4 Scapula and humerus in lateral view. The primitive conditions are found at left (*Heterodontosaurus*) and the derived conditions are found at right (*Tenontosaurus*). Numbers refer to characters described in the text. Scale=10 cm.

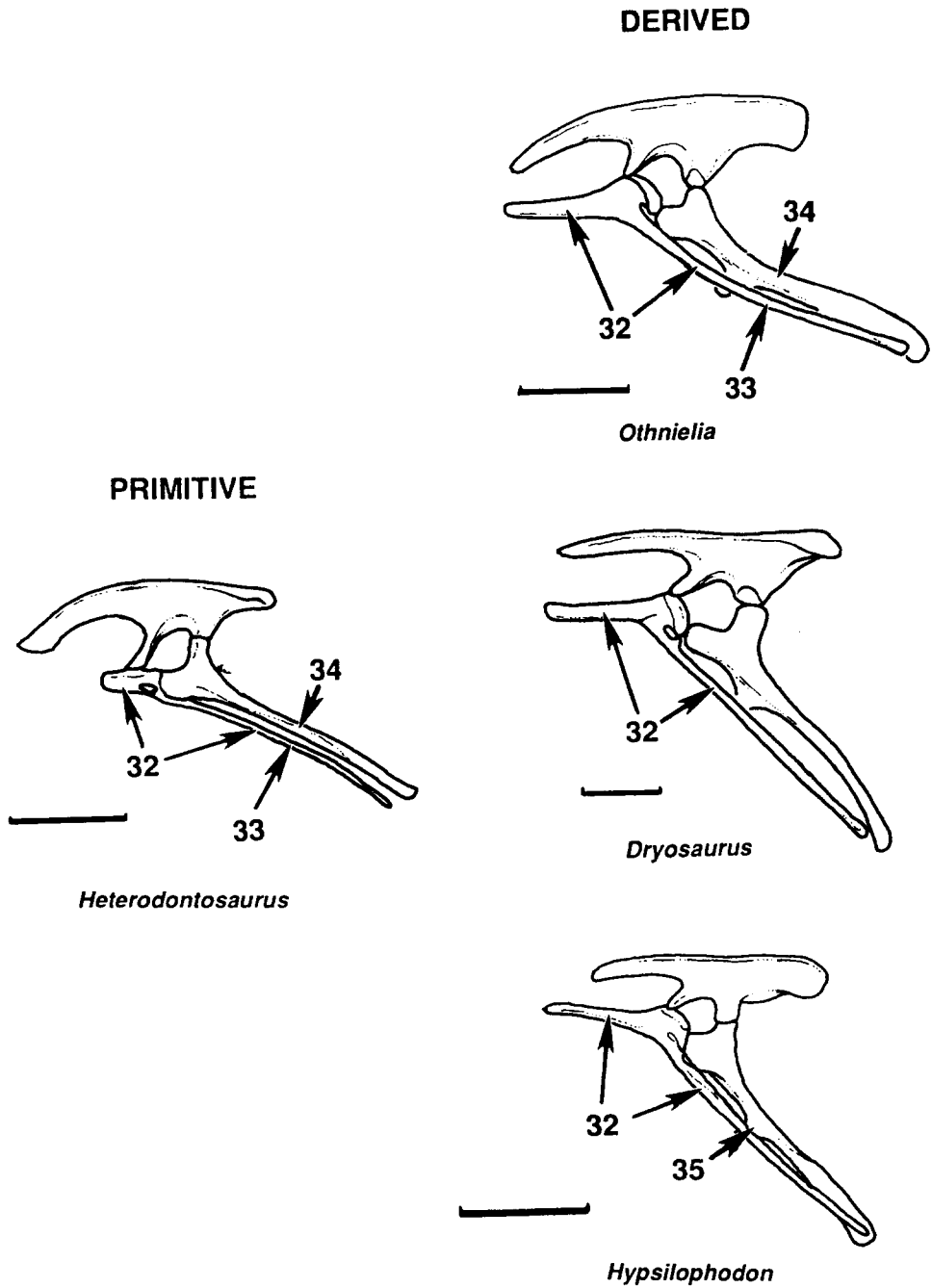


Figure 5 Pelvis in left lateral view. The primitive conditions are found at left (*Heterodontosaurus*, *Dryosaurus*) and the derived conditions are found at right (*Hypsilophodon*, *Othnielia*). Numbers refer to characters described in the text. Scale=10 cm.

Missing data comprise 28% of the character matrix used here. These missing data are not evenly distributed, but rather are clumped within the matrix. For example, *Zephyrosaurus* data are nearly 60% incomplete, due simply to the fact that this taxon is known almost exclusively from the skull. Other taxa suffer from similar limitations. How these missing data affect the levels of apomorphy within Hypsilophodontidae and between Hypsilophodontidae and Iguanodontia is of some concern.

Given the occurrence of missing data, it is important to understand how the phylogenetic algorithm deals with them. PAUP handles missing data in a reasonably straightforward manner. When information on a particular character is missing for a particular taxon, PAUP treats this non-information as equivalent to all possible states. The effect of this treatment is that all missing states are filled in according to what would be the most parsimonious character state had it not been missing, and the tree topology and length is then computed. Thus, a character with missing data will not affect the location to which an unplaced taxon is positioned in a given tree; its location is determined by those characters with on whose significance the tree is constructed.

The consequence of manipulating missing data in this fashion is that some of the synapomorphies at a given node may be absent in one of the two sister taxa. For instance, two of the three euornithopodan synapomorphies identified in this study are missing in basal members of Hypsilophodontidae. Likewise, a number of other nodes are characterized by synapomorphies that are not in fact present in one of the two sister taxa. As noted by Sanderson and Donoghue (1989), these phantom synapomorphies have the effect of artificially increasing the consistency index.

In order to assess the relative importance of missing data, those characters most

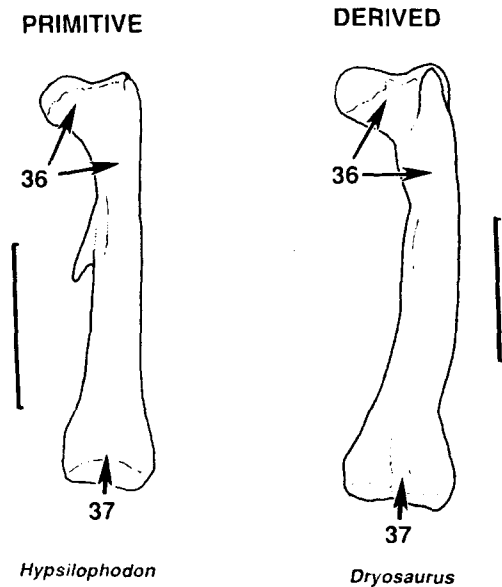


Figure 6 Femur in cranial view. The primitive conditions are found at left (*Dryosaurus*) and the derived conditions are found at right (*Hypsilophodon*). Numbers refer to characters described in the text. Scale=10 cm.

poorly known across taxa were eliminated from the character matrix. In our second set of analyses (Analysis 2), PAUP was run twice using only those characters complete in 55% (6 out of 11) and 64% (7 out of 11) of the taxa considered. In the first part of Analysis 2, four characters [3, 17, 18, 31] were removed from the original data matrix; in the second part, five additional characters [1, 2, 5, 27, 30] were removed. Thus, data matrices consisted of 33 and 28 characters respectively, resulting in data sets with successively more positive information about the character distribution among taxa.

The first part of Analysis 2 (55% completeness level) produced a single tree topologically identical to that described in Analysis 1 (Figure 8). The only structural differences are a reduction in tree length from 57 to 52 steps and a slight decrease in the consistency index from 0.649 to 0.635. Reduction of tree length is distributed in both Hypsilophodontidae and Iguanodontia. In Hypsilophodontidae, character 31 is lost, while in Iguanodontia characters 17 and 18 are lost. Character 3, which may be a euornithopodan synapomorphy or a derived character uniting *Dryosaurus* with "higher" iguanodontians is also lost.

Likewise, in the 64% completeness level there is a single tree that is identical with the previous two, although shorter (46 steps) and with a lower consistency index (0.609). In this second part of the culled analyses, reduction of tree length is concentrated principally within Iguanodontia. This group of euornithopodans loses an additional three synapomorphies [1, 2, 30] at its base and another synapomorphy [5] at Node 8. Character 27 is also lost as a synapomorphy at either Node 0 or Node 8. In contrast, Hypsilophodontidae loses no further synapomorphies at the 64% completeness level.

DISCUSSION

The study presented here, while upholding many of the phylogenetic relationships recently suggested for hypsilophodontids and basal iguanodontians, also documents that changes in tree length and consistency index are a function of the quality of the data base. Eliminating poorly known characters decreases both tree length and consistency index, because consistency index increases when PAUP replaces missing data with the most parsimonious character state (Sanderson and Donoghue, 1989). Consequently, it is not surprising that these consistency indices decrease in the culled analyses. Reduced consistency indices are to be expected when more complete subsets of data are run.

In view of the impact of missing data on tree structure and statistics, how complete data sets should be for numerical phylogenetic analyses becomes important. The way that PAUP handles missing data (i.e., designating features as synapomorphies though missing in one of the two united taxa) may be preferable (Analysis 1). These phantom synapomorphies then constitute predictions about their presence in these as yet incomplete taxa, should better material be found in the future. In contrast, it may be appropriate to use only those characters that have at least a minimal level of completeness among the taxa being considered, perhaps at a 50% level or better, to insure that available data provide positive information about a given character (Analysis 2). In this way, the impact of missing data on tree topology is reduced or eliminated. Finally, it is important that character completeness levels be explicitly noted by workers, given that there are alternative ways of viewing the impact of missing data on tree structure and statistics.

In addition to evaluating how character-set quality affects tree stability, we have

also identified characters that are ambiguous with respect to reversal and convergence. The probability that a feature is more likely to reverse or to arise independently in several lineages may prove to be character-specific and thus not knowable without additional information (e.g., functional linkages, developmental constraints) not found in the character matrix. Although we clearly have not solved this problem, we have at least identified where these ambiguities accrue by running in tandem the ACCTRAN and DELTRAN options of PAUP.

In an attempt to understand how complete the hypsilophodontid fossil record is at present, we calculated minimal times of divergence using the results of our phylogenetic analyses. Our approach to the combination of phylogeny and stratigraphy is somewhat similar to that of Norell (MS), who calculated temporal extensions of lineages as a function of sister relationship. Our stratigraphic data for hypsilophodontids and basal iguanodontians are taken from Weishampel (1990b), Sues and Norman (1990), and Norman and Weishampel (1990); these data are indicated in Table 1 (geochronology after Harland *et al.*, 1982). The cladogram portrayed in Figure 7 can be broken into pairwise assessments of minimal divergence times. Beginning at the top of the hypsilophodontid cladogram (Node 6), the affiliation of *Zephyrosaurus* with *Orodromeus* suggests that at least six biostratigraphic stages (about 40 million years) are missing from the history of this small clade. The stratigraphic distribution of *Parksosaurus* and *Hypsilophodon* implies that a minimum of seven stages (approximately 49 million years) of clade record (Node 5) are missing. Together, these two clades diverged at least by the Barremian/Aptian, indicating that only a short period of time (approximately 4 million years) separates Node 3 from included clades (Nodes 5

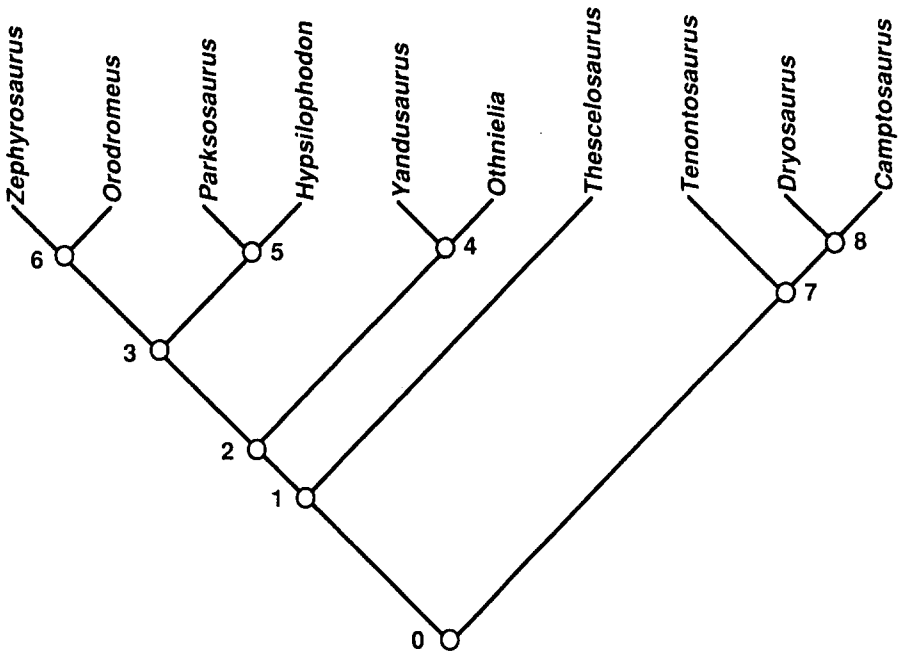


Figure 7 Cladogram of Hypsilophodontidae and basal Iguanodontia resulting from analyses of complete and culled data matrix.

and 6). This clade of *Orodromeus*+*Zephyrosaurus* and *Hypsilophodon*+*Parksosaurus* thus ranks among the more complete records of euornithopodan taxa.

The linking of *Othnielia* and *Yandusaurus* (Node 4) suggests that the fossil record of this small clade is missing on the order of three stages (approximately 19 million years). Hence, this clade falls within the middle range of completeness among euornithopodans. Furthermore, the *Othnielia*+*Yandusaurus* clade must have diverged from remaining higher hypsilophodontids (Node 2) by at least the Bathonian/Callovian (age of *Yandusaurus*), indicating that at least eight stages (approximately 50 million years) are missing from this portion of the hypsilophodontid fossil record.

Finally, the pairing of *Thescelosaurus* with remaining hypsilophodontids (Node 1) suggests that a great deal of the fossil history preceding the occurrence of this taxon is missing. That is, some 15 stages intervene between the oldest member of the sister taxon to *Thescelosaurus*, the clade of "higher" hypsilophodontids containing *Yandusaurus*, and *Thescelosaurus* itself. These 15 stages amount to approximately 105 million years.

Table 1 Stratigraphic and geographic distribution of Hypsilophodontidae and basal Iguanodontia

| Taxon | Stratigraphic distribution | Geographic distribution |
|---|-----------------------------------|--|
| <i>Yandusaurus hongheensis</i> He, 1979 | Bathonian/Callovian | Sichuan, People's Republic of China |
| <i>Othnielia rex</i> Marsh, 1877 | late Kimmeridgian-early Tithonian | Colorado, Utah, Wyoming, U.S.A. |
| <i>Dryosaurus altus</i> Marsh, 1878 | late Kimmeridgian-early Tithonian | Colorado, Wyoming, and Utah, U.S.A. |
| <i>Camptosaurus dispar</i> Marsh, 1879 | late Kimmeridgian-early Tithonian | Wyoming, Utah, Colorado, and Oklahoma, U.S.A. |
| <i>Hypsilophodon foxii</i> Huxley, 1869 | Barremian/Aptian | Isle of Wight, England |
| <i>Zephyrosaurus schaffi</i> Sues, 1980 | late Aptian | Montana, U.S.A. |
| <i>Tenontosaurus tilletti</i> Ostrom, 1970 | late Aptian | Wyoming and Montana, U.S.A. |
| <i>Orodromeus makelai</i> Horner et Weishampel, 1988 | late Campanian | Montana, U.S.A. |
| <i>Parksosaurus warreni</i> Parks, 1926 | early Maastrichtian | Alberta, Canada |
| <i>Thescelosaurus neglectus</i> Gilmore, 1913 | late Maastrichtian | Wyoming, Montana, South Dakota, and Colorado, U.S.A., and Alberta and Saskatchewan, Canada |

Within Iguanodontia, the union of *Dryosaurus* and *Camptosaurus* (Node 8) implies essentially no divergence time within the clade. Hence, the fossil record can be interpreted as being reasonably complete in this example. It is certainly the best record of euornithopodans. The larger clade of *Tenontosaurus*, *Dryosaurus*, and *Camptosaurus* (Node 7) indicates that at least six stages (approximately 35 million years) of missing information is present in this group of basal iguanodontians.

Finally, the union of Hypsilophodontidae and Iguanodontia to form Euornithopoda (Node 0) constitutes a minimal divergence time of approximately 19 million years.

These minimal divergence times were averaged across the euornithopodan cladogram, yielding a mean value of 35.5 million years accumulated per node. For Hypsilophodontidae alone, mean minimal divergence time is 44.5 million years. With the removal of *Thescelosaurus*, mean minimal divergence time for Hypsilophodontidae drops to 32.5 million years. It is interesting to note that this level of divergence times is well above that calculated for Dinosauria (13.5 million years; Weishampel, in prep.). Among these dinosaurian minimal divergence times, the node that unites *Thescelosaurus* with other hypsilophodontids in fact represents the highest minimal divergence time among all Dinosauria, slightly more than the 86 million years and 84 million years that constitute the minimal divergence times for Saurischia and Ornithopoda+Marginocephalia (Cerapoda *sensu* Sereno, 1986), respectively. Certainly for hypsilophodontids (and to a lesser degree for basal iguanodontians and Dinosauria in general), these mean minimal divergence times underscore the large amounts of evolution and numbers of taxa that are as of yet missing from the fossil record. Focussing on hypsilophodontids, the high values in each analysis are driven by the relatively great disparity in the ages between paired taxa, particularly *Thescelosaurus* and the clade of higher hypsilophodontids that includes *Yandusaurus* (i.e., Node 1 in Figure 7). New euornithopodan taxa, especially those whose relationships proved close to *Thescelosaurus*, *Yandusaurus*, and/or *Parksosaurus* and whose occurrences bridge their temporal distribution, would help immensely in reducing divergence times within the clade.

In summary, the analyses presented here uphold the status of Hypsilophodontidae as a monophyletic taxon. Within Hypsilophodontidae, all relationships among taxa appear to be stable irrespective of the completeness of the data set. Furthermore, *Tenontosaurus* stands as the basal member of Iguanodontia. It is also clear that the imperfections of the hypsilophodontid and basal iguanodontian fossil record are substantial and that the discovery of new taxa may alter these evaluations of affinity through the acquisition of new information.

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APPENDIX I

Alphabetical Listing of Species (and Specimens) Used in This Study

ABBREVIATIONS: AMNH: American Museum of Natural History, New York, New York, United States; BPI: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; BSP: Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Federal Republic of Germany; CCG: Chengdu College of Geology, Chengdu, Sichuan, People's Republic of China; CM: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, United States; GPIT: Geologisch-Paläontologisches Institut, Tübingen, Federal Republic of Germany; HMN: Humboldt Museum für Naturkunde, Berlin, Federal Republic of Germany; MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts, United States; MOR: Museum of the Rockies, Bozeman, Montana, United States; NHM: Natural History Museum, London, England; NMC: National Museum of Canada, Ottawa, Ontario, Canada; ROM: Royal Ontario Museum, Toronto, Ontario, Canada; SAM: South African Museum, Cape Town, South Africa; USNM: United States National Museum of Natural History, Washington, D.C., United States; YPM: Yale Peabody Museum, New Haven, Connecticut, United States; YPM-PU: Yale Peabody Museum—Princeton Collection, New Haven, Connecticut, United States.

Abrictosaurus consors (NHM UCL A.100, B.54)

Camptosaurus dispar (YPM 1880, 1886, 1887, 7416; USNM 5473, 5818, 5996, 5998, 7416)

Dryosaurus altus (CM 3392; YPM 1876)

Dryosaurus lettowvorbecki (HMN dyA, dyB, dy13, dy16, dy729; BSP AS I834; GPIT 1595/13-25)

Heterodontosaurus tucki (SAM 337, 1332)

Hypsilophodon foxii (NHM R196, R197, R2471, R2477, R8367, R8419)

Lanasaurus scalpridens (BPI 4244)

Orodromeus makelai (MOR 238, 294, 303, 403, YPM-PU 22412, 23431, 23432)

Othnielia rex (YPM 1882, 1915, USNM 5808, 5829, MCZ 4454)

Parksosaurus warreni (ROM 804)

Tenontosaurus tilletti (AMNH 3010, 3014, 3017, 3031, 3034, 3050, 3061; MCZ 4305, 4388, 7556, 7558; UPM 3201, 5456, 5461, 5463, 5465, 5468, 5472, 5478, 5481)

Thescelosaurus neglectus (NMC 8537; USNM 2944, 8258, 8259)

Yandusaurus hongheensis (CCG T6001, T6002)

Zephyrosaurus schaffi (MCZ 4392)

APPENDIX II

Character-Taxon Matrix

| | |
|--------------------------|---|
| Hypothetical Ancestor | 0000000000 0000000000 0000000000 00000000 |
| <i>Heterodontosaurus</i> | 0000000000 0000000000 9090900000 9000900 |
| <i>Camptosaurus</i> | 1100111901 1000101111 0100109101 0100001 |
| <i>Thescelosaurus</i> | 9999999999 0009909900 1011111090 9100000 |
| <i>Yandusaurus</i> | 9091900011 0100199999 1001999010 9011010 |
| <i>Othnielia</i> | 9999999999 9999999990 1011019019 9111010 |
| <i>Parksosaurus</i> | 9991911199 0109099909 1191911099 9991100 |
| <i>Hypsilophodon</i> | 0011000111 0111010000 0001011010 1100110 |
| <i>Zephyrosaurus</i> | 0919099910 1109919990 1001099999 9999999 |
| <i>Orodromeus</i> | 9999900010 0101019909 1091099019 1990100 |
| <i>Tenontosaurus</i> | 1111011111 0011001111 0000001111 0100001 |
| <i>Dryosaurus</i> | 1100111001 1000101111 0100000109 0100001 |

APPENDIX III

Cranial Characters

1. Everted oral margin of the premaxilla. In Ornithiscia ancestrally, the narial portion of the body of the premaxilla is relatively flat. This primitive condition is known to be retained in *Heterodontosaurus*, *Abriostosaurus*, *Hypsilophodon*, and *Zephyrosaurus*. By contrast, the ventral aspect of the body of the premaxilla expands laterally (i.e., is everted), so as to broaden the floor of the narial fossa in *Tenontosaurus*, *Dryosaurus* (viz., GPIT uncatalogued, HMN dy 14; *contra* Galton, 1983), and “higher” iguanodontians. Sereno (1986) interpreted eversion of the ventral premaxillary margin as a synapomorphy of Iguanodontia. However, Norman (1990b) noted that eversion of the premaxilla may be size-related. It may be true that premaxillary eversion is associated with positively allometric growth, but such a statement simply shifts emphasis to the consequences of size. Thus it could be argued that large size then takes value as a phylogenetically significant character. Given this size-related context and the absence of character 1 among basal ornithischians, eversion of the oral margin of the premaxilla is considered to be the modified state. This character constitutes a synapomorphy for Iguanodontia in our analyses of the entire data matrix. This evaluation supports the interpretation of Sereno (1986). Character 1 is lost as an iguanodontian synapomorphy due to its incomplete nature in the 64% culled analyses.

2. Enlarged external nares relative to the size of the orbit. Primitively, the external nares are small (less than 15% basal skull length) in *Lesothosaurus*, *Thyreophora*, *Heterodeontosaurus*, *Abriostosaurus*, *Yandusaurus*, and *Hypsilophodon* (other, more poorly preserved taxa may also have the condition, but this is not yet known). In contrast, the external nares are at least 20% basal skull length in *Tenontosaurus*, *Dryosaurus*, and “higher” iguanodontians. Although enlarged external nares may be positively allometrically related to body size (Norman, 1990b), this condition then becomes a consequence of large size,

which then becomes the phylogenetically significant character (see Character 1). In our analyses, character 2 is positioned as a synapomorphy of Iguanodontia, as originally indicated by Sereno (1986). Like character 1, however, this feature has a high level of missing data and was deleted in the 64% culled analysis.

3. Overlap of the dorsal process of the premaxilla onto the rostral process of the nasal (Figure 2). Primitively in *Heterodontosaurus*, *Dryosaurus*, and *Camptosaurus*, the dorsal process of the premaxilla fails to contact the rostral process of the nasal. Thus there is no bony union directly above the external naris. Compared to this ancestral condition, the dorsal premaxillary process forms a prominent scarf joint with the rostral process of the nasal in *Hypsilophodon*, *Zephyrosaurus*, and *Tenontosaurus*. This transformation is apparently unrelated to body size given the size-disparity between *Heterodontosaurus* and *Camptosaurus* (absence of contact) and between *Hypsilophodon* and *Tenontosaurus* (contact). Given its taxonomic distribution, character 3 is ambiguous with respect to the cladogram presented in this paper. It may constitute a synapomorphy for Euornithopoda or instead may be independently acquired by Hypsilophodontidae and *Tenontosaurus*. In the 55% culled analysis, character 3 is lost.

4. Absence of contact between the caudolateral process of the premaxilla and the lacrimal (Figure 2). The caudolateral premaxillary process (equivalent to the lateral premaxillary process of Weishampel, 1984; the posterolateral premaxillary process of Sereno, 1986) reaches and laterally overlaps the lacrimal primitively in *Heterodontosaurus*, *Dryosaurus*, and *Camptosaurus*. Compared to this ancestral condition, the caudolateral process of the premaxilla is reduced such that it terminates above the antorbital fossa some distance from the lacrimal in *Yandusaurus*, *Parksosaurus*, *Hypsilophodon*, and *Tenontosaurus*. Reduction of the caudolateral premaxillary process in these latter taxa is a reversal of the primitive condition found in Ornithischia (Gauthier, 1986; Sereno, 1986). Like character 3, however, character 4 is ambiguous with respect to its phylogenetic significance. It may be a synapomorphy for Euornithopoda or its acquisition may be independent in Hypsilophodontidae and *Tenontosaurus*.

5. Development of a second (rostromedial) maxillary process. Primitively in Ornithischia, the rostral end of the maxilla bears a single process that is lodged under or along the medial aspect of the body of the premaxilla. This ancestral condition is retained in *Heterodontosaurus*, *Hypsilophodon*, *Zephyrosaurus*, and *Tenontosaurus* (Weishampel, 1984; Sereno, 1986). In contrast, there is a second, rostromedial maxillary process in *Dryosaurus* (HMN dyB; *contra* Galton, 1983), *Camptosaurus*, and "higher" iguanodontians (although lost in lambeosaurine hadrosaurids; Weishampel, 1984; Sereno, 1986; see also Horner, 1990 for a somewhat different interpretation). The consequence of the evolution of this rostromedial process is to provide additional support to the premaxilla-maxilla joint, presumably related refinements of the pleurokinetic jaw mechanism in these animals (Weishampel, 1984; Norman, 1984; Norman and Weishampel, 1985). In our analyses of the complete data matrix, character 5 constitutes a synapomorphy of *Dryosaurus*+*Camptosaurus* (Node 8; *Dryomorpha sensu* Sereno, 1986). This feature is lost at the 64% completeness level.

6. Circular or ovate antorbital fossa (Figure 2). In Dinosauria ancestrally, the antorbital fossa is triangular, with the horizontal base of the triangle formed from the maxillary body directly above the tooth row. The dorsal process of the maxilla, directly under the maxilla-premaxilla contact, and the lacrimal form the remainder of the triangle. This primitive condition is retained in *Heterodontosaurus*, *Yandusaurus*, *Hypsilophodon*, and *Orodromeus*, among those euornithopodan taxa

for which there is appropriately preserved material. In contrast, the antorbital fossa in *Tenontosaurus* and *Dryosaurus* is circular or ovate, bounded ventrally, rostrally, and dorsally by the maxilla, and caudally by the lacrimal. Analysis of the complete data matrix identifies character 6 as a synapomorphy of Iguanodontia, thereby supporting Sereno's (1986) interpretation.

7. Relatively small external opening of the antorbital fossa. In the unnamed taxon consisting of *Euparkeria*+crown-group Archosauria (Benton, 1990), the external opening of the antorbital fossa is large. *Heterodontosaurus*, *Abrictosaurus*, *Yandusaurus*, *Hypsilophodon*, and *Orodromeus* have an antorbital fossa as much as 25% basal skull length, thus retaining this ancestral condition. In contrast to this condition, the external opening of the antorbital fossa is relatively small (10% basal skull length or less) in *Dryosaurus*, *Camptosaurus*, and *Tenontosaurus*. Reduction of the antorbital opening in *Parksosaurus* is convergent with respect to the relationships under consideration. This feature constitutes a synapomorphy for Iguanodontia, as indicated by Sereno (1986).

8. Exclusion of the jugal from the antorbital fossa by contact between the maxilla and jugal (Figure 2). The jugal forms a small portion of the caudal margin of the antorbital fossa primitively in Ornithischia. This feature is retained in *Heterodontosaurus*, *Yandusaurus*, *Orodromeus*, and *Dryosaurus*. *Parksosaurus*, *Hypsilophodon*, and *Tenontosaurus* differ from this ancestral condition; the jugal in these taxa is excluded from the antorbital fossa by the lacrimal-maxilla contact. The small clade of *Parksosaurus*+*Hypsilophodon* (Node 5) is united by character 8. Lack of participation of the jugal in the margin of the antorbital fossa in *Tenontosaurus* is then interpretable as an independent acquisition.

9. Relatively short palpebral (Figure 2). Ancestrally, the palpebral is 80–100% of the maximal rostrocaudal width of the orbit (viz., *Heterodontosaurus*, *Camptosaurus*, and *Dryosaurus*). In contrast, shortening of the palpebral (approximately 49–70% the maximal rostrocaudal width of the orbit) is seen in *Yandusaurus*, *Hypsilophodon*, *Zephyrosaurus*, *Orodromeus*, and *Tenontosaurus*. Given this taxonomic distribution, the significance of character 9 is ambiguous with the cladogram of Hypsilophodontidae and basal Iguanodontia. It may constitute a synapomorphy for Euornithopoda or it may have been independently acquired by Hypsilophodontidae and *Tenontosaurus*.

10. Absence of a jugal boss (Figure 2). In *Psittacosaurus*, possibly in Pachycephalosauria, and *Heterodontosaurus*, a boss is present along the ventral border of the body of the jugal (Weishampel and Witmer, 1990; Maryńska, 1990; Sereno, 1990). Consequently, this feature is regarded as primitive for Cerapoda (i.e., Ornithopoda+Marginocephalia; Sereno, 1986). This condition is also found in *Zephyrosaurus* and *Orodromeus*. In contrast, the derived state, loss of the jugal boss, is seen in *Yandusaurus*, *Hypsilophodon*, *Tenontosaurus*, and *Camptosaurus*. Character 10 constitutes a synapomorphy of Euornithopoda and its reversal a synapomorphy of *Zephyrosaurus*+*Orodromeus* (Node 6).

11. Partially laterally-facing jugal-postorbital articulation (Figure 2). In Ornithopoda ancestrally, the jugal-postorbital articulation is inturned so as to face rostrally. This condition is found in *Heterodontosaurus*, *Thescelosaurus*, *Yandusaurus*, *Parksosaurus*, *Hypsilophodon*, *Orodromeus*, and *Tenontosaurus* (Weishampel, 1984). The derived condition, a partially laterally-facing articulation between the jugal and postorbital, is found in *Camptosaurus*, *Zephyrosaurus*, and *Dryosaurus*. Character 11 stands as a synapomorphy for *Dryosaurus*+*Camptosaurus* (Node 8; Dryomorpha *sensu* Sereno, 1986). Independent acquisition of character 11 is seen in *Zephyrosaurus*.

12. Paired frontals longer than wide. Wide frontals (i.e., width of the paired frontals greater than or equal to their rostrocaudal length of the same elements) arose prior to the evolution of Heterodontosauridae among ornithopods. This ancestral condition is retained only in *Heterodontosaurus*, but also in *Camptosaurus*, *Thescelosaurus*, *Tenontosaurus*, and *Dryosaurus*. Narrowing of the frontals, the derived condition, is seen in *Yandusaurus*, *Parksosaurus*, *Hypsilophodon*, and *Orodromeus*. Character 12 constitutes a synapomorphy of Hypsilophodontidae above *Thescelosaurus* (Node 2), as also noted by Sereno (1986).

13. Ventral margin of the infratemporal fenestra well above the level of the orbit (Figure 2). As in *Ornithosuchia* ancestrally, the ventral margin of the infratemporal fenestra extends to or below the level of the base of the orbit in *Heterodontosaurus*, possibly in *Abrictosaurus*, and in *Camptosaurus*, *Thescelosaurus*, *Yandusaurus*, *Parksosaurus*, *Zephyrosaurus*, *Orodromeus*, and *Dryosaurus*. In contrast, elevation of the ventral margin of the infratemporal fenestra to a position well above the level of the base of the orbit is present in *Hypsilophodon* and *Tenontosaurus*. In our analyses, character 13 stands as an autapomorphy for both *Hypsilophodon* and *Tenontosaurus*.

14. Caudal process of the jugal limited to the ventral margin of the infratemporal fenestra (Figure 2). Because of its dorsal curvature, the caudal process of the jugal forms the caudoventral margin of the infratemporal fenestra ancestrally in Ornithopoda, where it is found in *Heterodontosaurus*, *Yandusaurus*, *Dryosaurus*, and *Camptosaurus*. Reduction of the caudal process of the jugal, possibly related to enlargement of the infratemporal fenestra and the adductor chamber, is apomorphically present in *Hypsilophodon*, *Orodromeus*, and *Tenontosaurus*. In our analyses, character 14 constitutes a synapomorphy at Node 3 (e.g., *Zephyrosaurus*+*Orodromeus*+*Parksosaurus*+*Hypsilophodon*). It is also independently derived in *Tenontosaurus*.

15. Reduced quadratojugal (Figure 2). In Archosauria ancestrally, the quadratojugal is large relative to the quadrate. Within Ornithopoda, the former element extends dorsally and contacts the prequadratic process of the squamosal in *Heterodontosaurus*. It is only slightly shorter in *Parksosaurus*, *Hypsilophodon*, *Orodromeus*, and *Tenontosaurus*, where it covers most of the rostral margin of the quadrate, but does not contact the prequadratic process of the squamosal. In contrast, a reduced quadratojugal with no contact with the prequadratic process of the squamosal is considered derived. This apomorphy is seen in *Yandusaurus*, *Camptosaurus*, and *Dryosaurus* (the last appears to have a very small—or absent?—quadratojugal). Character 15 independently diagnoses the small clade of *Yandusaurus*+*Othnielia* (Node 4), as well as the clade of *Dryosaurus*+*Camptosaurus* (Node 8; *Dryomorpha sensu* Sereno, 1986).

16. High angle between the base and long axis of the braincase. Primitively for Ornithopoda (Sereno, 1986), the long axis of the braincase makes an angle greater than 35° with the ventral margin of the braincase (i.e., occipital condyle, basal tubera, and basiptyergoid processes). Among these animals, *Heterodontosaurus*, *Thescelosaurus*, *Dryosaurus*, and *Camptosaurus* retain this ancestral condition. The derived condition, in which the long axis of the braincase makes an angle less than or equal to 35° with the ventral margin of the braincase, is seen in *Hypsilophodon*, *Zephyrosaurus*, and *Orodromeus*. As Sereno (1986) noted, character 16 constitutes a synapomorphy for Hypsilophodontidae above *Thescelosaurus* (Node 2).

17. Denticulate oral margin of the predentary. Ancestrally, the oral margin of

the predentary is relatively smooth (viz., *Marginocephalia*, *Stegosauria*, *Lesothosaurus*). This primitive condition is retained in *Heterodontosaurus*, *Abrictosaurus*, and *Hypsilophodon*, among well-preserved ornithopods. The development of a denticulate oral margin on the dentary is apomorphically found in *Camptosaurus*, *Tenontosaurus*, and *Dryosaurus*. In our analysis of the complete data matrix, character 17 forms a synapomorphy for Iguanodontia (see also Sereno, 1986). However, because of its relatively high levels of missing data, this character is lost in the 55% culled analysis.

18. Paired ventral process of the predentary. Primitively, the ventral process of the predentary is single among ornithischians, a condition retained in *Heterodontosaurus*, *Abrictosaurus*, and *Hypsilophodon*, among ornithopods for which there is direct fossil evidence. The apomorphic acquisition of a paired ventral process occurs in *Dryosaurus*, *Camptosaurus*, and *Tenontosaurus* (Sereno, 1986). As Sereno (1986) noted, this feature constitutes a synapomorphy for Iguanodontia in our analysis of the complete data matrix. However, like character 17, it is also lost as a derived feature in our 55% culled analysis.

19. Parallel margins of the dentary. Ancestrally for Ornithopoda (and in fact for Ornithischia), the dorsal and ventral margins of the dentary converge rostrally. Retention of this feature is found in *Heterodontosaurus*, less so in *Abrictosaurus*, and in *Thescelosaurus*, *Parksosaurus*, *Hypsilophodon*, and *Orodromeus*. A dentary with parallel dorsal and ventral margins is found in *Dryosaurus* (HMN dyB, BSP AS I834; *contra* Galton, 1983), *Camptosaurus*, and *Tenontosaurus* (Sereno, 1986). Biomechanical scaling may have an effect here (Norman, 1990b), but the same phylogenetic interpretations of body size may be applied here as they were in character 1 and 2. Character 19 stands as a synapomorphy for Iguanodontia in all of our analyses, in support of Sereno's (1986) prior interpretation.

Dental Characters

20. Absence of premaxillary teeth (Figure 2). Peg-like premaxillary teeth are present ancestrally in Ornithischia. Within Ornithopoda, this condition is retained in *Heterodontosaurus*, *Thescelosaurus*, *Othnielia*, *Hypsilophodon*, and *Zephyrosaurus*. Unlike these animals, *Dryosaurus*, *Tenontosaurus*, and *Camptosaurus* are known to have no premaxillary teeth (Sereno, 1986). This apomorphy arose convergently in the majority of neoceratopsians and ankylosaurs. As does Sereno (1986), all of our analyses position character 20 as a synapomorphy for Iguanodontia.

21. Presence of ridges confluent with marginal denticles of cheek teeth (Figure 3). In Ornithischia primitively, denticles are present along the mesial and distal margins of both maxillary and dentary teeth. These denticles, however, are not supported by (i.e., are not confluent with) ridges on the well-enameled buccal surface of maxillary teeth and lingual surface of dentary teeth. This condition is retained in *Abrictosaurus*, *Camptosaurus*, *Hypsilophodon*, *Tenontosaurus*, and *Dryosaurus*, among ornithopods. In contrast, marginal denticles are supported by ridges in *Thescelosaurus*, *Yandusaurus*, *Othnielia*, *Parksosaurus*, *Zephyrosaurus*, and *Orodromeus*. Character 21 constitutes a synapomorphy of Hypsilophodontidae. Within this taxon, it is reversed in *Hypsilophodon*.

22. Relatively high maxillary tooth crowns. In Ornithopoda ancestrally, maxillary tooth crowns are relatively stout (i.e., never more than 50% higher than mesiodistally wide; *Abrictosaurus*, *Heterodontosaurus*, *Thescelosaurus*,

Yandusaurus, *Othnielia*, *Hypsilophodon*, *Zephyrosaurus*, *Orodromeus*, *Tenontosaurus*). In contrast to these taxa, *Camptosaurus*, *Parksosaurus*, and *Dryosaurus* have maxillary tooth crowns 50% or more higher than mesiodistally wide. Character 22 stands as a synapomorphy to *Dryosaurus*+*Camptosaurus* (Node 8; Dryomorpha *sensu* Sereno, 1986). This feature also arose independently in *Parksosaurus*.

23. Central placement of the apex of maxillary crowns. In Ornithischia ancestrally, the apex of the crowns is placed distal to vertical mid-axis of the tooth. This condition is retained in *Abrictosaurus*, *Lanasaurus*, *Camptosaurus*, *Yandusaurus*, *Hypsilophodon*, *Zephyrosaurus*, *Tenontosaurus*, and *Dryosaurus*. *Thescelosaurus* and *Othnielia* constitute the only ornithopod taxa under consideration in which the apex of maxillary tooth crowns has migrated to a central position. Our analyses suggest that character 23 was gained autapomorphically in *Othnielia* and *Thescelosaurus*.

24. Presence of a cingulum on dentary teeth. Among ornithopods, absence of a cingulum on dentary teeth is ancestrally found in *Heterodontosaurus*, *Camptosaurus*, *Tenontosaurus*, and *Dryosaurus*. A cingulum at the base of dentary crowns, developed to some degree in *Thescelosaurus*, *Yandusaurus*, *Othnielia*, *Parksosaurus*, *Hypsilophodon*, *Zephyrosaurus*, and *Orodromeus*, consequently is interpreted as the apomorphic condition among these taxa. Character 24 constitutes a synapomorphy for Hypsilophodontidae.

25. Distal placement of the apex of dentary crowns (Figure 3). In *Abrictosaurus*, possibly in *Heterodontosaurus*, *Hypsilophodon*, *Zephyrosaurus*, *Orodromeus*, *Tenontosaurus*, *Dryosaurus*, and *Othnielia*, the apex of dentary crowns is centrally placed with respect to the mid-axis of the crown. This condition appears to be ancestral not only for Ornithopoda, but also for Ornithischia, as it is primitively present in basal Marginocephalia, basal Thyreophora, and *Lesothosaurus*. Shift of the apex to a more distal position is seen as independent acquisition in *Thescelosaurus* and *Camptosaurus*. The derived nature of character 25 in the latter taxon may indicate an ankylopollexian synapomorphy (*sensu* Sereno, 1986). Norman (1990b) interpreted the central placement of the primary ridge (which then culminates in the crown apex) as the derived condition for his Hypsilophodontia (our Hypsilophodontidae). This appears not to be the case if we have properly assessed character polarity.

Postcranial Characters

26. Partial ossification of the sternal segments of the cranial dorsal ribs. Primitively in Dinosauria, there appears to be no ossification of the sternal segments of the cranial dorsal ribs. Since there is no evidence of this kind of ossification in *Heterodontosaurus*, *Camptosaurus*, *Tenontosaurus*, and *Dryosaurus*, lack of sternal rib ossification is seen as primitive for these taxa within Ornithopoda. Such a condition contrasts with partial ossification of sternal rib segments in *Thescelosaurus*, *Othnielia*, and *Hypsilophodon*. Sereno (1986) and Forster (1990) interpreted this ossified condition as a synapomorphy of Hypsilophodontia, a conclusion borne out by our analyses.

27. Ossified hypaxial tendons. Ancestrally in Ornithischia, there is no ossification of the hypaxial tendons within the tail. *Heterodontosaurus* and *Dryosaurus* (taxa for which there is positive evidence) retain this condition. In contrast, *Hypsilophodon*, *Thescelosaurus*, *Parksosaurus*, and *Tenontosaurus*

ossify the hypaxial tendons in the caudal skeleton. Sereno (1986), Forster (1990), and Norman (1990b) diagnosed Hypsilophodontidae in part on this feature. However, Forster (1990) went on to note the potentially ambiguous nature of ossified hypaxial tendons, a view substantiated by these analyses. The presence of ossified hypaxial tendons can equally parsimoniously diagnose Euornithopoda or might independently be gained by Hypsilophodontidae and *Tenontosaurus*.

28. Humeral length less than scapular length (Figure 4). The length of the humerus is greater than or equal to the length of the scapula ancestrally in Ornithischia. Ornithopod taxa that retain this condition include *Heterodontosaurus*, *Thescelosaurus*, *Yandusaurus*, *Othnielia*, *Parksosaurus*, *Hypsilophodon*, and *Orodromeus*. In contrast, the proximal portion of the forelimb becomes abbreviated in *Camptosaurus*, *Tenontosaurus*, and *Dryosaurus*. This shortening of the humerus relative to the scapula is therefore considered derived for Iguanodontia (viz., Sereno, 1986; Forster, 1990; *contra* Norman, 1990b, who interpreted relative humeral lengthening as derived).

29. Caudal flexure of the humerus at the level of the deltopectoral crest (Figure 4). At the level of the deltopectoral crest, the caudal border of the humerus is primitively straight in *Heterodontosaurus*, *Camptosaurus*, and *Dryosaurus*. In contrast, the caudal border of the humerus develops a modest caudal flexure in *Yandusaurus*, *Othnielia*, *Hypsilophodon*, *Orodromeus*, and *Tenontosaurus*. Our analyses indicate that character 29 is ambiguous with respect to euornithopodan relationships being either a synapomorphy for Euornithopoda or an independent acquisition of Hypsilophodontidae and *Tenontosaurus*.

30. Loss of distal phalanx in manual digit II. Primitively for Ornithopoda, the manual digital formula is 2-3-4-3-2. *Heterodontosaurus*, *Thescelosaurus*, *Yandusaurus*, and *Hypsilophodon* all retain this plesiomorphy. However, in *Camptosaurus* and *Tenontosaurus*, digit II of the manus loses its distal phalanx. Consequently, character 30 constitutes a synapomorphy for Iguanodontia, confirming Sereno's (1986) interpretation.

31. Rod-shaped prepubic process. A short or flattened prepubic process has a primitive distribution for Ornithischia, a condition also retained in *Camptosaurus*, *Tenontosaurus*, and *Dryosaurus*. The apomorphic state, a rod-shaped prepubic process that is wider transversely than dorsoventrally, is seen in *Hypsilophodon* and *Orodromeus* (Sereno, 1986). Sereno (1986) and Forster (1990) diagnosed Hypsilophodontidae in part on this feature and our analyses confirm this interpretation.

32. Angle less than 100° between prepubic process and pubic shaft (Figure 5). Ancestrally in Ornithischia, the prepubic process makes a relatively large angle (greater than 150°) with the shaft of the pubis. This plesiomorphy is retained in a few ornithopod taxa, among them *Heterodontosaurus* and *Yandusaurus*. Decrease in angle (i.e., less than 100°) is found in *Camptosaurus*, *Thescelosaurus*, *Othnielia*, *Hypsilophodon*, *Tenontosaurus*, and *Dryosaurus*. Such a broad-based distribution for this derived condition allots it as a synapomorphy of Euornithopoda.

33. Dorsally-curved pubic shaft (Figure 5). The shaft of the pubis is primitively straight in Ornithischia, a condition retained in *Heterodontosaurus*, *Camptosaurus*, *Thescelosaurus*, *Hypsilophodon*, *Tenontosaurus*, and *Dryosaurus*, among ornithopods. In *Yandusaurus* and *Othnielia*, however, the pubic shaft becomes dorsally curved. In all of our analyses, character 33 constitutes a synapomorphy for *Yandusaurus*+*Othnielia* (Node 4).

34. Dorsal curvature of the ischial mid-shaft region (Figure 5). Ancestrally for

Ornithischia, the ischium is straight at its mid-shaft. This condition is also seen in some ornithopod taxa, among them *Heterodontosaurus*, *Dryosaurus*, *Tenontosaurus*, *Thescelosaurus*, *Hypsilophodon*, *Camptosaurus*, and *Orodromeus*. In contrast, the ischial shaft is dorsally curved in *Othnielia*, *Yandusaurus*, and *Parksosaurus*. Norman (1990b) interpreted a straight ischial shaft as a synapomorphy of Hypsilophodontia (our Hypsilophodontidae). However, our analyses suggest that a straight ischium at mid-shaft is primitive and that a dorsally curved ischial mid-shaft is a synapomorphy for the small clade of *Yandusaurus*+*Othnielia* (Node 4), independently evolved in *Parksosaurus*.

35. Distal position of obturator process (Figure 5). Because the sister-taxon to Euornithopoda and at least one successive outgroup lack an obturator process (it is absent in Heterodontosauridae, basally in Marginocephalia [absent in Pachycephalosauria and *Psittacosaurus*], and possibly basally in Thyreophora [absent in *Scelidosaurus*]), it is not possible to polarize the position of the obturator process at the level of basal euornithopodans. It can be analyzed, however, in an unordered fashion *a posteriori*. Among euornithopodans, obturator process position has the following distribution. The process is most often positioned within the proximal 20–35% of the length of the ischium (*Camptosaurus*, *Thescelosaurus*, *Yandusaurus*, *Othnielia*, *Tenontosaurus*, *Dryosaurus*). Only in *Parksosaurus*, *Hypsilophodon*, and *Orodromeus* is the obturator process positioned beyond a 40% demarcation. Our analyses of Euornithopoda, where we ran position of the obturator process as an unordered feature (UNORD option of PAUP), suggest the following polarity. The more proximal obturator process position is considered primitive in Euornithopoda, while a position beyond this 40% demarcation is derived. The derived condition thus becomes a synapomorphy of Node 3 (*Zephyrosaurus*, *Orodromeus*, *Parksosaurus*, *Hypsilophodon*). In contrast to our study, Norman (1990b) interpreted a position between one-third and one-half of the length of the ischial shaft as a synapomorphy of Hypsilophodontia (our Hypsilophodontidae). However, at the level of Euornithopoda, the position of the obturator process cannot be asserted as a synapomorphy for any of the subtaxa for the same reason that it cannot be applied at the level of basal Iguanodontia, except *a posteriori*. Finally, it should be noted that obturator process position can be *a priori* polarized at higher iguanodontian levels. For example, Sereno (1986) used his Hypsilophodontia (our Hypsilophodontidae) taxa and *Tenontosaurus* to polarize obturator position for his Dryomorpha.

36. Angle greater than 100° between the femoral neck and shaft (Figure 6). The neck of the femur makes an angle of not more than 100° with the femoral shaft plesiomorphically in Ornithopoda, retained not only in *Heterodontosaurus*, but also in *Camptosaurus*, *Thescelosaurus*, *Parksosaurus*, *Orodromeus*, *Tenontosaurus*, and *Dryosaurus*, among ornithopod taxa under consideration. In contrast, in *Yandusaurus*, *Othnielia*, and *Hypsilophodon*, the femoral neck makes an angle greater than 100° with the shaft. In our analyses, character 36 stands as a synapomorphy for *Yandusaurus*+*Othnielia* (Node 4), a condition that is independently evolved in *Hypsilophodon*.

37. Deep cranial intercondylar groove on the distal femur (Figure 6). Primitively in Ornithischia, the cranial intercondylar (extensor) groove on the distal femur is virtually nonexistent. This condition is plesiomorphically retained in *Heterodontosaurus*, *Yandusaurus*, *Othnielia*, *Orodromeus*, *Hypsilophodon*, and *Thescelosaurus*. In contrast, the cranial intercondylar groove is well developed in *Camptosaurus*, *Dryosaurus*, and *Tenontosaurus*. As noted by Sereno (1986), the

evolution of a deep cranial intercondylar groove constitutes a synapomorphy for Iguanodontia (Node 7).

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