

THE PHYLOGENY OF THE ORNITHISCHIAN DINOSAURS

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SYNOPSIS Ornithischia is a familiar and diverse clade of dinosaurs whose global phylogeny has remained largely unaltered since early cladistic analyses in the mid 1980s. Current understanding of ornithischian evolution is hampered by a paucity of explicitly numerical phylogenetic analyses that consider the entire clade. As a result, it is difficult to assess the robustness of current phylogenetic hypotheses for Ornithischia and the effect that the addition of new taxa or characters is likely to have on the overall topology of the clade.

The new phylogenetic analysis presented here incorporates a range of new basal taxa and characters in an attempt to rigorously test global ornithischian phylogeny. Parsimony analysis is carried out with 46 taxa and 221 characters. Although the strict component consensus tree shows poor resolution in a number of areas, application of reduced consensus methods provides a well-resolved picture of ornithischian interrelationships. Surprisingly, Heterodontosauridae is placed as the most basal group of all well-known ornithischians, phylogenetically distant from a stem-defined Ornithopoda, creating a topology that is more congruent with the known ornithischian stratigraphical record. There is no evidence for a monophyletic ‘Fabrosauridae’, and *Lesothosaurus* (the best-known ‘fabrosaur’) occupies an unusual position as the most basal member of Thyreophora. Other relationships within Thyreophora remain largely stable. The primitive thyreophoran *Scelidosaurus* is the sister taxon of Euryopoda (stegosaurs and ankylosaurs), rather than a basal ankylosaur as implied by some previous studies.

The taxonomic content of Ornithopoda differs significantly from previous analyses and basal relationships within the clade are weakly supported, requiring further investigation. ‘Hypsilophodontidae’ is paraphyletic, with some taxa (*Agilisaurus*, *Hexinlusaurus*, *Othnielia*) placed outside of Ornithopoda as non-cerapodans. Ceratopsia and Pachycephalosauria are monophyletic and are united as Marginocephalia; however, the stability of these clades is reduced by a number of poorly preserved basal taxa.

This analysis reaffirms much of the currently accepted ornithischian topology. Nevertheless, instability in the position and content of several clades (notably Heterodontosauridae and Ornithopoda) indicates that considerable future work on ornithischian phylogeny is required and causes problems for several current phylogenetic definitions.

KEY WORDS vertebrate palaeontology, Ornithischia, systematics, cladistics, Dinosauria

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INTRODUCTION

The clade Ornithischia represents a major grouping within Dinosauria, the most familiar and widely popularised of all extinct organisms. An ornithischian, *Iguanodon* Mantell, 1825, was the second dinosaur genus to be named, while of the three taxa explicitly included within Dinosauria by Owen (1842), two (*Iguanodon* and *Hylaeosaurus*) were later recognised as ornithischians. Since these early discoveries, a large number of genera and species of ornithischians have been named: a recent review (Weishampel *et al.* 2004a) recognised over 180 valid genera. The earliest ornithischians are known from the Carnian stage of the Late Triassic (Casamiquela 1967) and the clade disappeared in the mass extinctions at the end of the Cretaceous. During this time ornithischians achieved a global distribution and are now known from every continent, including Antarctica (e.g. Hooker *et al.* 1991; Weishampel *et al.* 2004b).

Ornithischians appear to have been extremely scarce during the Late Triassic (Serenó 1997) and remained uncommon (although apparently more diverse) during the Early and Middle Jurassic; during this time interval terrestrial ver-

tebrate faunas are dominated by saurischians (Weishampel *et al.* 2004b). Ornithischians became much more abundant during the Late Jurassic and Early Cretaceous and ornithischian diversity peaked during the Campanian stage of the Late Cretaceous. Late Triassic–Early Jurassic ornithischians were generally small-bodied (1–2 m in length) bipedal cursors (e.g. *Lesothosaurus diagnosticus*: Thulborn 1972; Sereno 1991a), but during the rest of the Mesozoic they diversified into a considerable range of morphologies and sizes, with many groups reverting to quadrupedality. The vast majority of ornithischians are believed to have been herbivorous, although some basal forms have been interpreted as potentially omnivorous (Barrett 2000).

One major problem in understanding ornithischian evolution is that, to date, there are few published numerical phylogenetic analyses dedicated solely to Ornithischia (Weishampel 2004). It is difficult, therefore, to assess the relative phylogenetic support for ornithischian clades, to look at the effects upon phylogenetic results of adding or deleting taxa or characters, or to test alternative hypotheses of taxon or character evolution. Here, we present a new phylogenetic analysis of Ornithischia, as part of an on-going study of ornithischian phylogeny.

Institutional abbreviations

- BMNH** = Natural History Museum, London, UK
BRSMG = Bristol City Museum and Art Gallery, Bristol, UK
BP = Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa
BYU = Earth Science Museum, Brigham Young University, Provo, Utah, USA
CAMSM = Sedgwick Museum, University of Cambridge, Cambridge, UK
CEUM = Prehistoric Museum, College of Eastern Utah, Price, Utah, USA
CV = Chongqing Natural History Museum, Chongqing, People's Republic of China
GCC = Museum of the Chengdu University of Technology (formerly Chengdu College of Geology), Chengdu, People's Republic of China
GI = Geological Institute, Ulaanbaatar, Mongolia
GSM = Geological Survey Museum, Keyworth, UK
GZG = Geowissenschaftliches Zentrum der Universität Göttingen, Göttingen, Germany
IGCAGS = Institute of Geology, Chinese Academy of Sciences, Beijing, People's Republic of China
IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
MCZ = Museum of Comparative Zoology, Harvard, USA
MB = Museum für Naturkunde, Berlin, Germany
MCF-PVPH = Museo Carmen Funes, Paleontología de Vertebrados Plaza Huinul, Argentina
MNA = Museum of Northern Arizona, Flagstaff, USA
MOR = Museum of the Rockies, Bozeman, Montana, USA
MPM = Museo Padre Molina, Rio Gallegos, Santa Cruz, Argentina
MWC = Museum of Western Colorado, Grand Junction, Colorado, USA
OUM = University Museum of Natural History, Oxford, UK
PVL = Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina
ROM = Royal Ontario Museum, Toronto, Ontario, Canada
SAM-PK = Iziko South African Museum, Cape Town, South Africa
SDSM = South Dakota School of Mines, Rapid City, South Dakota, USA
SGWG = Sektion Geologische Wissenschaften Greifswald, Ernst-Moritz Universität, Greifswald, Germany
UC = University of Chicago, Chicago, USA
UCMP = University of California Museum of Paleontology, Berkeley, USA
YPM = Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

ZDM = Zigong Dinosaur Museum, Dashanpu, People's Republic of China

ZPAL = Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

PREVIOUS ANALYSES OF ORNITHISCHIAN PHYLOGENY

Traditional classifications

Although material from the clade began to be described and named in the early 19th century (Mantell 1822, 1825, 1833), the recognition that ornithischians formed a grouping distinct from other reptiles (including other dinosaurs) was not reached until the work of Seeley (1887). Seeley was the first to identify and articulate a fundamental morphological dichotomy within the then described dinosaurian taxa. He recognised two orders, distinguished mainly on the basis of pelvic anatomy, that he named Ornithischia and Saurischia. Major subdivisions of Seeley's Ornithischia (Stegosauria, Ornithopoda, Ceratopsia) were identified by Marsh (1877*a*, 1881, 1890) and Marsh (1894) later grouped these subdivisions together as the order Predentata, generally considered synonymous with Ornithischia.

Nopcsa (1915) proposed a subdivision within Ornithischia, between the bipedal, unarmoured forms (ornithopods) and a new suborder that he named Thyreophora (comprising ankylosaurs, stegosaurs and ceratopsians). The grouping Thyreophora was often ignored by later workers, but the name was revived by Norman (1984) and Sereno (1984, 1986), although its current usage (for a clade consisting of all armoured ornithischians) differs somewhat from that proposed by Nopcsa (i.e. in current usage ceratopsians are not members of Thyreophora).

Romer (1956) divided Ornithischia into four suborders: Ornithopoda (including all bipedal forms), Stegosauria, Ankylosauria and Ceratopsia. Most bipedal and relatively 'unspecialised' taxa were included within Ornithopoda; other suborders were believed to be derived from within the ornithopods, although only the ceratopsians were explicitly linked with a particular group of ornithopods (the psittacosaurids).

Thulborn (1971) suggested that most of the major groups of ornithischians (e.g. iguanodontids, pachycephalosaurs, ceratopsians) were descended from a Late Triassic–Late Cretaceous 'hypsilophodont plexus', an implicitly paraphyletic grade of small, primitive, bipedal ornithopods. Ankylosaurs and stegosaurs were considered to occupy a primitive position outside of this plexus, sharing ancestors with the earliest hypsilophodontids. The details of this classification were questioned by Galton (1972), who removed *Echinodon becklesii* and *Fabrosaurus australis* from the family Hypsilophodontidae to form the family Fabrosauridae (see also Galton 1978), which included those taxa he considered to represent the most basal known ornithischians. Maryńska & Osmólska (1974) emphasised the morphological distinctness of the pachycephalosaurs, previously included as the family Pachycephalosauridae within Ornithopoda, and created a new suborder of Ornithischia, Pachycephalosauria.

In summary, pre-cladistic ornithischian classifications tended to recognise either four (Romer 1956) or five

(Maryańska & Osmólska 1974) suborders within Ornithischia. One of these suborders (Ornithopoda) was an implicitly paraphyletic grouping of taxa, defined on the basis of plesiomorphic characters (e.g. bipedality). Only a few workers (e.g. Thulborn 1971; Galton 1972) attempted to identify the pattern of interrelationships between or within these clades.

Cladistic studies

The first cladistic studies of ornithischian phylogeny were published simultaneously by Norman (1984), Milner & Norman (1984) and Sereno (1984); the results of Norman (1984) and Sereno (1984) are shown in Fig. 1A, B. Norman (1984) proposed that Ornithischia could be divided into two major groupings: Thyreophora, comprising the ankylosaurs and stegosaurs, and Ornithopoda, which Norman expanded to include ceratopsians. Norman positioned fabrosaurs as basal ornithopods, suggested that ceratopsians and iguanodontians (referred to as 'dryosauroideans' in his cladogram) shared a common ancestor to the exclusion of hypsilophodontids, but considered the position of heterodontosaurids and pachycephalosaurs to be problematic and unresolved. The phylogeny of Milner & Norman (1984) concentrated on relationships within Ornithopoda and effectively represented a subset of the analysis of Norman (1984).

The phylogeny presented by Sereno (1984) differed significantly from that of Norman (1984). Sereno proposed that Fabrosauridae was polyphyletic and positioned *Lesothosaurus diagnosticus* (previously included within Fabrosauridae) as the most basal known ornithischian. His conception of Ornithopoda was much more restrictive than that of previous workers and excluded ceratopsians, pachycephalosaurs and 'fabrosaurs', while including heterodontosaurids. His conception of Thyreophora also differed substantially from that of Norman (1984), comprising a clade consisting of ankylosaurs, stegosaurs, pachycephalosaurs and ceratopsians.

The phylogeny of Cooper (1985) was similar in many aspects (Fig. 1C) to that of Sereno (1984). However, Cooper positioned Heterodontosauridae as the sister group to the Pachycephalosauria–Ceratopsia clade and considered Fabrosauridae to represent the most basal clade within Ornithopoda.

Maryańska & Osmólska (1985) outlined a phylogeny (Fig. 1D) that differed in several key points from that of Norman (1984) and Sereno (1984). Maryańska & Osmólska proposed that ankylosaurs and stegosaurs did not share a common ancestor but, instead, represented serial outgroups to more derived ornithischians, and that heterodontosaurids formed the sister group to a clade consisting of Ornithopoda (including *Lesothosaurus diagnosticus*), Pachycephalosauria and Ceratopsia. Following Sereno (1984), Maryańska & Osmólska united Pachycephalosauria and Ceratopsia to form a clade to the exclusion of ornithopods.

The most influential published work on ornithischian phylogeny was produced by Sereno (1986) and his results (Fig. 1E) have dominated subsequent understanding of ornithischian phylogeny (see, e.g. Weishampel *et al.* 1990, 1992, 2004a; Fastovsky & Weishampel 1996, 2005; Currie & Padian 1997; Sereno 1997, 1999a). Sereno (1986) modified his earlier (Sereno 1984) hypothesis by uniting ornithopods, pachycephalosaurs and ceratopsians (following Norman (1984) and Maryańska & Osmólska (1985)) in a clade that he termed Cerapoda. Within Cerapoda, hetero-

odontosaurids were positioned as basal ornithopods, while the clade containing Pachycephalosauria and Ceratopsia was named Marginocephalia. Sereno followed Norman (1984) in restricting Thyreophora to ankylosaurs, stegosaurs and two basal armoured forms (*Scutellosaurus lawleri*, *Scelidosaurus harrisonii*), while thyreophorans and cerapodans were united as the clade Genasauria. Sereno continued to consider Fabrosauridae polyphyletic and positioned *Lesothosaurus diagnosticus* as the sister taxon of Genasauria.

Following the work of Sereno (1986), ornithischian workers tended to focus on relationships within the major ornithischian clades; e.g. the phylogeny of basal Ornithopoda has been analysed by Weishampel & Heinrich (1992), Winkler *et al.* (1997), Scheetz (1998, 1999), Weishampel *et al.* (2003) and Norman *et al.* (2004c), amongst others. However, there have been only a few attempts to test the global phylogeny of Ornithischia.

Sereno (1997: figs 1, 2) presented an ornithischian cladogram, but this was not supported by a data matrix or information about analyses. In a review paper, Sereno (1999a) considered ornithischians within a larger scale analysis of dinosaurian phylogeny. This included nine separate data sets, each of which analysed separate portions of the dinosaurian tree. Four of these data sets (data sets 1–4) dealt with ornithischians. Data set 1 analysed basal dinosaurian phylogeny and, within this framework, tested both ornithischian monophyly and interrelationships. Data sets 2–4 analysed the within-clade phylogeny of Thyreophora, Ornithopoda and Marginocephalia. Results generally supported the findings of Sereno (1986) and differed only in the inclusion of additional taxa (e.g. the basal thyreophoran *Emausaurus ernsti*) and the identification of the Late Triassic taxon *Pisanosaurus mertii* as the most basal ornithischian. Monophyly of Thyreophora, Ornithopoda and Marginocephalia (and a taxonomic content for these clades consistent with the phylogenetic results of Sereno (1986)), was assumed prior to analysis.

Buchholz (2002) carried out an ornithischian analysis with 27 taxa and 97 characters. Taxonomic sampling was restricted mostly to taxa generally considered as ornithopods, with Marginocephalia coded as a composite taxon and basal thyreophorans excluded from the analysis. Buchholz found support for a sister-grouping of heterodontosaurids and marginocephalians and for paraphyly of hypsilophodontids. Unfortunately, although a character-list was published, a matrix was not provided and these results cannot be reassessed.

Liu (2004) tested the global phylogeny of Ornithischia with a large-scale analysis including 44 taxa and 326 characters. Interesting results were reported: Fabrosauridae and Hypsilophodontidae were found to be paraphyletic, *Lesothosaurus* was positioned as a basal member of Thyreophora, *Agilisaurus louderbacki* (often considered to represent a basal ornithopod, e.g. Norman *et al.* 2004c) grouped outside of Cerapoda and Marginocephalia and Iguanodontia were united as sister groups. Unfortunately, this analysis has, to date, been published in abstract form only. It is, therefore, impossible, at this stage, to reanalyse the data. However, the reported results of Liu (2004) clearly highlight the importance of new phylogenetic analyses.

One of us (Butler 2005) included a cladistic analysis (23 taxa, 73 characters) of Ornithischia within a review of the 'fabrosaurid' ornithischians of the upper Elliot Formation of southern Africa. That analysis recovered interesting results, including positioning heterodontosaurids and the Middle

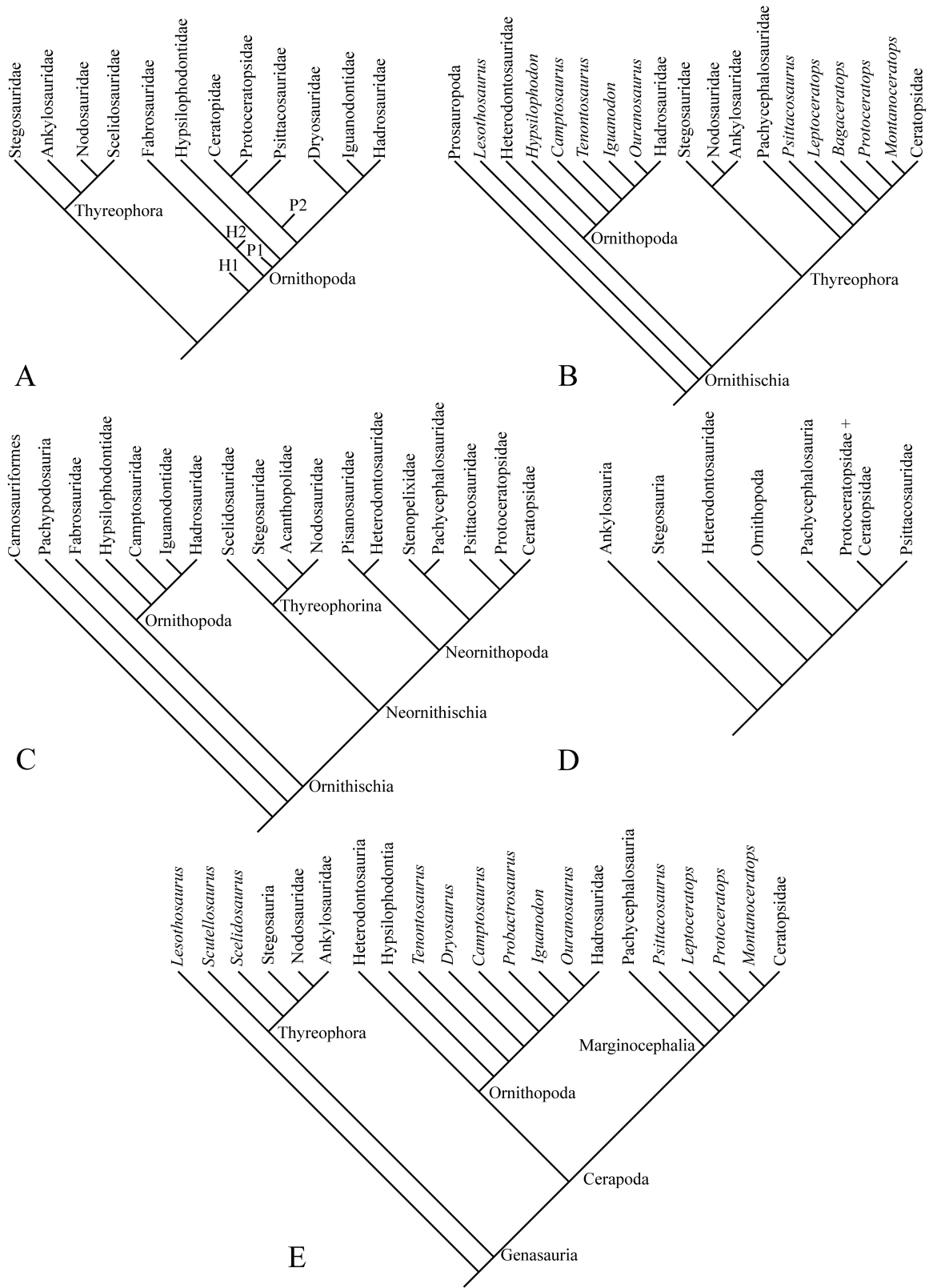


Figure 1 Previous numerical ornithischian phylogenies, simplified and redrawn from the original publications. **A**, Norman (1984); **B**, Sereno (1984); **C**, Cooper (1985); **D**, Maryńska & Osmólska (1985); **E**, Sereno (1986). H1, H2, alternative positions proposed by Norman (1984) for the clade Heterodontosauridae; P1, P2, alternative positions proposed by Norman (1984) for the clade Pachycephalosauria.

Jurassic taxa *Agilisaurus louderbacki* and *Hexinlusaurus multidentis* outside of Cerapoda; that analysis represented an early iteration of the analysis presented here and is superseded by the present study.

Although a number of major phylogenetic studies of Ornithischia have been published (Norman 1984; Sereno 1984, 1986, 1999a; Cooper 1985; Maryańska & Osmólska 1985), the majority have failed to include crucial information, including: (1) a character–taxon data matrix; (2) details of the specimens and references used in coding operational taxonomic units; (3) tree searching methods; (4) the number and scores of the most parsimonious trees recovered by search methods; (5) tests of data robustness and support for particular clades (e.g. bootstrapping, decay analysis). Most previous studies have simply presented a fully-resolved tree and lists of apomorphies for particular clades. It is neither possible to independently rerun these analyses and recover their results, nor is it possible to assess data robustness, the relative support for clades, or the support for alternative phylogenetic hypotheses.

With the exception of the preliminary study of Butler (2005), Sereno (1999a) is the only published ornithischian analysis that includes a data matrix that can be rerun and reanalysed. However, there are problems with this analysis. Only a limited number of ornithischian taxa were included and, in addition, monophyly of major clades (such as Marginocephalia) was assumed prior to analysis; unfortunately, monophyly of clades such as Marginocephalia are questions that ornithischian analyses still need to resolve.

MATERIAL AND METHODS

The aim of the analysis

The aim of this analysis is to test the global phylogeny of Ornithischia, concentrating on the phylogenetic relationships of basal forms. Questions concerning the monophyly of the Dinosauria, the phylogenetic relationships of basal ‘dinosauriformes’ and basal saurischians, and the relationships of derived taxa within the major ornithischian clades, are beyond the scope of this analysis. The intention is to test the phylogenetic framework upon which the current understanding of ornithischian evolution is based.

Phylogenetic framework

All published cladistic analyses have shown Dinosauria to form a monophyletic clade (e.g. Gauthier 1986; Benton & Clark 1988; Novas 1996; Sereno 1999a; Benton 2004; Langer 2004; Langer & Benton 2006). Dinosauria includes two subclades: Saurischia and Ornithischia (Gauthier 1986; Sereno 1986). A number of outgroups to Dinosauria have been identified; the most proximate of which appear to be several ‘dinosauriform’ taxa, exemplified by *Lagerpeton* (Sereno & Arcucci 1993), *Marasuchus* (Sereno & Arcucci 1994) and *Silesaurus* (Dzik 2003; Langer & Benton 2006). Successively more distant outgroups to Dinosauria within Archosauria include Pterosauria (although see Bennett 1996; Peters 2000), *Scleromochlus*, Crurotarsi, Proterochampsidae, *Euparkeria*, *Erythrosuchus* and *Proterosuchus* (Sereno 1991b; Benton 2004).

Table 1 provides phylogenetic definitions for ornithischian clade names discussed in the text (modified from Sereno 1998, 1999b; Wagner 2004). There is a conflict in the literature between the names Neornithischia (Cooper 1985) and Cerapoda (Sereno 1986), which have both been applied to the clade consisting of ornithopods, pachycephalosaurs and ceratopsians (e.g. Sereno 1999a; Weishampel 2004). Here, we follow Buchholz (2002) and Barrett *et al.* (2005) by using both names: Neornithischia is applied to a stem-based clade, while Cerapoda is used for a node-based clade. In addition, our use of Ornithopoda differs from that of those authors who have defined this taxon as a node-based clade utilising *Heterodontosaurus* as an internal specifier (e.g. Sereno 1998); we instead use Ornithopoda for a stem-based clade (Buchholz 2002; Wagner 2004; Norman *et al.* 2004c).

Selection of ingroup taxa

A taxonomic review of Ornithischia was carried out and a number of supraspecific, species level and outgroup operational taxonomic units (OTUs) were selected. Weishampel *et al.* (1990, 1992, 2004a) served as the source for this review. Coding of taxa for cladistic analysis was based, where possible, on first-hand examination of specimens, supplemented with information from the literature. Appendix 1 provides details of the references and specimens used for coding OTUs. The choice of ingroup taxa is discussed in greater detail below and outgroup taxa are discussed in the following section.

Supraspecific taxa

A number of authors (e.g. Wiens 1998; Prendini 2001) have suggested that supraspecific taxa should be avoided in phylogenetic analysis when possible, as the coding of such taxa is problematic, and simulations tend to suggest that splitting such taxa into species level terminals provides better results. Ideally, therefore, any analysis of Ornithischia should utilise only species level terminal taxa. Nevertheless, the use of species level taxa as exemplars for major clades was considered impractical for this analysis for a number of reasons. First, the choice of exemplar taxa is not always obvious. For instance, the clade Ankylosauria is nearly universally accepted as monophyletic and is well-supported by anatomical evidence. However, there is little consensus as to phylogenetic relationships within Ankylosauria (e.g. Kirkland 1998; Carpenter 2001; Vickaryous *et al.* 2001, 2004; Parish 2003) and justifying the use of one taxon, or several taxa, as exemplars is difficult. In addition, many of the apparently basal ankylosaur taxa that might be used as exemplars are fragmentary (e.g. *Cedarpelta bilbeyhallorum*, *Mymoorapelta maysi*), incompletely described in the literature (*Gastonia burgei*), or based upon juvenile material (*Liaoningosaurus paradoxus*). In such a situation it can be advantageous to code a supraspecific taxon to represent the clade. The use of supraspecific taxa has the additional advantage of reducing the number of OTUs that must be included in the analysis. This is important, because it allows heuristic searches to be carried out in an acceptable timeframe and allows much more detailed examination of the data. For these reasons, selected supraspecific taxa were included in this analysis.

As outlined by Bininda-Emonds *et al.* (1998), the correct use of supraspecific taxa in phylogenetic analyses has two requirements. Firstly, the taxa must be monophyletic. Only supraspecific taxa that are generally accepted as

Table 1 Phylogenetic definitions for the major ornithischian clades discussed in this analysis (modified from: Sereno 1998, 1999b; Buchholz 2002; Wagner 2004).

Clade name	Phylogenetic definition
Dinosauria Owen, 1842	<i>Triceratops horridus</i> Marsh, 1889, <i>Passer domesticus</i> (Linnaeus, 1758), their most recent common ancestor and all descendents.
Saurischia Seeley, 1887	All dinosaurs more closely related to <i>Passer domesticus</i> (Linnaeus, 1758) than to <i>Triceratops horridus</i> Marsh, 1889.
Ornithischia Seeley, 1887	All dinosaurs more closely related to <i>Triceratops horridus</i> Marsh, 1889 than to either <i>Passer domesticus</i> (Linnaeus, 1758), or <i>Saltasaurus loricatus</i> Bonaparte & Powell, 1980.
Genasauria Sereno, 1986	<i>Ankylosaurus magniventris</i> Brown 1908, <i>Stegosaurus stenops</i> Marsh, 1877a, <i>Parasaurolophus walkeri</i> Parks, 1922, <i>Triceratops horridus</i> Marsh, 1889, <i>Pachycephalosaurus wyomingensis</i> (Gilmore, 1931), their most recent common ancestor and all descendents.
Thyreophora Nopcsa, 1915	All genasaurians more closely related to <i>Ankylosaurus magniventris</i> Brown, 1908 than to <i>Parasaurolophus walkeri</i> Parks, 1922, <i>Triceratops horridus</i> Marsh, 1889, or <i>Pachycephalosaurus wyomingensis</i> (Gilmore, 1931).
Euryroda Sereno, 1986	<i>Ankylosaurus magniventris</i> Brown, 1908, <i>Stegosaurus stenops</i> Marsh, 1877a, their most recent common ancestor and all descendents.
Ankylosauria Osborn, 1923	All ornithischians more closely related to <i>Ankylosaurus magniventris</i> Brown, 1908 than to <i>Stegosaurus stenops</i> Marsh, 1877a.
Stegosauria Marsh, 1877a	All ornithischians more closely related to <i>Stegosaurus stenops</i> Marsh, 1877a than to <i>Ankylosaurus magniventris</i> Brown, 1908.
Neornithischia Cooper, 1985	All genasaurians more closely related to <i>Parasaurolophus walkeri</i> Parks, 1922, than to <i>Ankylosaurus magniventris</i> Brown, 1908 or <i>Stegosaurus stenops</i> Marsh, 1877a.
Cerapoda Sereno, 1986	<i>Parasaurolophus walkeri</i> Parks, 1922, <i>Triceratops horridus</i> Marsh, 1889, their most recent common ancestor and all descendents.
Ornithopoda Marsh, 1881	All genasaurians more closely related to <i>Parasaurolophus walkeri</i> Parks, 1922, than to <i>Triceratops horridus</i> Marsh, 1889
Marginocephalia Sereno, 1986	<i>Triceratops horridus</i> Marsh, 1889, <i>Pachycephalosaurus wyomingensis</i> (Gilmore, 1931), their most recent common ancestor and all descendents.
Ceratopsia Marsh, 1890	All marginocephalians more closely related to <i>Triceratops horridus</i> Marsh, 1889 than to <i>Pachycephalosaurus wyomingensis</i> (Gilmore, 1931).
Pachycephalosauria Maryańska & Osmólska, 1974	All marginocephalians more closely related to <i>Pachycephalosaurus wyomingensis</i> (Gilmore, 1931) than to <i>Triceratops horridus</i> Marsh, 1889.

monophyletic were utilised here. Secondly, it must be possible to code them as a single OTU in a manner that maintains their position on a cladogram with respect to a solution including all species. Several authors (e.g. Bininda-Emonds *et al.* 1998; Wiens 1998) suggest that the ‘ancestral’ method, whereby the character states of a hypothetical ancestor (the ‘groundplan’) are reconstructed on the basis of prior phylogenetic analyses, is the most successful method of coding supraspecific taxa. The ‘ancestral’ method (the methodology is outlined by Langer & Benton 2006) was used in this analysis. The eight supraspecific OTUs used are discussed in greater detail below:

1. *Ankylosauria*. Ankylosauria is defined as all taxa more closely related to *Ankylosaurus magniventris* than to *Stegosaurus stenops* (Sereno 1998) and includes the subclades Ankylosauridae and Nodosauridae. Included taxa and diagnostic features are listed by Vickaryous *et al.* (2004). The known temporal range of the clade is Callovian to Maastrichtian (Middle Jurassic–Late Cretaceous).

The most recent review of Ankylosauria (Vickaryous *et al.* 2004) recognised over 40 valid species. The phylogeny assumed here for character coding represents a consensus of the following published phylogenies: Kirkland

(1998), Vickaryous *et al.* (2001), Hill *et al.* (2003) and Vickaryous *et al.* (2004). The phylogenetic analysis of Carpenter (2001) is not used, because it utilised a compartmentalisation technique and does not, therefore, represent a global phylogeny.

2. *Stegosauria*. Stegosauria is defined as all taxa more closely related to *Stegosaurus stenops* than to *Ankylosaurus magniventris* (Sereno 1998). A full listing of included taxa and synapomorphies supporting monophyly of the clade is given in Galton & Upchurch (2004b). Stegosaurians form a relatively small but well-known and well-supported clade of ornithischians, known mostly from the Middle to Late Jurassic, with fragmentary forms known from the Early Cretaceous.

Sereno & Dong (1992) provided the first phylogenetic analysis of stegosaurians, but considered only a few taxa. They proposed that *Huayangosaurus taibaii* represents the most basal member of the clade, with *Dacentrurus armatus* positioned as the sister-group to all more derived stegosaurians. Galton & Upchurch (2004b) have provided the most complete analysis to date; the basal positions of *Huayangosaurus* and *Dacentrurus* were confirmed by their analysis, but little resolution was found amongst more derived stegosaurians.

3. *Rhabdodontidae*. Rhabdodontidae is defined as *Zalmoxes robustus*, *Rhabdodon priscus*, their common ancestor and all of its descendents (Weishampel *et al.* 2003) and the temporal range of the clade extends from the Late Santonian to the Maastrichtian (Late Cretaceous). Synapomorphies supporting the clade are given by Weishampel *et al.* (2003).
4. *Dryosauridae*. Dryosauridae includes the taxa *Dryosaurus altus*, *Dryosaurus lettowvorbecki*, *Valdosaurus canaliculatus* and *Valdosaurus nigeriensis* (Norman 2004) and is defined as *Dryosaurus altus* and all taxa more closely related to it than to *Parasaurolophus walkeri* (Sereno 1998). The clade is known from the Late Jurassic and Early Cretaceous. Potential synapomorphies of this clade include: lacrimal inserts into notch in the maxilla; very wide brevis shelf on the ilium; large, deep pit on the femoral shaft, at the base of the fourth trochanter; digit I of the pes is absent or vestigial.
5. *Ankylopollexia*. Ankylopollexia is defined as *Camptosaurus dispar*, *Parasaurolophus walkeri*, their common ancestor and all descendents (Sereno 1998). A listing of included taxa and synapomorphies supporting monophyly of the clade is given by Norman (2004). The clade extends from the Kimmeridgian to the Maastrichtian (Late Jurassic–Late Cretaceous).
Ankylopollexia was erected by Sereno (1986) for ornithopods exhibiting derived features of the teeth and manus, in particular the modification of manual digit I to accommodate a spine-like pollex. Within this clade are Camptosauridae and Styracosterna, both of which have been given stem-based phylogenetic definitions by Sereno (1998). The monophyly of Ankylopollexia is universally supported by phylogenetic analysis and its interrelationships are relatively well understood (e.g. Norman 2002, 2004).
6. *Pachycephalosauridae*. Pachycephalosauridae is defined as all taxa more closely related to *Pachycephalosaurus wyomingensis* than to either *Homalocephale calathocercos* or *Goyocephale lattimorei*. Known taxa are restricted to the Late Cretaceous (Campanian–Maastrichtian) and synapomorphies are given in Sereno (2000).
A number of explicit, numerical phylogenetic analyses of Pachycephalosauridae have been carried out in recent years (Sereno 2000; Williamson & Carr 2002; Sullivan 2003; Maryańska *et al.* 2004). These studies indicate a basal position for *Stegoceras* and the existence of a derived clade containing *Tylocephale*, *Prenocephale* and *Pachycephalosaurus*, amongst others.
7. *Psittacosauridae*. Psittacosauridae is defined as all taxa more closely related to *Psittacosaurus mongoliensis* than to *Triceratops horridus* and contains the genera *Hongshanosaurus* and *Psittacosaurus*. Synapomorphies of the clade are given by Sereno (2000). The genus *Psittacosaurus* is probably the most speciose and diverse of all dinosaur genera, although the exact number of species recognised is controversial (Sereno 1990b; You & Dodson 2004). Relationships within the clade are poorly understood. Members of Psittacosauridae are known from the Early Cretaceous.
8. *Unnamed taxon (Coronosauria + Leptoceratopsidae)*. This unnamed clade is defined as *Leptoceratops gracilis*, *Protoceratops andrewsi* and *Triceratops horridus*, their common ancestor and all of its descendents and includes

taxa ranging from the Turonian to the Maastrichtian (Late Cretaceous). Synapomorphies of this node are given by Sereno (2000), Makovicky (2001) and Makovicky & Norell (2006).

Neoceratopsian phylogeny has undergone a number of rigorous studies in recent years (Sereno 2000; Makovicky 2001; Xu *et al.* 2002; You & Dodson 2003, 2004; Chinnery 2004; Makovicky & Norell 2006) and a broad-scale consensus has been reached that *Liaoceratops* and *Archaeoceratops* represent basal taxa and that other neoceratopsian taxa form a distinct clade. This clade of more derived neoceratopsians remains unnamed and, generally, comprises a clade known as Leptoceratopsidae and a clade known as Coronosauria, which in turn comprises Protoceratopsidae and Ceratopsoidea (Sereno 2000; Makovicky 2001; Xu *et al.* 2002; Chinnery 2004).

Included species level taxa

Following the selection and definition of supraspecific taxa, the status of all taxa not included in one of these derived clades was assessed, using first-hand observations and the literature. For each taxon a decision was made as to whether it should be included in phylogenetic analysis or not. Included species level taxa are discussed in this section; excluded species level taxa (and the reasons for exclusion) are discussed in the following section.

Abrictosaurus consors (Thulborn, 1974) is known from a single partial skull and postcranial skeleton (BMNH RUB54, holotype; formerly UCL B54) from the upper Elliot Formation of Lesotho (Early Jurassic: Hettangian–Sinemurian). Autapomorphies have not previously been defined for *Abrictosaurus* and this taxon is provisionally diagnosed by the following combination of characters: arched diastema between premaxilla and maxilla present; enlarged caniniform teeth absent from the premaxilla and dentary. The single specimen of *Abrictosaurus* was initially described as a new species of the heterodontosaurid *Lycorhinus* (Thulborn 1974); however, it can clearly be distinguished from *Lycorhinus* on the basis of dental characters (Hopson 1975). Hopson (1975) tentatively referred the specimen BMNH A100 (discussed below) to *Abrictosaurus*; however, this referral has not been supported by subsequent work. *Abrictosaurus* and BMNH A100 are included here as separate OTUs.

Agilisaurus louderbacki Peng, 1990 is known from a complete, articulated skull and postcranial skeleton (ZDM T6011, holotype) from the Lower Shaximiao Formation of Sichuan Province, People's Republic of China (Middle Jurassic: ?Bajocian, Chen *et al.* 1982; ?Bathonian–Callovian, Dong & Tang 1984). *Agilisaurus* can be distinguished by the following autapomorphies: presence of a palpebral/supraorbital bar that traverses the width of the orbit; anteriormost dentary teeth conical, resembling premaxillary teeth; presence of a series of low, anterolaterally directed ridges on the orbital portion of the frontal; presence of an excavated area immediately anterior to the antorbital fossa (modified from Barrett *et al.* 2005).

Anasibetia saldiviai Coria & Calvo, 2002 is known from a partial skeleton with skull fragments (MCF-PVPH-74, holotype) as well as a number of referred specimens (see Coria & Calvo 2002) from the Lisandro Formation of Neuquén Province, Argentina (Late Cretaceous: Cenomanian). This taxon can be diagnosed on the basis of its

anteroventrally orientated occipital condyle and the presence of an ilium with preacetabular process longer than 50% of the total ilium length (modified from Coria & Calvo 2002).

Archaeoceratops oshimai Dong & Azuma, 1997 is known from a well-preserved skull and postcranial material (IVPP V11114, holotype; IVPP V11115, paratype) from the Xinminbao Group of Gansu Province, China (Early Cretaceous: Aptian–Albian) and is characterised by the presence of an excavation on the lateral surface of the ischiadic peduncle of the ilium, as well as by a unique character combination (modified from You & Dodson 2003).

The specimen BMNH A100 (formerly UCL A100) comprises a partial, disarticulated skull from the upper Elliot Formation of South Africa. Assignment of this specimen to *Lycorhinus* (Thulborn 1970b, 1974; Gow 1990) was not based on unique characters, but on general similarity. A number of subsequent authors criticised the referral of this specimen to *Lycorhinus*: Galton (1973a: caption to fig. 2) referred BMNH A100 to *Heterodontosaurus* sp.; Charig & Crompton (1974) considered BMNH A100 to be generically distinct from both *Heterodontosaurus* and *Lycorhinus*; while Hopson (1975) provisionally referred BMNH A100 to *Abrictosaurus*.

The taxonomy of the Elliot Formation heterodontosaurids is poorly resolved and requires further work. At present there is no consensus as to the taxonomic status of BMNH A100; however, this specimen is known from relatively complete and informative cranial remains and has received a detailed description (Thulborn 1970b) and is thus included in the phylogenetic analysis here as a separate OTU.

Bugenasaura infernalis Galton, 1995 was erected for a partial skull and postcranial fragments (SDSM 7210, holotype) from the Hell Creek Formation of South Dakota, USA (Late Cretaceous: Maastrichtian). This taxon is diagnosed by the following features: no edentulous region at the anterior end of the premaxilla; very deeply recessed cheek tooth row, with a massive and deep dentary and a very prominent overhanging ridge (with a braided appearance) on the ventral part of the maxilla; distal end of palpebral obliquely truncated with ridges medially (modified from Galton 1999). A new skeleton of *Bugenasaura* is known (MOR 979; R.J.B. pers. obs. 2004); however, this specimen has not been fully prepared and is currently undescribed.

Chaoyangsaurus youngi Zhao *et al.* 1999 is based upon a partial skull and fragmentary postcranial elements (IG-CAGS V371, holotype) from the Tuchengzi Formation of Liaoning Province, China (Middle or Late Jurassic: Middle Jurassic, Zhao *et al.* 1999; Tithonian, Weishampel *et al.* 2004b). *Chaoyangsaurus* is distinguished by the following autapomorphic features: quadratojugal overlaps posterior side of the quadrate shaft; quadrate slopes strongly anteriorly; ridge present between the planar lateral and ventral surfaces of the angular (modified from Zhao *et al.* 1999).

Echinodon becklesii Owen, 1861b is based upon fragmentary cranial material (see Norman & Barrett 2002) from the Purbeck Formation of England (Early Cretaceous: Berriasian). *Echinodon* can be diagnosed by the presence of one, or possibly two, caniniform teeth situated at the anterior end of the maxilla (Norman & Barrett 2002).

Emausaurus ernsti Haubold, 1990 is known from a partial skull and postcranial fragments (SGWG 85, holotype), from an unnamed unit in Germany (Early Jurassic: Toarcian). *Emausaurus* can be diagnosed by the possession of a large,

triangular plate-like palpebral, the robust lateral margin of which bears a number of low ridges.

Gasparinisaura cincosaltensis Coria & Salgado, 1996 is known from numerous specimens (see Coria & Salgado 1996; Salgado *et al.* 1997) from the Rio Colorado Formation of Patagonia, Argentina (Late Cretaceous: Coniacian–Santonian) and is diagnosed by the following characters: anteroposteriorly wide ascending process of lacrimal contacts ventral process of postorbital posteriorly; infratemporal fenestra bordered entirely ventrally by quadratojugal; apex of arched dorsal margin of infratemporal fenestra positioned posterior to mandibular articulation; fully fused greater and lesser trochanters; condylid of femur laterally positioned (modified from Coria & Salgado 1996).

Goyocephale lattimorei Perle *et al.* 1982 is known from a relatively complete skeleton with partial skull (GI SPS 100/1501, holotype), from an unnamed unit, Mongolia (Late Cretaceous: ?late Santonian or early Campanian). One autapomorphy has been identified: the lateral margin of the skull is sinuous in dorsal view (Serenó 2000).

Heterodontosaurus tucki Crompton & Charig, 1962 is known from a nearly complete skull (SAM-PK-K337, holotype) from the Clarens Formation (= Cave Sandstone) of South Africa (Early Jurassic: Sinemurian) and a referred skull and postcranial skeleton (SAM-PK-K1332, Santa Luca *et al.* 1976; Santa Luca 1980) from the upper Elliot Formation of South Africa. A number of features may be autapomorphic for this taxon, although it is possible that some may prove to be present in other, poorly known, heterodontosaurids, or may eventually prove to be ornithischian plesiomorphies. These possible autapomorphies include: dorsal process of premaxilla does not form contact with nasals; anterior, accessory opening present within the antorbital fossa; squamosal–quadratojugal contact is anteroposteriorly broad; paroccipital processes are very deep dorsoventrally; paired, deep recesses on the ventral surface of the basisphenoid; basisphenoid processes are extremely elongated; cingulum is completely absent on cheek-teeth; ischium with elongate flange on lateral margin.

Hexinlusaurus multidens (He & Cai, 1983) is known from two partial skulls and postcranial skeletons (ZDM T6001, holotype; ZDM T6002, paratype) from the Lower Shaximiao Formation of China. *Hexinlusaurus* can be distinguished by the presence of a marked concavity that extends over the lateral surface of the postorbital (Barrett *et al.* 2005).

Homalocephale calathoceros Maryańska & Osmólska, 1974 is known only from a skull and partial postcranial skeleton (GI SPS 100/1201, holotype) from the Nemegt Formation of Mongolia (Late Cretaceous: ?late Campanian or early Maastrichtian). *Homalocephale* is diagnosed by the presence of a postacetabular process of the ilium that is crescent-shaped and ventrally deflected (Serenó 2000).

Hypsilophodon foxii Huxley, 1869 is known from numerous specimens (see Galton 1974a) from the Wessex Formation of the Isle of Wight, UK (Early Cretaceous: Barremian). Autapomorphies have not been previously defined for *Hypsilophodon*, but include the presence of a large foramen in the ascending process of the maxilla that communicates medially with the antorbital fossa (Galton 1974a: fig. 3). Although material of *Hypsilophodon* has been reported from continental Europe (Sanz *et al.* 1983) and North America (Galton & Jensen 1979), none of this material can be

confidently referred to this taxon and, at present, *Hypsilophodon* is only known from the UK.

Jeholosaurus shangyuanensis Xu *et al.* 2000 is known from two specimens (IVPP V12529, holotype; IVPP V12530, referred) from the Yixian Formation of Liaoning Province, China (Early Cretaceous) and is characterised by the following combination of characters: six premaxillary teeth; foramina present on dorsal surface of nasal; large foramen present in quadratojugal; preantary about 1.5 times as long as the premaxilla; pedal phalanx 3–4 times longer than other phalanges of pedal digit 3 (modified from Xu *et al.* 2000).

Lesothosaurus diagnosticus Galton, 1978 is known from a number of nearly complete skulls and disarticulated postcranial skeletons, while *Stormbergia dangershoeki* Butler, 2005 is known from three partial skeletons. Both taxa are from the upper Elliot Formation of South Africa and Lesotho. A full discussion of the hypodigm and diagnosis of each taxon can be found in Butler (2005).

Liaoceratops yanzigouensis Xu *et al.* 2002 is known from two complete skulls (IVPP V12738, holotype; IVPP V12633, referred specimen) from the Lower Yixian Formation of Liaoning Province, China (Early Cretaceous). *Liaoceratops* is characterised by the following features: sutures between premaxilla, maxilla, nasal and prefrontal intersecting at a common point high on the side of the snout; possession of several tubercles on the ventral margin of the angular; a foramen on the posterior face of the quadrate near the articulation with the quadratojugal; small tubercle on the dorsal border of the foramen magnum; thick posterior border of the parietal frill (Xu *et al.* 2002).

Lycorhinus angustidens Houghton, 1924 is known from a left dentary (SAM-PK-K3606, holotype) and two provisionally referred specimens (BP/1/4244, left maxilla, holotype of *Lanasaurus scalpridens* Gow, 1975, referred to *Lycorhinus angustidens* by Gow 1990; BP/1/5253, left maxilla, referred to *Lycorhinus angustidens* by Gow 1990) from the upper Elliot Formation of South Africa. There has been considerable controversy over the validity of *Lycorhinus angustidens*. Houghton (1924) named *Lycorhinus* for a partial left dentary that he believed represented a cynodontid synapsid. Crompton & Charig (1962) reidentified *Lycorhinus* as a heterodontosaurid and, later Charig & Crompton (1974) considered it a *nomen dubium*. Thulborn (1970b) assigned the specimen BMNH A100 to *Lycorhinus*; however, this assignment was not supported by most subsequent authors (Galton 1973a; Charig & Crompton 1974; Hopson 1975, 1980). Hopson (1975) demonstrated that *Lycorhinus* could be distinguished from other heterodontosaurids (*Abrietosaurus* and *Heterodontosaurus*). Finally, Gow (1990) referred the maxillae BP/1/4244 (holotype of *Lanasaurus* Gow, 1975) and BP/1/5253 to *Lycorhinus*.

The validity of *Lycorhinus* requires reassessment and only a preliminary diagnosis is suggested here, based upon the marked medial curvature of the dentary and maxillary tooth rows (Gow 1990). As discussed by Hopson (1975), a unique combination of plesiomorphic and derived characters is probably also diagnostic for *Lycorhinus*.

Micropachycephalosaurus hongtuyanensis Dong, 1978 is known from a partial skull and skeleton (IVPP V5542, holotype) from the Wangshi Formation of Shandong Province, People's Republic of China (Late Cretaceous: Campanian). The holotype of *Micropachycephalosaurus* is

extremely fragmentary and many elements were erroneously identified in the original description. A full review and redescription is being prepared (R. J. B. & Q. Zhao, unpublished results). Although Sereno (2000) has suggested that autapomorphic features are absent, the presence of prominent ventral grooves on the most posterior dorsal vertebrae appears to be autapomorphic for *Micropachycephalosaurus* and this taxon is here included in the phylogenetic analysis.

Orodromeus makelai Horner & Weishampel, 1988 is known from abundant and well-preserved material (see Scheetz 1999) from the Upper Two Medicine and Judith River formations of Montana, USA (Late Cretaceous: ?Late Campanian). *Orodromeus* is characterised by the following combination of characters: prominent boss on anterolateral maxilla; subnarial depression on premaxilla–maxilla boundary; midline depression on nasals; boss on jugal; postorbital with distinct projection into orbit; dentition plesiomorphic with ridges absent lingually and labially.

Othnielia rex (Marsh, 1877b) is known from a number of specimens (YPM 1915, holotype, left femur; referred specimens (see Galton 1983) include: BYU ESM-163R, articulated, near-complete postcranial skeleton described by Galton & Jensen 1973) from the Morrison Formation of the USA (Late Jurassic: Kimmeridgian–Tithonian). YPM 1915 is the holotype of *Nanosaurus rex* Marsh, 1877b, which was made the type species of the genus *Othnielia* by Galton (1977). This specimen (an isolated femur) lacks obvious autapomorphies, although it may be diagnosable on the basis of a unique character combination. Referral of specimens to *Othnielia* follows Galton (1983), pending a review of the validity of this taxon.

Parksosaurus warreni (Parks, 1926) is known from a single, relatively complete, skull and skeleton (ROM 804, holotype) from the Horseshoe Canyon Formation of Alberta, Canada (Late Cretaceous: Maastrichtian). *Parksosaurus* is distinguished by a dorsoventrally broad posterolateral process of the premaxilla and a postorbital process of the jugal that expands posterodorsally.

Pisanosaurus mertii Casamiquela, 1967 is known from a single partial skeleton (PVL 2577, holotype) from the Ischigualasto Formation (Late Triassic: Carnian) of Argentina. As discussed by Sereno (1991a), this taxon can be diagnosed by the following characters: anteroposterior depth of distal end of the tibia is greater than maximum transverse width; calcaneum is transversely narrow.

Scelidosaurus harrisonii Owen, 1861a is known from several partial skeletons from the Lower Lias of Dorset, England (Early Jurassic: late Sinemurian). Owen (1861a) described material which he referred to *Scelidosaurus*, including a femur (GSM 109560), articulated knee-joint (BMNH 39496), ungual phalanx (GSM 10956), a partial juvenile skeleton (Philpott Museum, Lyme Regis, unnumbered, casts are catalogued as BMNH R5909) and a near-complete skull (BMNH R1111). Owen (1863) described the near-complete postcranial skeleton associated with the skull BMNH R1111, while Lydekker (1888) later designated the articulated knee-joint as the lectotype. Newman (1968) recognised that the material described by Owen (1861a) represents a composite of theropod (GSM 109560; BMNH 39496; GSM 10956) and ornithischian (Philpott Museum, juvenile skeleton; BMNH R1111) material, and Charig & Newman (1992) formally designated the skull and postcranial skeleton (BMNH R1111) as a replacement lectotype. The juvenile described by Owen

(1861*a*) probably represents a second individual of *Scelidosaurus* (Galton 1975). Further material has come to light in recent years, including BMNH R6704 (Rixon 1968; Charig 1972: fig. 6A; considered as a possible new taxon of basal thyreophoran by Coombs *et al.* 1990), BRSMG Ce12785 (Barrett 2001) and CAMSM X 39256. Reports of the genus *Scelidosaurus* in the Kayenta Formation of Arizona (Padian 1989) and the Lower Lufeng of China (Lucas 1996: see *Tatisaurus*, below) cannot be substantiated at present. No diagnosis based upon synapomorphies has ever been published for *Scelidosaurus* and a full diagnosis must await redescription of this taxon (D. B. Norman, unpublished results).

Scutellosaurus lawleri Colbert, 1981 is known from several partial skeletons (MNA P1.175, holotype; MNA P1.1752, paratype; for referred material see Rosenbaum & Padian 2000) described by Colbert (1981) and Rosenbaum & Padian (2000) from the Kayenta Formation of Arizona, USA (Early Jurassic: Sinemurian–Pliensbachian). Unique features include: dorsal and ventral margins of the preacetabular process of the ilium are drawn out medially into distinct flanges which converge upon one another anteriorly; elongate tail of at least 58 caudal vertebrae (R. J. B. & S. C. R. Maidment, unpublished results).

Stenopelix valdensis Meyer, 1857 is known from a single partially articulated postcranial skeleton, preserved as impressions in sandstone blocks, from the Obernkirchen Sandstein of Germany (Early Cretaceous: Berriasian); latex casts prepared by Sues & Galton (1982) make detailed examination of the material possible. The ischium of *Stenopelix* has the following autapomorphies: distinct bend at mid-shaft; broadest at mid-shaft and tapers anteriorly and posteriorly; blade is transversely arched distally, being ventrally convex and dorsally concave (modified from Sereno 1987).

Talenkauen santacrucensis Novas *et al.* 2004 is based upon a partial skull and postcranial skeleton (MPM-10001, holotype) from the Pari Aike Formation, Santa Cruz Province, Argentina (Late Cretaceous: Maastrichtian). This taxon can be diagnosed by the presence of well-developed epiphyses on cervical 3 and plate-like uncinat processes on the rib-cage (Novas *et al.* 2004).

The genus *Tenontosaurus* Ostrom, 1970 is characterised by the following features: dorsoventrally tall maxilla, nearly full height of the rostrum; orbit square; 12 cervical vertebrae; elongate tail (59+ caudals). Two species are recognised and included here: *Tenontosaurus tilletti* Ostrom, 1970 is known from abundant material (see Forster 1990) from the Cloverly Formation of Montana, USA (Early Cretaceous: Aptian–Albian) and *Tenontosaurus dossi* Winkler *et al.* 1997 is known from two specimens from the Twin Mountains Formation of Texas, USA (Early Cretaceous). The species are distinguished by the retention in *Tenontosaurus dossi* of premaxillary teeth and a postpubic process equal in length to the ischium (Winkler *et al.* 1997).

Thescelosaurus neglectus Gilmore, 1913 is known from numerous specimens (see Galton 1997) from the Lance Formation of Wyoming, the Hell Creek Formation of Montana, the Scollard Formation of Alberta and the Frenchman Formation of Saskatchewan (Late Cretaceous: ?late Campanian–Maastrichtian). The taxonomic history of *Thescelosaurus* has been summarised by Galton (1995, 1997) and his taxonomic assignments are followed provisionally here, with *Thescelosaurus edmontonensis* being considered a junior synonym of *T. neglectus*. It should be noted that

synonymy is based on general similarity, rather than on autapomorphic features (see Galton 1995); future revision of the *Thescelosaurus* material may indicate the presence of two, or more, distinct taxa. One possible autapomorphy is recognised here: a large notch or foramen within the supraoccipital, dorsal to the foramen magnum (see Galton 1997).

Wannanosaurus yansiensis Hou, 1977 is known from a partial skull and postcranial skeleton (IVPP V4447, holotype) and some referred postcranial elements (IVPP V4447.1, paratype), from the Xiaoyan Formation of Anhui Province, China (Late Cretaceous: Campanian). *Wannanosaurus* is distinguished by the extreme flexure of the humerus, with proximal and distal ends set at approximately 30° to one another (modified from Sereno 2000).

Yandusaurus hongheensis He, 1979 is known from a partial skull and postcranial material (GCC V20501, holotype) from the Upper Shaximiao Formation of Sichuan, People's Republic of China (Late Jurassic: ?Oxfordian, Weishampel *et al.* 2004*b*). All of the anatomical features previously used to diagnosis *Yandusaurus* (He & Cai 1984) have wider distributions amongst basal ornithopods. However, one autapomorphic feature is apparent in the holotype (R. J. B., pers. obs. 2004; Barrett *et al.* 2005); the mid–posterior cervicals have circular, pit-like depressions developed at the base of their postzygapophyses.

Zephyrosaurus schaffi Sues, 1980 is known from an incomplete skull and postcranial fragments (MCZ 4392, holotype) from the Cloverly Formation of Montana, USA (Early Cretaceous: Aptian–Albian) and is characterised by the following unique combination of characters: prominent boss on anterolateral maxilla; short, massive, triangular palpebral; boss on jugal; postorbital with distinct projection into orbit; dentary/maxillary teeth with numerous subparallel ridges connecting to marginal denticles.

Excluded species level taxa

A number of taxa have been considered non-diagnosable *nomina dubia* by most recent reviews and are here excluded from analysis. These taxa include ‘*Camptosaurus*’ *leedsii*, *Fabrosaurus australis*, *Geranosaurus atavus*, ‘*Hypsilophodon*’ *wielandi*, *Laosaurus celer*, *Laosaurus minimus*, *Lusitanosaurus liasicus*, *Nanosaurus agilis* and *Sanpasaurus yaoi*.

Many ornithischian or putative ornithischian taxa have been erected solely or largely on the basis of dental remains, including: *Alocodon kuehnei*, *Crosbysaurus harrissae*, *Drinker nisti*, *Ferganocephale adenticulatum*, *Galtonia gibbidens*, *Gongbusaurus shiyii*, *Krzyzanowskisaurus hunti*, *Lucianosaurus wildi*, *Pekinosaurus olseni*, *Phyllodon henkeli*, *Protecovasaurus lucasi*, *Revueltosaurus callenderi*, *Siluosaurus zhangqiani*, ‘*Stegosaurus*’ *madagascariensis*, *Taveirosaurus costai*, *Tecovasaurus murreyi* and *Trimucrodon cuneatus*. Recent work has demonstrated that at least some of these taxa pertain to non-ornithischian clades (Parker *et al.* 2005*a*; Irmis *et al.* 2007) and the taxonomic validity of many of these tooth taxa is additionally questionable (Weishampel *et al.* 2004*a*). Furthermore, tooth taxa add little new anatomical information to the analysis and suffer from extremely high (more than 95%) levels of missing data. For these reasons these taxa have been excluded.

Technosaurus smalli, from the Cooper Canyon Formation (Late Triassic: Norian) of Texas, was described as a ‘fabrosaurid’ ornithischian by Chatterjee (1984) on the basis

of a single fragmentary skeleton. Sereno (1991a) suggested that the holotype of *Technosaurus* contains elements of both an ornithischian and a sauropodomorph. Irmis *et al.* (2005, 2007) agreed that the specimen is a composite of at least two taxa, but suggested that the posterior portion of the lower jaw is referable to the pseudosuchian *Shuvosaurus*, whereas other parts of the holotype may represent a *Silesaurus*-like taxon. They do not consider any of the material to be ornithischian. In view of the considerable confusion as to the association of the holotype of *Technosaurus*, it is here excluded from phylogenetic analysis.

Norman *et al.* (2004b) considered *Tatisaurus oehleri* and *Bienosaurus lufengensis* from the Lower Lufeng Formation (Early Jurassic: Sinemurian) of China as valid taxa and possible basal thyreophorans. However, reassessment of *Tatisaurus* (Norman *et al.* 2007) suggests that it is a *nomen dubium*. Autapomorphic characters are not evident in the original description of *Bienosaurus* (Dong 2001) and the validity of this taxon is uncertain. As a result, both taxa are excluded from the current phylogenetic analysis.

Xiaosaurus dashanpensis from the Lower Shaximiao Formation of Sichuan Province, China (Middle Jurassic: ?Bajocian, Chen *et al.* 1982; ?Bathonian–Callovian, Dong & Tang 1984) is based upon very fragmentary remains, but appears to be diagnosable on the basis of the possession of a proximally straight humerus that lacks the medial curvature seen in all other basal ornithischians (Barrett *et al.* 2005). However, the whereabouts of the holotype and referred material are currently unknown (Barrett *et al.* 2005) and unavailable for further study and the original description (Dong & Tang 1983) provides few anatomical details. As a result, we do not include *Xiaosaurus* in the present study.

The location of the holotype of '*Gongbusaurus*' *wucaiwansensis* is currently unknown (X. Xu, pers. comm., 2004) and the original description (Dong 1989) is brief and poorly figured and does not allow the recognition of autapomorphies, or a unique character combination. Therefore, despite the fact that recent reviews (e.g. Norman *et al.* 2004c) retain '*Gongbusaurus*' *wucaiwansensis* as a valid taxon, we here exclude it from the phylogenetic analysis.

Notohypsilophodon comodorensis was described by Martínez (1998) on the basis of a partial skeleton from the Bajo Barreal Formation, Chubut Province, Argentina (Late Cretaceous: ?Cenomanian). Martínez (1998) listed a number of potential autapomorphies of *Notohypsilophodon*; however, most of these appear to have wider distributions within Ornithischia (e.g. the reduction of the deltopectoral crest of the humerus is seen in other South American ornithopods, Novas *et al.* 2004) or represent plesiomorphies (distal end of fibula reduced, astragalus with 'stepped' proximal surface). *Notohypsilophodon* may represent a valid taxon, but this cannot be ascertained from the published description and this taxon is provisionally excluded from the phylogenetic analysis.

Four taxa (*Atlascopcosaurus loadsi*, *Fulgurotherium australe*, *Leaellynasaura amicagraphica*, *Quantassaurus intrepidus*) have been named on the basis of cranial and postcranial material from the Early Cretaceous of Australia (Rich & Vickers-Rich 1989, 1999). Although all of these taxa have been considered valid by a recent review (e.g. Norman *et al.* 2004c), the type specimens of all four taxa are fragmentary and unambiguous autapomorphies have not yet been defined. Referral of additional material to any one of these taxa is problematic. Although we accept that some or all of these

taxa may prove to be diagnostic with further study, we here provisionally exclude them from phylogenetic analysis as we have been unable to examine the majority of the material first-hand.

A number of taxa (*Auroraceratops rugosus*, *Changchunsaurus parvus*, *Xuanhuaceratops niei*, *Yamaceratops dorngobiensis*, *Yinlong downsi*) were described after the current analysis was carried out and thus have not been included. We plan to include these taxa in future iterations of this analysis.

Selection of outgroup taxa

Three outgroup taxa were chosen, based upon the phylogenetic framework outlined above. Recent, comprehensive, phylogenetic analyses of basal dinosaurs have demonstrated that *Herrerasaurus ischigualastensis* Reig, 1963 is the most basal known member of Saurischia (Langer 2004; Langer & Benton 2006). In addition, this taxon is known from well-preserved complete material and has been extensively described (Novas 1993; Sereno 1993; Sereno & Novas 1993). *Marasuchus talampayensis* (Romer, 1972) represents a well-known dinosaurian outgroup and *Euparkeria capensis* Broom, 1913 represents a basal archosaur, phylogenetically distant from Dinosauria and lacking the numerous derived specialisations seen in many other more proximate dinosaurian outgroups, such as pterosaurs and crurotarsans.

ANALYSES

Search methods

The full matrix (Appendix 3) consists of 46 taxa (43 in-group taxa and 3 outgroup taxa), coded for 221 characters (Appendix 2). The data matrix was constructed using the NEXUS Data Editor (<http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html>). Prior to analysis, safe taxonomic reduction (Wilkinson 1995c) was carried out using the program TAXEQ3 (Wilkinson 2001a). Safe taxonomic reduction identifies taxa that can be excluded without affecting the inferred relationships of the remaining taxa. The matrix does not contain any taxonomic equivalents and all taxa were included in subsequent analyses.

Analyses were carried out in PAUP* 4.0b10 (Swofford 2002); all characters are treated as unordered and equally weighted and polymorphisms are treated as uncertainty. Branches with a minimum length of zero were collapsed during searches (the '-amb' option); this setting recovers only 'strictly supported' trees (Nixon & Carpenter 1996; Kearney & Clark 2003), but can result in trees that are not of minimum length and cannot be considered as most parsimonious trees (MPTs); (Wilkinson 1995a). As a result we filtered the resultant set of trees to ensure that only minimum length trees were retained. Analysis was conducted using a heuristic search with 10,000 replicates and TBR branch-swapping, each starting tree being produced by random stepwise addition.

The analysis recovered 3787 trees; filtering these trees so that only minimum length trees were retained resulted in 756 MPTs of 477 steps (Consistency Index (CI) = 0.505, Retention Index (RI) = 0.732, Rescaled Consistency Index (RC) = 0.370). Strict and 50% majority-rule component



Figure 2 Strict component consensus (left) and 50% majority-rule consensus (right) of 756 most parsimonious trees (MPTs) produced by analysing a data matrix of 46 taxa and 221 characters. Values above nodes on the Strict component consensus represent bootstrap proportions. Values beneath nodes on the Strict component consensus indicate Bremer support. Bremer support values of +1 or less are not shown. Numbers beneath nodes on the 50% majority-rule consensus indicate the percentage of MPTs in which that node appears (nodes with no values beneath them appear in all MPTs).

consensus trees (Fig. 2) and an Adams consensus tree, were calculated using PAUP*. The strict component consensus (SCC) tree contains two major polytomies and contains a much lower degree of resolution than the majority-rule or Adams consensus trees; the latter observation suggests that the low degree of resolution in the SCC tree results from a number of taxa acting as ‘wildcards’, as a result of high

amounts of missing data, or character conflict, or both. A maximum agreement subtree was also calculated that excludes 8 taxa (*Echinodon*, *Lycorhinus*, *Bugenasaura*, *Jeholosaurus*, *Talekauen*, *Thescelosaurus*, *Yandusaurus*, *Zephyrosaurus*; see Fig. 3).

An additional search was carried out using a demonstration version of TNT (Tree Analysis Using New Technology)

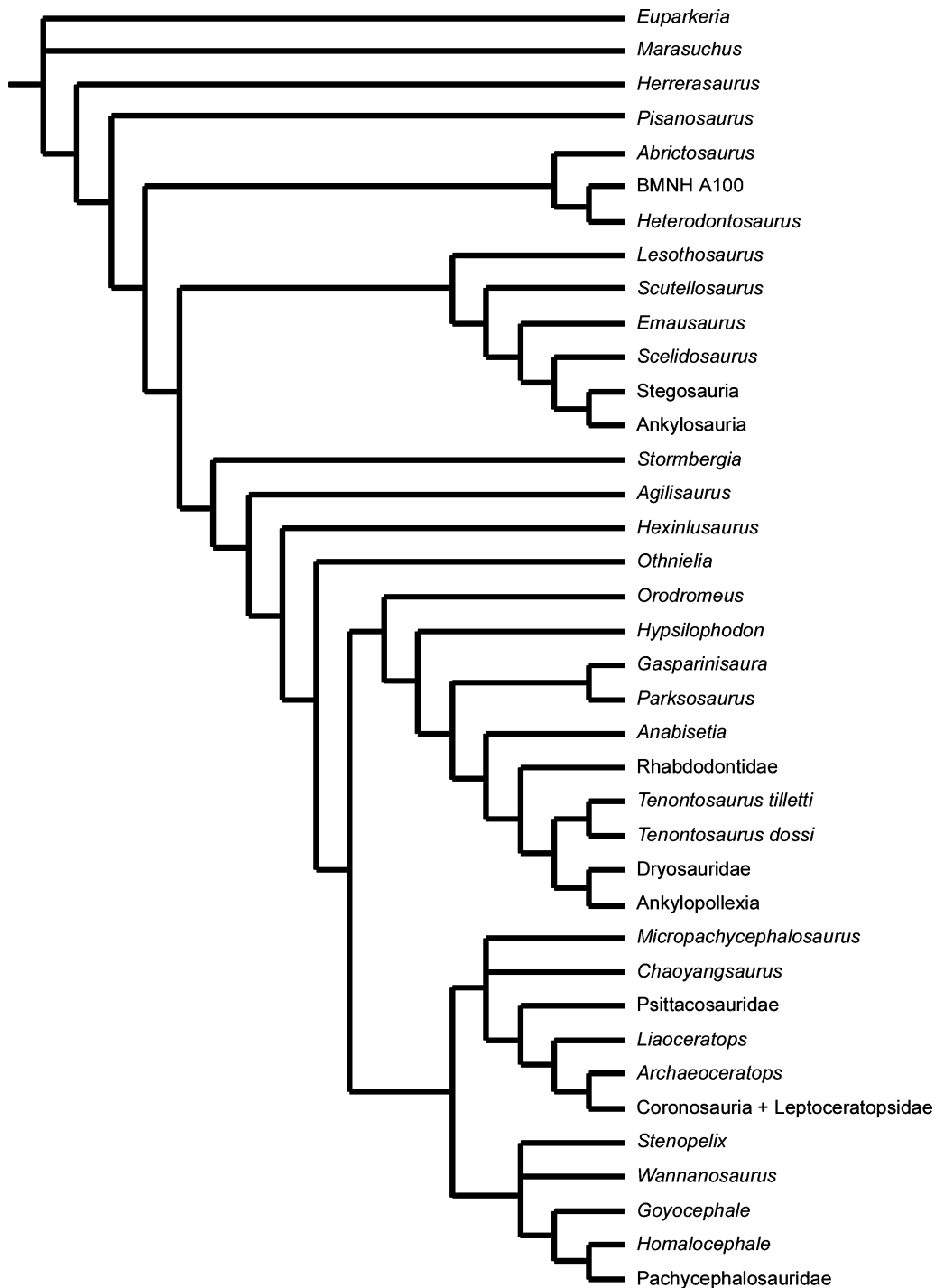


Figure 3 Maximum agreement subtree of 756 most parsimonious trees (MPTs) produced by analysing a data matrix of 46 taxa and 221 characters. Eight (*Echinodon*, *Lycorhinus*, *Bugenasaura*, *Jeholosaurus*, *Talekauen*, *Thescelosaurus*, *Yandusaurus* and *Zephyrosaurus*) of the original taxa are excluded.

v1.0, downloaded from www.zmuc.dk/public/phylogeny. A 'New Technology' search was carried out, using a random addition-sequence, 1000 replicates and default settings for the 'Sect. Search', 'Ratchet', 'Drift' and 'Tree Fusing' options. The search recovered 119 trees of 477 steps; the consensus of these trees matched the consensus of the 756 MPTs recovered by PAUP*. That TNT failed to find trees shorter than 477 steps suggests that this is the minimum tree length.

The set of 756 MPTs recovered by PAUP* forms the basis for subsequent discussion.

In an attempt to resolve further relationships common to all 756 MPTs and to identify the most unstable taxa, reduced consensus techniques (Wilkinson 1994, 1995*b*, 2003) were applied to the data. The most commonly used consensus methods are strict component consensus (SCC) trees, which include all terminal taxa and all the clades

(components) common to all MPTs. However, the strict component method has problems of insensitivity and may fail to represent relationships that are common to the set of MPTs, but cannot be expressed as shared clades (Wilkinson 2003). Reduced consensus methods identify 'n-taxon statements'; n-taxon statements express cladistic relationships (e.g. A and C are more closely related to each other than either is to E), but need not include all terminal taxa. Reduced consensus methods delete unstable taxa to produce more informative consensus trees, which represent n-taxon statements.

Reduced consensus was applied using the 'strict' program of REDCON 3.0 (Wilkinson, 2001b) and the results corroborated using RADCON (Thorley & Page 2000), identifying a profile of eight strict reduced consensus (SRC) trees, the first of which includes all taxa and corresponds in topology to the SCC tree of the 756 MPTs. The remaining SRC trees exclude one or more unstable 'wildcard' taxa, resulting in an increase in resolution. Seven taxa (*Echinodon*, *Lycorhinus*, *Zephyrosaurus*, *Talenkauen*, *Yandusaurus*, *Gaspardinisaura*, *Parksosaurus*) are identified as unstable by these analyses. We combined six of the SRC trees (those excluding *Echinodon*, *Lycorhinus*, *Zephyrosaurus*, *Talenkauen* and *Yandusaurus*) to produce an informative derivative SRC tree (Fig. 4). We use this derivative SRC tree as the basis for optimisation of synapomorphies (Appendix 4) and for much of the subsequent discussion, and it represents our preferred hypothesis of interrelationships.

Testing the support for relationships

Randomisation tests

PAUP* was used to run a Permutation Tail-Probability (PTP) test using 1000 randomised replicates of the reduced data set (Faith & Cranston 1991; Kitching *et al.* 1998). The randomised replicates are created by randomly permuting the character states assigned to taxa, decreasing character congruence to a level that would be expected by chance alone. The MPT length is then calculated for each replicate and the distribution of MPT lengths for the replicates is compared to the length of the original MPT. The PTP test has been criticised (Bryant 1992; Carpenter 1992) and Kitching *et al.* (1998) suggested that it could best be used as an independent evaluation of the explanatory power of the data set, rather than as a criterion for acceptance or rejection of any particular cladogram. In this case, the results of this test indicate that the most parsimonious tree length (477 steps) lies outside the range of minimum tree lengths obtained from the randomised data ($P = 0.001$). This indicates that a significant phylogenetic signal is present in the data set and is not completely obscured by character conflict and missing data.

Bremer support

'Traditional' decay analysis, or Bremer support, measures the number of additional steps required before the clade is lost from the strict consensus of near-minimum length cladograms (Bremer 1988; Kitching *et al.* 1998). Bremer support was calculated for nodes present in the SCC tree by searching in PAUP* for the shortest trees not compatible with a particular node, using the CONVERSE option.

Bremer support values are shown in Fig. 2. Most nodes have a decay index of +1, i.e. they are absent from the strict consensus of all trees of 478 steps or less. Stronger support is

found only within the clades Thyreophora and Iguanodontia, but even here support is relatively low. However, it is possible that a few unstable 'wildcard' taxa, such as those identified by reduced consensus techniques (see above), can obscure support for relationships, resulting in lower decay indices than might be otherwise expected.

Wilkinson *et al.* (2000) proposed a new technique, double decay analysis (DDA), which provides Bremer support for all strictly supported n-taxon relationships. An attempt was made to apply DDA using RADCON (Thorley & Page 2000); however, the large size of the data set meant that this approach was not feasible due to time and memory constraints. For particular areas of interest PAUP* was used to write backbone constraints that could then be used to test the decay indices of n-taxon statements (see individual examples below). This allowed an assessment of the effect that wildcard taxa have upon the Bremer support for clades.

Bootstrapping

Bootstrap analysis generates 'pseudoreplicate' data sets by randomly sampling with replacement a proportion of the characters, deleting some characters randomly and reweighting other characters randomly. The MPTs are generated for each pseudoreplicate and the degree of conflict between resulting MPTs is assessed using a 50% majority rule consensus tree. Clades that are supported by a large number of characters, with low levels of homoplasy, would be expected to have high bootstrap values, whereas bootstrap values should be lower for clades supported by only a few, or by homoplastic, characters. The bootstrap should, therefore, be considered as a one-sided test of a cladogram (Kitching *et al.* 1998): groups that are recovered are supported by the data, but groups that are not recovered (or that have low bootstrap values) cannot be rejected.

A bootstrap analysis was carried out using PAUP* with 1000 replications. To allow the analysis to be carried out within a reasonable length of time the MAXTREES option of PAUP was set to 1000. This means that for each pseudoreplicate data set the search for MPTs was truncated once 1000 trees had been found. Figure 2 shows the results of the bootstrap analysis. Bootstrap support is weak throughout much of the tree.

Unstable 'wildcard' taxa can obscure levels of bootstrap support for relationships (Wilkinson 2003). One potential solution is to use the majority-rule bootstrap reduced consensus (MBRC) technique developed by Wilkinson (1996). The MBRC method provides bootstrap proportions for all 'n-taxon statements' and is implemented in the REDBOOT program of REDCON 3.0. Unfortunately, REDBOOT could not be used for this analysis due to the large size of the data matrix. An alternative method for assessing the impact of 'wildcards' on bootstrap support is used here. All trees recovered by the bootstrap analysis were saved to a NEXUS treefile. The five unstable taxa removed in the derivative SRC tree (*Echinodon*, *Lycorhinus*, *Zephyrosaurus*, *Talenkauen* and *Yandusaurus*) were pruned *a posteriori* from this set of bootstrap trees, with duplicate topologies created by this deletion being collapsed. Following pruning of these five taxa a new majority-rule bootstrap reduced consensus tree was generated containing recalculated bootstrap values (Fig. 4). For further areas of particular interest additional potentially unstable taxa were identified and pruned

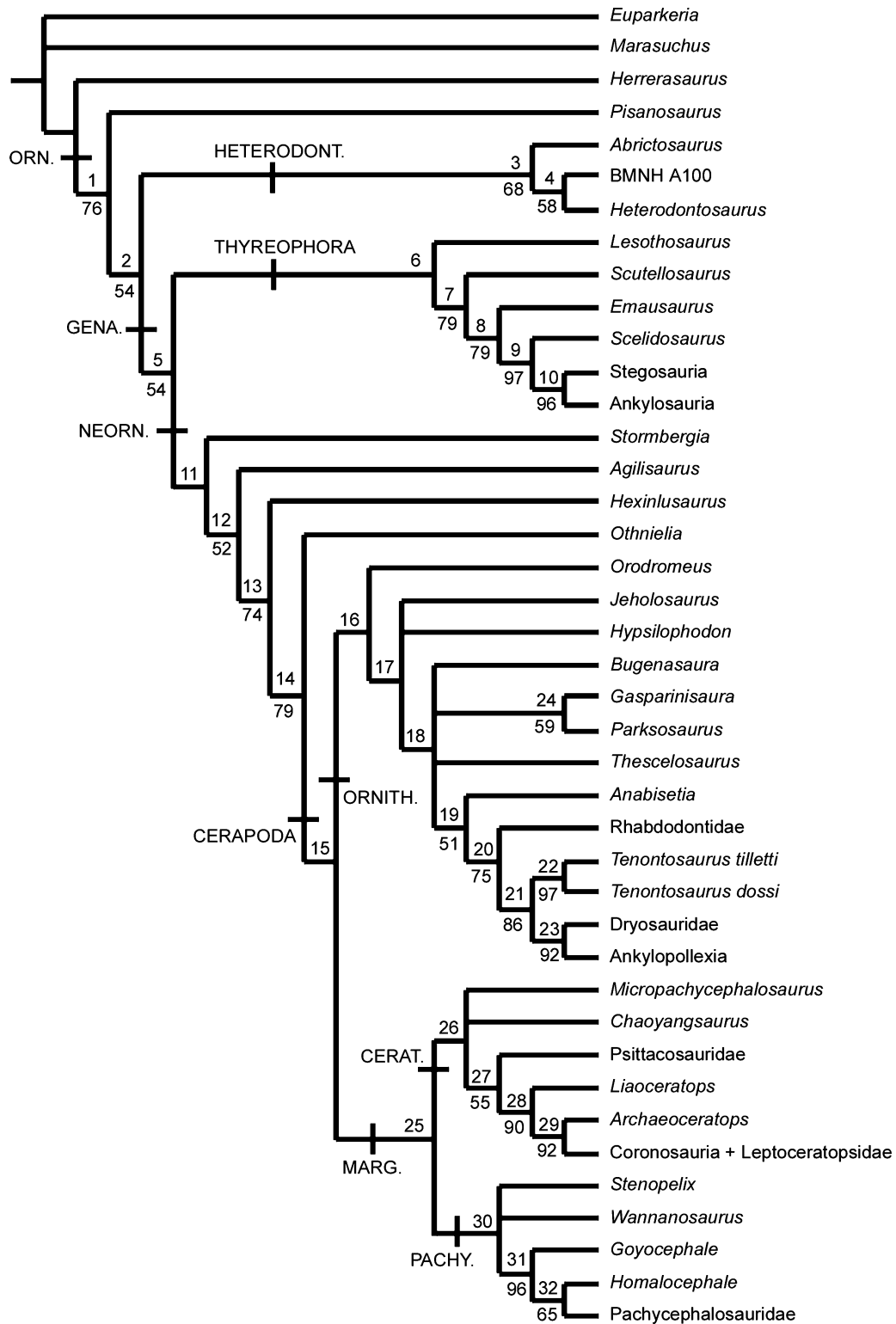


Figure 4 Derivative strict reduced consensus tree derived by *a posteriori* pruning of five unstable taxa (*Echinodon*, *Lycorhinus*, *Zephyrosaurus*, *Talenkauen* and *Yandusaurus*) from the set of 756 most parsimonious trees (MPTs) generated by the full analysis. The number above each node is a unique identifier used in the tree description (see Appendix 4). The number beneath a node represents the bootstrap proportion for that node (taken from the reduced bootstrap analysis). Note the increased levels of bootstrap support for a number of nodes when compared to Fig. 2. Abbreviations: ORN., Ornithischia; HETERODONT., Heterodontosauridae; GENA., Genasauria; NEORN., Neornithischia; ORNITH., Ornithopoda; MARG., Marginocephalia; CERAT., Ceratopsia; PACHY., Pachycephalosauria.

and bootstrap values recalculated. The effect of ‘wildcards’ on bootstrap values is discussed further below.

RESULTS

Ornithischian monophyly

Most of the characters identified as synapomorphic for Ornithischia (Appendix 4) have been identified by previous authors (Norman 1984; Sereno 1984, 1986, 1991a, 1999a; Cooper 1985; Maryańska & Osmólska 1985; Weishampel 2004; Norman *et al.* 2004a; Butler 2005). Some new potential ornithischian synapomorphies are proposed by this analysis. The presence of a buccal emargination has previously been considered (Sereno 1986, 1999a) to be synapomorphic for a less inclusive clade of ornithischians, Genasauria, and absent in the basal ornithischian *Lesothosaurus diagnosticus*. This analysis alternatively suggests that the presence of a weak or incipient buccal emargination (generally correlated with the presence of ‘cheeks’, see Galton 1973a) is a synapomorphy of Ornithischia. As noted by Butler (2005: 204), in *Lesothosaurus* there is a weak anteroposteriorly extending ridge (referred to, below, as the ‘maxillary ridge’) above the row of external maxillary foramina, forming the ventral margin of the external antorbital fenestra. Below this eminence the lateral surface of the maxilla is gently bevelled such that the maxillary tooth row is slightly inset along at least the posterior two-thirds of its length. A similar weak medial offset of the tooth row is seen in other basal ornithischians such as *Abriktosaurus consors* (BMNH RUB54) and *Scutellosaurus lawleri* (Colbert 1981) and is proposed here to be homologous with the well-developed buccal emargination seen in many other ornithischians. Irmis *et al.* (2007) criticised Butler (2005) for using the same coding for the weak buccal emargination of *Lesothosaurus* and the well-defined buccal emargination of taxa such as *Heterodontosaurus tucki*. However, the coding of Butler (2005) referred only to the presence of an emargination (not how well-developed it was), which we propose is homologous in *Lesothosaurus* and *Heterodontosaurus*. Irmis *et al.* (2007) additionally stated that in ornithischians the maxillary ridge was separated from the ventral margin of the external antorbital fenestra. This is true for some ornithischians (e.g. *Hypsilophodon foxii*, Galton 1974a) but in many basal ornithischians such as *Lesothosaurus* (BMNH R8501) and *Heterodontosaurus* (SAM-PK-K1332; Norman *et al.* 2004c: fig. 18.1) the maxillary ridge does form the ventral margin of the external antorbital fenestra.

Another potential ornithischian synapomorphy is the size and position of the posttemporal foramen. In ornithischian outgroups the posttemporal foramen is relatively large and positioned on the boundary between the parietal and the paroccipital process (e.g. *Euparkeria capensis*, Ewer 1965: fig. 2B; basal sauropodomorphs, Galton & Upchurch 2004a; *Herrerasaurus ischigualastensis*, Sereno & Novas 1993: fig. 8C), whereas in basal ornithischians (e.g. *Lesothosaurus diagnosticus*, Sereno 1991a, Sereno 1991a: fig. 11C; *Heterodontosaurus tucki*, Weishampel & Witmer 1990b: fig. 23.1), the posttemporal foramen is reduced in size and entirely enclosed by the paroccipital process. This character was independently identified as an ornithischian synapomorphy by Langer & Benton (2006).

Some previously suggested ornithischian synapomorphies are not supported by this analysis. For example Sereno (1999a) suggested that an elongate posterolateral process of the premaxilla diagnoses the clade; however, an elongate posterolateral process is present in the basal archosaur *Euparkeria* (Ewer 1965), the basal saurischian *Herrerasaurus* (Sereno & Novas 1993) and the problematic non-ornithischian ‘dinosauriform’ *Silesaurus opolensis* (Dzik 2003), and may be plesiomorphic for Dinosauria (Maryańska & Osmólska 1985).

Many of the characters identified by this and previous analyses as synapomorphic for Ornithischia describe the anatomy of the dentary and maxillary teeth. These synapomorphies have been used to refer taxa named on the basis of isolated teeth to Ornithischia (e.g. Hunt & Lucas 1994). However, recent discoveries suggest that ornithischian-like teeth have evolved a number of times within Archosauria. For instance, recently discovered cranial and postcranial material of the putative ornithischian *Revueltosaurus callenderi* suggests that this taxon is actually a non-ornithischian archosaur that appears to be phylogenetically closer to crocodylomorphs than to dinosaurs and that its ornithischian-like dentition evolved independently (Parker *et al.* 2005a, b; Irmis *et al.* 2007). In addition, ornithischian-like teeth have been described in *Silesaurus opolensis* (Dzik 2003), while many of the characteristic features of the ornithischian dentition also occur in taxa as diverse as therizinosaurs, basal sauropodomorphs and aetosaurs, suggesting that dental characters (perhaps not surprisingly) may be subject to particularly high levels of homoplasy.

The identification of ornithischian-like dental character states in non-ornithischian taxa highlights the problems inherent in referring fragmentary material to specific clades. As noted by Butler *et al.* (2006) and Irmis *et al.* (2007), most Triassic taxa named upon the basis of isolated teeth cannot, in general, be referred to Ornithischia with certainty unless they demonstrate, or are associated with material demonstrating, unique synapomorphies of an ornithischian clade (i.e. features that are not independently synapomorphic for other clades).

Pisanosaurus mertii

Pisanosaurus mertii is generally believed to be the oldest known ornithischian (Casamiquela 1967), but both the association of the material included within the holotype specimen and its phylogenetic position, have proved controversial. Sereno (1991a) proposed that the holotype specimen contained material from more than one individual; he suggested that the skull fragments, partial impression of the pelvis and distal hind limb might belong together, but that the fragmentary scapula and other postcranial bones were too small to be referred to the same individual. However, Bonaparte (1976) noted that the vertebrae were recovered in articulation with the skull and that the skeleton may have been complete prior to weathering, and a recent review supported the idea that the type specimen represents a single individual (Irmis *et al.* 2007).

Bonaparte (1976) referred *Pisanosaurus* to Heterodontosauridae on the basis that both share subcylindrical, closely packed cheek teeth, with wear facets forming a more or less continuous surface extending along the tooth row. However, Weishampel & Witmer (1990a) and Sereno (1991a)

considered *Pisanosaurus* to be the most basal known ornithischian. Weishampel & Witmer (1990a) suggested that the similarities between *Pisanosaurus* and heterodontosaurids are plesiomorphic, while Sereno (1991a: 174) noted that: 'The [wear] facets . . . do not form a continuous occlusal surface as occurs in *Heterodontosaurus* [tucki].' More recently, Norman *et al.* (2004a) have once again emphasised the morphological similarities between the cranial material of *Pisanosaurus* and that of heterodontosaurids.

The SCC tree (Fig. 2) recovered by this analysis positions *Pisanosaurus* in an unresolved polytomy at the base of Ornithischia. However, the 50% majority-rule consensus tree (Fig. 2), maximum agreement subtree (Fig. 3) and the derivative SRC tree (Fig. 4) all support the position of *Pisanosaurus* as the most basal known ornithischian. These consensus trees additionally position heterodontosaurids as a monophyletic clade of non-genasaurians, close to the base of Ornithischia (discussed below). *Pisanosaurus* and heterodontosaurids are not separated in the SCC (this is the result of the instability of the fragmentary wildcard taxon *Echinodon becklesii*); only one node separates *Pisanosaurus* from heterodontosaurids in the derivative SRC tree. This node is weakly supported by bootstrap proportions: it does not appear in the total-evidence bootstrap analysis (support of only 37%) and has support of only 54% in the reduced bootstrap analysis (Fig. 4). Only one character (Character 206, Appendix 2) unambiguously supports this node. Constraining *Pisanosaurus* and heterodontosaurids to form a monophyletic clade requires only one additional step. This suggests that the two opposing phylogenetic positions for *Pisanosaurus*, as either a non-genasaurian basal ornithischian (Sereno 1991a) or a heterodontosaurid (Bonaparte 1976), are not necessarily mutually exclusive. *Pisanosaurus* may indeed represent a heterodontosaurid and the evidence for this should be reconsidered by future work.

Heterodontosauridae

The position of heterodontosaurids within Ornithischia is one of the most problematic areas in ornithischian phylogeny and there is no current consensus on this topic. Four alternative phylogenetic positions have been proposed: (1) as basal ornithopods (e.g. Crompton & Charig 1962; Thulborn 1971; Galton 1972; Santa Luca *et al.* 1976; Sereno 1984, 1986, 1999a; Gauthier 1986; Weishampel 1990; Weishampel & Witmer 1990b; Smith 1997; Norman *et al.* 2004c); (2) as the sister group to Marginocephalia (Maryńska & Osmólska 1984; Cooper 1985; Olshevsky 1991; Zhao *et al.* 1999; Buchholz 2002; You *et al.* 2003; Norman *et al.* 2004c; Xu *et al.* 2006); (3) as the sister group to Ornithopoda + Marginocephalia (Cerapoda) (Norman 1984; Maryńska & Osmólska 1985; Butler 2005); (4) as the most basal well-known ornithischians (Bakker & Galton 1974; Olsen & Baird 1986). This analysis supports the fourth of these positions and the phylogenetic support for this is discussed below, although a full review of the anatomical evidence will be presented elsewhere (R. J. B., unpublished results).

Four taxa (*Heterodontosaurus tucki*, *Abriotosaurus consors*, *Echinodon becklesii*, *Lycorhinus angustidens*) and one specimen (BMNH A100) previously referred to Heterodontosauridae were included in this analysis. These taxa do not form a clade in the SCC tree, but are included in a large polytomy at the base of Ornithischia (Fig. 2). However, reduced consensus trees indicate that this basal polytomy is

the result of the unstable and problematic taxon *Echinodon* (which is highly fragmentary, with 83% missing data); exclusion of *Echinodon* results in the remaining four OTUs forming a heterodontosaurid clade, while further exclusion of *Lycorhinus* (86% missing data) in the derivative SRC tree resolves relationships within Heterodontosauridae (Fig. 4).

The heterodontosaurid node is weakly supported by bootstrap proportions in the total-evidence bootstrap analysis (support of only 19%); however, bootstrap support is considerably higher (68%) in the reduced bootstrap analysis (Fig. 4), suggesting that low bootstrap support for Heterodontosauridae is probably the result of fragmentary and unstable wildcard taxa. To test whether similar 'hidden' Bremer support exists for Heterodontosauridae we wrote a backbone constraint that specified that *Heterodontosaurus*, *Abriotosaurus* and BMNH A100 form a clade to the exclusion of other ornithischians, but did not specify the position of the five unstable taxa (*Echinodon*, *Lycorhinus*, *Zephyrosaurus*, *Talenkauen* and *Yandusaurus*) discussed above and removed in the derivative SRC tree. The Bremer support for this backbone constraint was +2, again suggesting that low support for Heterodontosauridae is the result of unstable wildcard taxa.

The MPTs recovered in this analysis do not support a link between heterodontosaurids and ornithopods (phylogenetic hypothesis 1, above). In order to test this further we ran the following constrained analyses: firstly, Ornithopoda (*sensu* Weishampel 1990; Sereno 1999a), containing heterodontosaurids, 'hypsiphodontids' and iguanodontids, was constrained as monophyletic, although Hypsiphodontidae (*sensu* Weishampel & Heinrich 1992) was not constrained as a monophyletic clade; secondly, a backbone constraint was specified that required that *Heterodontosaurus* and Ankylopollexia be more closely related to each other than either is to marginocephalians, thyreophorans or ornithischian outgroups. This constraint does not specify the complete content of Ornithopoda.

Templeton non-parametric tests were carried out using PAUP* that compared trees within the profile of 756 MPTs generated by the unconstrained analysis with all trees recovered by the constrained analyses. Ideally all MPTs should be compared with all trees recovered by the constrained analyses; however, as this is time intensive (this would involve 756 separate Templeton tests) a subset of the MPTs (every 25th MPT) was used.

Under the first constraint, 1812 trees of 500 steps were found, 23 steps longer than the most parsimonious tree length. These trees were a significantly worse ($p = 0.0004$ – 0.01) explanation of the data than the most parsimonious topology. The second constraint recovered 2034 trees of 490 steps (13 extra steps). Some, but not all, of these trees were significantly ($p = 0.03$ – 0.07) worse explanations of the data than the most parsimonious topology.

A sister group relationship between heterodontosaurids and marginocephalians (phylogenetic hypothesis 2, above) is not found by this analysis; instead heterodontosaurids are positioned more basally within Ornithischia (Fig. 4). To test if any support is present in the data for a Heterodontosauridae–Marginocephalia sister grouping we constrained such a clade to be monophyletic and 420 trees of 487 steps (10 extra steps) were recovered; Templeton tests indicate that these trees are not a significantly worse explanation of the data ($p = 0.128$ – 0.1803).

A number of derived character states are absent in heterodontosaurids, but occur in all cerapodan ornithischians. These include: loss of the squamosal–quadratojugal contact; closure of the external mandibular fenestra (reversed in some psittacosaurids); reduction of the pubic peduncle of the ilium; development of an elongated rod-like prepubic process; modification of the *fossa trochanteris* into a distinct constriction separating the femoral head and greater trochanter; and the anteroposterior expansion of the greater trochanter of the femur relative to the anterior trochanter (Characters 52, 104, 178, 193, 194, 198, 199; Appendix 2). If heterodontosaurids are positioned within Cerapoda, as either basal marginocephalians or basal ornithopods, then a substantial amount of homoplasy must be invoked to explain the distribution of these derived character states.

This analysis finds support for an alternative position, not suggested by previous cladistic phylogenetic analyses (although suggested by the non-cladistic work of Bakker & Galton 1974; Olsen & Baird 1986), that heterodontosaurids are not members of Genasauria and are actually situated close to the base of Ornithischia. This basal position is supported by a number of characters (Appendix 4), including: absence of a spout-shaped mandibular symphysis; premaxillary crowns not expanded mesiodistally or apicobasally above the root; alveolar foramina absent medial to maxillary and dentary tooth rows; retention of epiphyses on cervical vertebrae; manus length more than 40% of the combined length of the humerus and radius; penultimate phalanges of the second and third manual digits more elongate than the proximal phalanges; extensor pits present on the dorsal surface of the distal end of metacarpals and manual phalanges; manual unguals strongly recurved with prominent flexor tubercles (Characters 97, 113, 126, 133, 156, 159, 162, 163; Appendix 2).

A basal position for heterodontosaurids is more consistent with the stratigraphic record than previous hypotheses and has important implications for our understanding of early ornithischian anatomy, palaeobiology and evolution that will be explored by future work. However, substantial further work is required on heterodontosaurid anatomy and character homology before this hypothesis can be considered well-supported.

'Fabrosaurids'

Sereno (1984, 1986, 1991a, 1999a) proposed that the plesiomorphic ornithischian *Lesothosaurus diagnosticus* is the sister group of Genasauria, a position similar to that proposed by Galton (1972) and this interpretation has been followed by later authors (e.g. Weishampel & Witmer 1990a; Norman *et al.* 2004a). This contrasts with previous views of ornithischian phylogeny (Thulborn 1971; Norman 1984; Cooper 1985; Maryańska & Osmólska 1985) that usually considered *Lesothosaurus* to have affinities with Ornithopoda and, sometimes, a larger group that additionally included pachycephalosaurs and ceratopsians (Norman 1984; Butler 2005). The interpretation of the position of *Lesothosaurus* suggested by Sereno (1984, 1986, 1991a, 1999a) is based upon a number of putative synapomorphies supposedly shared by Genasauria and absent in *Lesothosaurus*; Butler (2005) recently demonstrated that most of these characters are either present in *Lesothosaurus* or absent in some basal thyreophorans/neornithischians. Butler (2005) suggested three characters that might group *Lesothosaurus* with

basal neornithischians. Of these characters, reduction of the forelimb (character 153, Appendix 2) is here optimised as independently gained in *Lesothosaurus*, *Agilisaurus louderbacki* and pachycephalosaurs; the presence of a dorsal groove on the ischium (character 183, Appendix 2) may be a genasaurian plesiomorphy as it appears to be present in the thyreophoran *Scutellosaurus lawleri* (UCMP 130580, R. J. B., pers. obs., 2005); while the reduction of metatarsal one (character 211, Appendix 2) optimises as an ornithischian plesiomorphy, present in heterodontosaurids.

This analysis resolves *Lesothosaurus* as the most basal thyreophoran (Figs 2–4; see also Liu 2004); however, only one unambiguous character (character 106, Appendix 2) supports this position. In *Lesothosaurus* an anteroposteriorly extending ridge is present on the lateral surface of the surangular, immediately anterodorsal to the glenoid and dorsal to the surangular foramen (BMNH RUB17; a previous reconstruction (Sereno 1991a) shows this feature as less prominent than actually occurs in the syntype and referred specimens). This feature is also present in the basal thyreophorans *Scelidosaurus* (BMNH R1111), *Emausaurus* (Haubold 1990) and *Scutellosaurus* (UCMP 130580). In all four taxa the ridge is prominent and transversely thickened, overhangs the lateral surface of the angular and laterally delimits a narrow, dorsally facing shelf. Statistical support for this position of *Lesothosaurus* is weak (total-evidence bootstrap proportion = 40%; Bremer support = +1), with the low bootstrap support reflecting the fact that this node is supported by only a single character.

All previous and current interpretations of the exact phylogenetic position of *Lesothosaurus* are problematic and poorly supported. However, it seems clear that *Lesothosaurus* is positioned close to the base of Genasauria, as either the sister-taxon to this clade (Sereno 1986, 1999a), the most basal known neornithischian (Butler 2005), or the most basal thyreophoran (this analysis). In addition, autapomorphies appear to be difficult to delimit for *Lesothosaurus* (Butler 2005). Taken in combination, these observations suggest that the anatomy of *Lesothosaurus* may be close to that of the ancestral genasaurian and that this taxon remains a good 'ancestral' taxon for ornithischian functional studies.

A monophyletic Fabrosauridae was not supported by this analysis. Peng (1997) identified a number of characters that he suggested linked *Lesothosaurus* and *Agilisaurus* to the exclusion of other ornithischians. While some of these characters have more widespread distributions within Ornithischia (e.g. Characters 173, 176, 183, 211, Appendix 2), one character (humerus strongly reduced in length, Character 153, Appendix 2) is only known in *Lesothosaurus* and *Agilisaurus* amongst basal ornithischians. This character, therefore, provides some evidence for a monophyletic Fabrosauridae. However, *Agilisaurus* is more derived than *Lesothosaurus* in a large number of other character states (e.g. Characters 101, 104, 178, 184, 194, Appendix 2), suggesting that Fabrosauridae *sensu* Peng (1997) is defined largely on the basis of symplesiomorphies and is probably paraphyletic. Five additional steps are required for *Lesothosaurus* and *Agilisaurus* to form a clade to the exclusion of other taxa.

Neither Butler (2005) nor this analysis have been able to find anatomical evidence for a South African 'fabrosaurid' clade (*sensu* Knoll 2002a, b), consisting of *Lesothosaurus* and *Stormbergia dangershoeki*, although only one additional

step is required for such a clade to be recovered. One unambiguous synapomorphy positions *Stormbergia* as a basal neornithischian, separate from *Lesothosaurus*: presence of a tab-shaped obturator process on the ischium (Character 184, Appendix 2).

Thyreophora

The monophyly of Thyreophora (ignoring, at present, the possible most basal thyreophoran *Lesothosaurus diagnosticus*, discussed above) is well-established and uncontroversial and the clade including *Scutellosaurus lawleri*, *Emausaurus ernsti*, *Scelidosaurus harrisonii* and Euryopoda (Ankylosauria + Stegosauria) is comparatively well-supported by total-evidence bootstrap proportions and Bremer support (Fig. 2). The characters that unambiguously support the monophyly of this clade (Appendix 4) have already been identified by Sereno (1986, 1999a), with the exception of the presence of cortical remodelling of cranial elements (Character 89, Appendix 2), which has been previously considered to be limited to ankylosaurs, but is also known in *Scutellosaurus* (UCMP 130580, jugal; Rosenbaum & Padian 2000: fig. 5C), *Emausaurus* (SGWG 85) and *Scelidosaurus* (BMNH R1111; Carpenter 2001).

The phylogenetic position of *Scelidosaurus harrisonii* has proved controversial, despite being known from a number of well-preserved specimens. This is probably because no comprehensive description of the taxon has been carried out since the work of Owen (1861a, 1863), although a redescription is in progress (D.B.N. unpublished results). Sereno (1986, 1999a) suggested 16 characters that link ankylosaurs and stegosaurs (as the clade Euryopoda) to the exclusion of *Scelidosaurus*. Carpenter (2001) made the most extensive case to date in favour of positioning *Scelidosaurus* as the most basal ankylosaur; however, Carpenter did not include the euryopodan characters of Sereno (1999a) in his analysis. At least four of the five synapomorphies identified by Carpenter as linking *Scelidosaurus* with ankylosaurs appear to have a more widespread distribution within Thyreophora (Maidment *et al.*, 2006; R. J. B. & S. C. R. Maidment, unpublished results).

This analysis does not find a sister group relationship between *Scelidosaurus* and ankylosaurs. A large number of anatomical features are shared by stegosaurs and ankylosaurs, but are absent in *Scelidosaurus* (Appendix 4; see also Sereno 1986, 1999a). It is possible that a number of these features could have evolved in parallel in both clades as adaptations to large size (e.g. development of the preacetabular process of the ilium, Character 166, Appendix 2; reduction of the fourth trochanter, Character 201, Appendix 2), but that this homoplasy has not yet been recognised as a result of the scarcity of well-preserved Early and Middle Jurassic euryopodans. It is also possible that the distribution of character states has been complicated by coding both Stegosauria and Ankylosauria as supraspecific clades: a full consideration of the phylogenetic position of *Scelidosaurus* requires an analysis that includes a large number of stegosaur and ankylosaur taxa. Unfortunately such an analysis has not yet been carried out and is beyond the scope of this work. However, the evidence presented by this analysis casts doubts upon interpretation of *Scelidosaurus* as a basal ankylosaur. Constraining *Scelidosaurus* to be the sister group of Ankylosauria results in 2270 trees of 485 steps (8 extra steps), but is

not a significantly worse explanation of the data (Templeton test, $p = 0.04\text{--}0.13$).

Basal neornithischians

Most previous analyses have included all neornithischian taxa within Cerapoda, as members of either Ornithopoda or Marginocephalia (e.g. Sereno 1999a). Only Butler (2005) has previously identified non-cerapodan neornithischians. This analysis finds four OTUs (*Stormbergia dangershoeki*, *Agilisaurus louderbacki*, *Hexinlusaurus multidentis*, *Othnielia rex*; the lattermost is identified as a non-cerapodan neornithischian in the derivative SRC tree: Fig. 4) that form a pectinate series of successively closer sister taxa to Cerapoda.

Referral of *Stormbergia* to Neornithischia is supported by only a single unambiguous character (possession of an obturator process on the ischium, Character 184, Appendix 2), and measures of support for this node are weak (Bremer support = +1, bootstrap = 33%). Referral of this taxon to Neornithischia is, therefore, preliminary (although we have not yet been able to identify evidence that might support its referral to any other ornithischian clade) and a better supported phylogenetic position must await the discovery of specimens of this taxon with cranial material.

Apparent support is also weak for the position of *Agilisaurus* and *Hexinlusaurus* as basal neornithischians. However, bootstrap support for the node supporting the clade *Othnielia* + Cerapoda, to the exclusion of *Agilisaurus* and *Hexinlusaurus*, is relatively high (79%) in the reduced bootstrap analysis (Fig. 4). Five unambiguous characters (Appendix 4) suggest that *Hexinlusaurus* is more closely related to cerapodans than *Agilisaurus*. This is of interest as many authors have synonymised the two, although recent work (Barrett *et al.* 2005) supports generic-level distinction. Four additional steps are required for *Agilisaurus* and *Hexinlusaurus* to group as sister taxa, although this does not represent a significantly worse explanation of the data (Templeton test, $p = 0.10\text{--}0.35$). Constraining these taxa as ornithopods (as suggested by previous authors, e.g. Weishampel & Heinrich 1992; Norman *et al.* 2004c) requires 13 additional steps and is a significantly worse explanation of the data than the most parsimonious topology (Templeton test, $p = 0.01\text{--}0.02$).

The phylogenetic position of *Othnielia* is problematic. *Othnielia* has been invariably referred to Ornithopoda, usually as a member of Hyspilophodontidae (e.g. Weishampel & Heinrich 1992); by contrast, the derivative SRC tree (Fig. 4) recovered by this analysis excludes *Othnielia* from Cerapoda, as a result of the retention of a relatively short postacetabular process (Character 174, Appendix 2) and a relatively reduced and splint-like first metatarsal (Character 211, Appendix 2). However, the position of *Othnielia* appears to be unstable and weakly supported and this may reflect the near-absence of cranial data for this taxon.

Ornithopoda

A monophyletic Ornithopoda is not recovered in the SCC tree (Fig. 2), but is present in the derivative SRC tree (Fig. 4) following the *a posteriori* pruning of five unstable taxa, including the putative ornithopods *Yandusaurus*, *Zephyrosaurus* and *Talenkauen*. However, the content of the ornithopod clade recovered in the derivative SRC tree (Fig. 4) differs significantly from that suggested by previous analyses. A number of

taxa generally referred to Ornithopoda (heterodontosaurids, *Agilisaurus*, *Hexinlusaurus*, *Othnielia*) are here positioned elsewhere within Ornithischia; this suggests that Ornithopoda, as conceived by some previous authors (e.g. Sereno 1986, 1999a; Norman *et al.* 2004c), may be polyphyletic; alternatively, although we do not promote this view (we prefer the stem-based definition for Ornithopoda given in Table 1), it is conceivable that the definition of Ornithopoda could be expanded to include some, or all, of these taxa, as well as ceratopsians and pachycephalosaurs.

Hypsilophodontidae, as generally conceived (Weishampel & Heinrich 1992), does not form a monophyletic clade; instead 'hypsilophodontids' appear to represent a paraphyletic grade of basal neornithischian and basal ornithopod taxa (see below). More derived ornithopod relationships generally follow that suggested by previous authors (e.g. Weishampel *et al.* 2003).

The derivative SRC tree (Fig. 4) suggests that Ornithopoda includes a paraphyletic assemblage of 'hypsilophodontids' (*Orodromeus makelai*, *Jeholosaurus shangyuanensis*, *Hypsilophodon foxii*, *Parksosaurus warreni*, *Gasparinisaura cincosaltensis*, *Bugenasaura infernalis*, *Thescelosaurus neglectus*) and Iguanodontia (comprising rhabdodontids, tenontosaurus, dryosaurids and ankylopollexians). However, support is weak at the base of Ornithopoda, with most basal nodes having very low (less than 50%) total-evidence bootstrap values. The characters that support basal nodes in the derivative SRC tree tend to have limited or poorly understood distributions. For example, Ornithopoda is supported by the presence of a fossa-like depression on the premaxilla–maxilla boundary (Character 13, Appendix 2), the possession of narrow and elongate (more than twice as long as wide) frontals that contact the nasals anterior to the orbits (Character 64, Appendix 2), and the possession of a foramen positioned on the dorsal part of the surangular–dentary joint (Character 105, Appendix 2). The first character is only known in *Orodromeus*, *Jeholosaurus* and *Hypsilophodon*. It appears to be absent in more derived ornithopods and a similar distribution occurs for the second character (also present in *Zephyrosaurus*, Sues 1980).

This analysis suggests that Ornithopoda is a poorly supported clade and the weak support at the base of Ornithopoda may be a result of the instability of fragmentary (e.g. *Zephyrosaurus*, *Yandusaurus*) or incompletely described (e.g. *Talenkauen*) taxa. A further cause of the weak support for Ornithopoda may be the repositioning of heterodontosaurids as basal ornithischians. Heterodontosaurids have effectively acted as an outgroup for analyses of ornithopod phylogeny. For instance, Sereno (1999a) suggested that the following characters were derived features of Euornithopoda: reduction of the external antorbital fenestra; closure of the external mandibular fenestra; reduction of the deltopectoral crest of the humerus; enlargement of the prepubic process of the pubis; presence of an obturator process on the ischium. The plesiomorphic state for each of these characters is present in Heterodontosauridae. However, if heterodontosaurids are repositioned basally within Ornithischia it becomes apparent that each of the above characters suggested by Sereno (1999a) as diagnostic for Euornithopoda actually has a more widespread distribution within Cerapoda. For instance, the external mandibular fenestra is closed in basal neornithischians (e.g. *Agilisaurus*, Peng 1992), ceratopsians (e.g. Zhao *et al.* 1999; You & Dodson 2004) and pachyceph-

alosaurs (Maryańska *et al.* 2004), the prepubic process of the pubis is elongated in some basal neornithischians (*Hexinlusaurus*, He & Cai 1984), pachycephalosaurs (Maryańska *et al.* 2004: fig. 21.4C) and basal ceratopsians (e.g. Psittacosauridae, Sereno 1987; *Archaeoceratops*, You & Dodson 2003) and the obturator process is present on the ischium in basal neornithischians (*Stormbergia*, SAM-PK-K1105, BMNH R11000, Butler 2005; *Agilisaurus*, ZDM T6011; *Hexinlusaurus*, He & Cai 1984, ZDM T6001). Thus the apparently strong support for Ornithopoda found by previous analyses (e.g. Sereno 1999a) may be in part an artefact of an incorrect phylogenetic placement of heterodontosaurids.

Hypsilophodontidae

Early conceptions of Hypsilophodontidae were of an implicitly paraphyletic 'plexus' of plesiomorphic, small, bipedal ornithischians (e.g. Thulborn 1971). Such a grouping was incompatible with cladistic study and a number of authors attempted to develop a more restrictive, monophyletic, definition of the group (e.g. Norman 1984; Sereno 1984, 1986; Cooper 1985; Sues & Norman 1990; Weishampel & Heinrich 1992). Sereno (1986) and Weishampel & Heinrich (1992) considered the following taxa as members of Hypsilophodontidae: *Thescelosaurus neglectus*, *Othnielia rex*, *Hypsilophodon foxii*, *Zephyrosaurus schaffi*, *Orodromeus makelai* and *Yandusaurus* (the taxa *Yandusaurus hongheensis* and *Hexinlusaurus multidentis* were included as a single OTU; however, these taxa are distinguishable at generic level: Barrett *et al.* 2005). Sues & Norman (1990) referred a number of other small ornithopods (e.g. *Agilisaurus louderbacki*, *Gongbusaurus shiyii*, '*Gongbusaurus wucaiwansensis*') to Hypsilophodontidae, while *Bugenasaura infernalis* has been referred to the clade by Galton (1999). However, recent analyses (Schetz 1998, 1999; Winkler *et al.* 1998; Weishampel *et al.* 2003; Norman *et al.* 2004c) have found little evidence for hypsilophodontid monophyly.

A monophyletic Hypsilophodontidae was not recovered by this analysis (Figs 2–4). Although 'hypsilophodontids' are generally thought of as rather anatomically conservative, it is clear that they are actually relatively diverse, with some taxa (e.g. *Thescelosaurus*) showing greater similarities to more derived, iguanodontian ornithopods, while other taxa appear to have much more plesiomorphic morphologies (e.g. *Orodromeus*) and some may not even be referable to Ornithopoda (e.g. *Agilisaurus*, *Hexinlusaurus*, *Othnielia*).

'Hypsilophodontids' appear to represent a grade of basal neornithischian and basal ornithopod taxa. Further work should be carried out on the relationships of these basal taxa. This analysis finds weak support for some groupings, such as *Gasparinisaura* and *Parksosaurus* and more in depth work in this part of the tree might clarify such possibilities.

Marginocephalia

Only limited character evidence has been discovered previously for Marginocephalia (although see Xu *et al.* 2006), leading some authors to doubt its validity (Dodson 1990; Sullivan 2006). This analysis supports marginocephalian monophyly; however, total-evidence bootstrap values (less than 50%) and Bremer support (+1) are very low for this clade. This might suggest that the clade is supported by a relatively low number of characters. However, character optimisation

(Appendix 4) indicates that Marginocephalia is supported by 8 unambiguous synapomorphies and as many as 17 characters under accelerated transformation (ACCTRAN). This suggests that there is considerable character evidence for Marginocephalia, but that support for the clade is obscured by one or more wildcard taxa. The putative basal pachycephalosaur *Stenopelix valdensis* and the problematic cerapodan *Micropachycephalosaurus hongtuyanensis* are identified below as wildcard taxa and it is possible that the apparent low support for Marginocephalia may result, in part, from the instability of these taxa. To test this possibility a backbone constraint was written that did not specify the position of *Stenopelix*, *Micropachycephalosaurus*, or the five unstable taxa identified in the derivative SRC tree (Fig. 4), but specified that all other pachycephalosaurs and ceratopsians were more closely related to one another than any of them were to ornithopods, thyreophorans, or non-cerapodan neornithischians. This constraint had a Bremer support of +4. This increased Bremer support suggests that there is relatively strong 'hidden' support for Marginocephalia. To confirm this, we pruned the five unstable taxa identified in the derivative SRC tree, *Micropachycephalosaurus* and *Stenopelix* from the set of trees recovered by the bootstrap analysis and generated a new 50% majority-rule bootstrap reduced consensus tree, which demonstrates increased (70%) bootstrap support for Marginocephalia.

Three key characters have been identified by previous authors (Serenó 1984, 1986, 1987, 1999a, 2000; Cooper 1985; Maryańska & Osmólska 1985) as supporting marginocephalian monophyly: posterior expansion of the parietosquamosal obscures the occiput in dorsal view, premaxillae excluded from the border of the internal nares, postpubis reduced or absent (Characters 68, 84, 188/189, Appendix 2). Other suggested marginocephalian synapomorphies (see, e.g., Cooper 1985; Serenó 1987) have not been supported by subsequent work. This analysis supports the validity of these three marginocephalian characters.

A number of other potential marginocephalian synapomorphies are identified here. Unambiguous synapomorphies include: absence of elliptic fossa on the nasals (although a fossa is present in at least one basal ceratopsian, *Liaoceratops yanzigouensis*), three premaxillary teeth, elongate and strap-like scapula blade and the absence of an obturator process on the ischium (Characters 19, 112, 150, 184, Appendix 2). ACCTRAN indicates additional potential synapomorphies, most of which have rather uncertain distributions and suffer from missing data. For example, node-like ornamentation is present on the jugal–postorbital bar and angular (Characters 41, 108, Appendix 2) of pachycephalosaurs and the basal ceratopsians *Chaoyangsaurus youngi* and *Archaeoceratops oshimai*. However, the distribution of this character remains uncertain as ornamentation is absent in other basal ceratopsians such as Psittacosauridae.

Ceratopsia

Ceratopsia is recovered as a monophyletic clade in this analysis, although decay indices and bootstrap values suggest that support for the clade is weak. However, this may result from the inclusion within the clade of the fragmentary and problematic taxon *Micropachycephalosaurus hongtuyanensis*, which appears to act as a 'wildcard', or the unstable position of the putative basal pachycephalosaur *Stenopelix valdensis* (see below), or both. The Bremer support for the

ceratopsian node (including *Micropachycephalosaurus*) is +1. To test the effect of *Micropachycephalosaurus* and *Stenopelix* upon the apparent support for Ceratopsia an n-taxon backbone constraint was defined which specified that *Chaoyangsaurus*, Psittacosauridae and neoceratopsians were more closely related to each other than to ornithopods, pachycephalosaurs, or non-cerapodans; however, it did not specify the position of *Micropachycephalosaurus*, *Stenopelix*, or the five wildcard taxa identified by the derivative SRC tree (Fig. 4). PAUP* was then used to search for the shortest trees incompatible with the backbone constraint. The shortest tree recovered was of 481 steps (Bremer support of +4), suggesting that strong support exists for the ceratopsian clade, but is obscured by the unstable nature of several taxa. To confirm this, we pruned seven taxa (see above) including *Micropachycephalosaurus* and *Stenopelix* from the set of trees recovered by the bootstrap analysis and generated a new majority-rule bootstrap reduced consensus tree, which demonstrates very high (89%) bootstrap support for Ceratopsia.

Why does *Micropachycephalosaurus* act as a wildcard and why does this taxon group with ceratopsians when it has been traditionally referred to Pachycephalosauria (Dong 1978; Maryańska *et al.* 2004)? The holotype of *Micropachycephalosaurus* (IVPP V 5542), originally described by Dong (1978), is extremely fragmentary and comprises a quadrate and partial tooth row, vertebral elements (including an incomplete sacrum), a partial ilium and the partial left femur and tibia. Dong (1978) referred *Micropachycephalosaurus* to Pachycephalosauria on the basis of a supposedly thickened skull roof; however, no material of the skull roof is currently present in the holotype specimen (R. J. B. pers. obs., 2004; R. J. B. & Q. Zhao, unpublished results). In addition, other pachycephalosaurian synapomorphies (e.g. preacetabular process of ilium expands mediolaterally anteriorly in dorsal view; elongate caudal ribs) are absent. Cerapodan features (particularly of the femur) are present, but few characters can be identified that unambiguously link *Micropachycephalosaurus* with pachycephalosaurs, ornithopods or ceratopsians. The only character that can be identified as potentially linking *Micropachycephalosaurus* with ceratopsians is the enlargement of the lateral condyle of the quadrate (Character 63, Appendix 2); however, this character is homoplastic, with the derived state also known in heterodontosaurids (*Heterodontosaurus*, SAM-PK-K337) and some ornithopods (e.g. Weishampel *et al.* 2003). Only one additional step is required for *Micropachycephalosaurus* to group with either pachycephalosaurs or ornithopods, instead of ceratopsians. A ceratopsian identity appears to be poorly supported and the position of *Micropachycephalosaurus* within Cerapoda cannot be clarified with any certainty (R. J. B. & Q. Zhao, unpublished results).

Pachycephalosauria

Pachycephalosauria is a well-established clade and all published ornithischian phylogenetic analyses have found it to be monophyletic. This analysis finds Pachycephalosauria to be a monophyletic clade including *Stenopelix valdensis*, *Wannanosaurus yansiensis*, *Goyocephale lattimorei*, *Homocephale calathocercos* and Pachycephalosauridae; however, Bremer support (+1) and total-evidence bootstrap values (55%) show surprisingly low support for Pachycephalosauria (Fig. 2), although bootstrap support is stronger for more derived groupings within the clade. However, as

with Ceratopsia, the real support for the clade may be obscured by the presence of one or more ‘wildcard’ taxa. The most obvious candidate is the problematic basal taxon *Stenopelix*. To test this possibility, a backbone constraint was defined that specified that *Wannanosaurus*, *Goyocephale*, *Homalocephale* and Pachycephalosauridae are more closely related to one another than to ceratopsians, ornithopods, or non-ceratopodans (the phylogenetic positions of the five wildcard taxa identified by reduced consensus, *Stenopelix* and the problematic taxon *Micropachycephalosaurius* were not specified by this constraint). The shortest tree incompatible with this constraint was 480 steps long (3 steps longer than the MPTs), suggesting that unstable taxa are decreasing the apparent support for Pachycephalosauria. A new majority-rule bootstrap reduced consensus tree, following the pruning of seven taxa (see above) demonstrates exceptionally high (95%) bootstrap support for Pachycephalosauria (*Wannanosaurus*, *Goyocephale*, *Homalocephale*, Pachycephalosauridae). Thus, although support for pachycephalosaurian monophyly may be strong, it is obscured by the presence in the data set of a number of wildcard taxa of uncertain position.

CONCLUSIONS

Stability, instability, and future directions in ornithischian phylogeny

The results of this phylogenetic analysis differ in many respects from those of previous analyses and reinforce the importance of constant reassessment of phylogenetic hypotheses. Furthermore, the results of this analysis highlight areas of stability within ornithischian phylogeny and also problematic areas in which future efforts should be concentrated.

At a broad-scale, the widely accepted framework of ornithischian phylogeny, developed by Norman (1984), Sereno (1984, 1986, 1991a, 1999a), Cooper (1985) and Maryańska & Osmólska (1985), amongst others, has proved relatively stable (Fig. 4). There appears to be a basal split within Ornithischia between thyreophorans and neornithischians. Within Neornithischia two monophyletic clades occur, Ornithopoda and Marginocephalia; the latter is subdivided into Ceratopsia and Pachycephalosauria. In many cases this analysis has strengthened this basic framework; for example, by identifying additional marginocephalian synapomorphies. However, a number of unstable and problematic areas within this framework have also been identified.

Heterodontosaurids have long been recognised as the most unstable of ornithischian taxa and the clade has been positioned in four very different positions within Ornithischia. This analysis positions heterodontosaurids as non-genasaurian basal ornithischians, but we additionally note that recent authors have found anatomical evidence and phylogenetic support for the idea that heterodontosaurids may form the sister clade to Marginocephalia (e.g. Xu *et al.* 2006). Resolving the position of heterodontosaurids within Ornithischia is one of the most important tasks facing ornithischian phylogeneticists and future work should aim to combine the data set provided here with that of Xu *et al.* (2006).

The removal of heterodontosaurids from the base of Ornithopoda highlights another major area of instability within

Ornithischia: basal ornithopod phylogeny. Removing heterodontosaurids here results in a number of taxa long considered as ornithopods (e.g. *Agilisaurus louderbacki*, *Hexinlusaurus multidentis*, *Othnielia rex*) grouping outside of Cerapoda, as non-ornithopods. This analysis suggests that the number of taxa that can be referred to Ornithopoda is more restrictive than hypothesised by previous workers. In addition, recognising robust ornithopod synapomorphies is extremely difficult and basal relationships (amongst the ‘hypsilophodontid’ taxa) are poorly resolved and weakly supported. Considerable future work is required to determine exactly which taxa can be referred with confidence to this clade, what characters diagnose the clade and how basal taxa are related to one another.

Implications for phylogenetic taxonomy of Ornithischia

Sereno (1998, 1999b) provided node-based and stem-based phylogenetic definitions for a large number of ornithischian clades; alternative definitions for a number of major ornithischian clades have since been provided by Buchholz (2002), Wagner (2004), various authors in Weishampel *et al.* (2004a) and this study (Table 1). The results of this analysis highlight some of the problems that can occur when clade names are given phylogenetic definitions on the basis of assumed stability and later phylogenetic analyses generate alternate topologies. For instance, this analysis positions heterodontosaurids near to the base of Ornithischia, rather than as ornithopods as suggested by many previous authors. Sereno (1998) provided a node-based definition for the clade Ornithopoda: ‘*Heterodontosaurus*, *Parasaurolophus*, their most recent common ancestor and all descendents’. When this definition is applied to the phylogeny produced by this analysis (Fig. 4), virtually all ornithischians (with the exception of *Pisanosaurus mertii*), including ankylosaurs, stegosaurs, ceratopsians and pachycephalosaurs, are included within Ornithopoda. This is a radically different, and rather unsatisfactory, taxonomic content to that currently understood. The problem is avoided if a conservative stem-based definition is used for Ornithopoda (see Table 1; Buchholz 2002; Wagner 2004; Norman *et al.* 2004c). Likewise, Sereno (1998) provided a stem-based definition for the clade Euornithopoda: ‘All ornithopods closer to *Parasaurolophus* than to *Heterodontosaurus*.’ Applying this definition to the phylogeny produced by this analysis results in Euornithopoda effectively referring to the same clade as Genasauria. Again, this is an unsatisfactory taxonomic content for Euornithopoda, radically different from its currently understood content. In this case it would probably have been better not to provide a phylogenetic definition for Euornithopoda, given the known unstable phylogenetic position of the external specifier, *Heterodontosaurus tucki*.

Another taxonomic problem is highlighted by this analysis. Iguanodontia has generally been used for those taxa more derived within Ornithopoda than Hypsilophodontidae. However, such a definition is problematic if, as suggested by this analysis, Hypsilophodontidae is paraphyletic. Sereno (1998) proposed the stem-based definition, ‘All euornithopods closer to *Parasaurolophus* than to *Hypsilophodon*’. Application of this definition to the phylogeny produced by this analysis suggests that taxa such as *Thescelosaurus neglectus* and *Parksosaurus warreni* are iguanodontians. However, such taxa have generally been considered as

'hypsilophodontid' basal ornithopods, outside of Iguanodontia. In response to this problem, Norman (2004) used the name Iguanodontia for: 'all euornithopods closer to *Edmontosaurus* than to *Thescelosaurus*'. Such a definition may be satisfactory, provided that the relatively derived position for *Thescelosaurus* suggested by Norman *et al.* (2004c) is accurate. If future analyses find that *Thescelosaurus* groups more basally within Ornithischia than other 'hypsilophodontids' (see, for instance, Buchholz 2002) then the definition of Iguanodontia will again be problematic and a node-based definition for the clade (e.g. Weishampel *et al.* 2003) may be preferable. At present we refrain from proposing an alternative phylogenetic definition for Iguanodontia, due to the instability of basal ornithopod phylogeny.

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APPENDIX 1: SPECIMENS AND REFERENCES USED FOR CODING OPERATIONAL TAXONOMIC UNITS

- Euparkeria capensis Broom, 1913**: Ewer (1965), Gower & Weber (1998).
- Marasuchus liloensis (Romer, 1972)**: Bonaparte (1975), Sereno & Arcucci (1994).
- Herrerasaurus ischigualastensis Reig, 1963**: Novas (1993), Sereno (1993), Sereno & Novas (1993); MCZ 7063, 7064.
- Abriotosaurus consors (Thulborn, 1974)**: Thulborn (1974), Hopson (1975); BMNH RUB54 (holotype).
- Agilisaurus louderbacki Peng, 1990**: Peng (1992, 1997), Barrett *et al.* (2005); ZDM 6011 (holotype).
- Anasibetia saldiviai Coria & Calvo, 2002**: Coria & Calvo (2002).
- Ankylopollexia Sereno, 1986**: Gilmore (1909), Galton & Powell (1980), Norman (1980, 1986, 2002, 2004), Norman & Weishampel (1990); OUM J330 (holotype, ‘*Cumnoria prestwichii*’); BMNH, numerous specimens referable to *Iguanodon* spp.
- Ankylosauria Osborn, 1923**: Ostrom (1970), Maryańska (1977), Coombs (1978), Coombs & Maryańska (1990), Lee (1996), Carpenter (2001, 2004), Carpenter *et al.* (2001), Xu *et al.* (2001), Vickaryous *et al.* (2001, 2004); BMNH R175, *Polacanthus foxii* (holotype); BYU, material of *Gastonia burgei* (many specimens); CEUM, holotypes and referred material of *Gastonia burgei*, *Animantarx ramaljonesi*, *Cedarpelta bilbeyhallorum* (see Kirkland 1998; Carpenter *et al.* 1999, 2001); MWC, holotype and referred material of *Mymoorapelta maysi* (see Kirkland & Carpenter 1994; Kirkland *et al.* 1998); IVPP V12560 (holotype of *Liaoningosaurus paradoxus*).
- Archaeoceratops oshimai Dong & Azuma, 1997**: Dong & Azuma (1997), You & Dodson (2003); IVPP V11114 (holotype); IVPP V11115 (paratype).
- Bugenasaura infernalis Galton, 1995**: Galton (1995, 1999); SDSM 7210 (holotype), MOR 979.
- Chaoyangsaurus youngi Zhao et al., 1999**: Zhao *et al.* (1999); IGCAGS V371 (holotype).
- Dryosauridae Milner & Norman, 1984**: Janensch (1955), Galton (1981, 1983, 1989), Galton & Taquet (1982); BMNH R185, R186, holotype of *Valdosaurus canaliculatus*; MB, numerous cranial and postcranial specimens of *Dysalotosaurus lettowvorbecki* (see Galton 1981, 1983).
- Echinodon becklesii Owen, 1861b**: Galton (1978), Norman & Barrett (2002); BMNH 48209, 48210 (lectotypes); BMNH 48211–48215 (paralectotypes).
- Emausaurus ernsti Haubold, 1990**: Haubold (1990), Norman *et al.* (2004b); SGWG 85 (holotype).
- Gasparinisaura cincosaltensis Coria & Salgado 1996**: Coria & Salgado (1996), Salgado *et al.* (1997).
- Goyocephale lattimorei Perle et al., 1982**: Perle *et al.* (1982), Sereno (2000), Maryańska *et al.* (2004).
- Heterodontosaurus tucki Crompton & Charig, 1962**: Crompton & Charig (1962), Santa Luca *et al.* (1976), Santa Luca (1980), Weishampel & Witmer (1990b), Norman *et al.* (2004c); SAM-PK-K337 (holotype); SAM-PK-K1332 (referred specimen).
- Hexinlusaurus multidentis (He & Cai, 1983)**: He & Cai (1984), Barrett *et al.* (2005); ZDM T6001 (holotype).
- Homalocephale calathocercos Maryańska & Osmólska, 1974**: Maryańska & Osmólska (1974), Maryańska (1990), Sereno (2000), Maryańska *et al.* (2004).
- Hypsilophodon foxii Huxley, 1869**: Galton (1974a); BMNH R197 (holotype); other BMNH specimens (see Galton 1974a).
- Jeholosaurus shangyuanensis Xu et al., 2000**: Xu *et al.* (2000); IVPP V12529 (holotype); IVPP V12530.
- Lesothosaurus diagnosticus Galton, 1978**: Thulborn (1970a, 1972), Santa Luca (1984), Weishampel & Witmer (1990a), Sereno (1991a), Norman *et al.* (2004a), Butler (2005); BMNH RUB17, RUB23 (syntypes); BMNH R11956, R8501 (referred specimens); SAM-PK-K400, K401, K1106 (referred specimens).
- Liaoceratops yanzigouensis Xu et al., 2002**: Xu *et al.* (2002); IVPP V12738 (holotype).
- Lycorhinus angustidens Houghton, 1924**: Gow (1975, 1990), Hopson (1975, 1980); SAM-PK-K3606 (holotype); BP/1/4244, BP/1/5253 (referred, Gow 1990).
- Micropachycephalosaurus hongtuyanensis Dong, 1978**: Dong (1978); IVPP V5542 (holotype).
- Othnielia rex (Marsh, 1877b)**: Galton & Jensen (1973), Galton (1983); BYU ESM-163R.
- Orodromeus makelai Horner & Weishampel, 1988**: Horner & Weishampel (1988), Scheetz (1999); MOR 294 (holotype), MOR 403, 473, 623, 1141 (referred specimens).
- Pachycephalosauridae Sternberg, 1945**: Brown & Schlaikjer (1943), Maryańska & Osmólska (1974), Sues & Galton (1987), Maryańska (1990), Sereno (2000), Maryańska *et al.* (2004); BMNH R10055 (cast of

- holotype skull of *Stegoceras*), ZPAL MgD-I/104 (holotype of *Prenocephale prenes*).
- Parksosaurus warreni** (Parks, 1926): Parks (1926), Sternberg (1940), Galton (1973*b*).
- Pisanosaurus mertii** Casamiquela, 1967: Casamiquela (1967), Bonaparte (1976), Weishampel & Witmer (1990*a*), Sereno (1991*a*), Báez & Marsicano (2001), Norman *et al.* (2004*a*).
- Psittacosauridae** Osborn, 1923: Sereno (1987, 1990*a, b*, 2000), Sereno & Chao (1988), Sereno *et al.* (1988), You *et al.* (2003); IVPP V12704 (*Hongshanosaurus* holotype); IVPP V738, 740–1, 749 (*Psittacosaurus sinensis* holotype and referred specimens); IVPP V7705 (*Psittacosaurus meileyingensis* holotype).
- Rhabdodontidae** Weishampel *et al.*, 2003: Pincemaille-Quillévéré (2002), Weishampel *et al.* (2003); BMNH specimens of *Zalmoxes robustus* (see Weishampel *et al.* 2003 for full list).
- Scelidosaurus harrisonii** Owen, 1861*a*: Owen (1861*a*, 1863), Norman *et al.* (2004*b*); BMNHR1111 (lectotype); BMNH R5909, R6704; BRSMG Ce12785; CAMSM X 39256.
- Scutellosaurus lawleri** Colbert, 1981: Colbert (1981), Coombs *et al.* (1990), Sereno (1991*a*), Rosenbaum & Padian (2000), Norman *et al.* (2004*b*); MNA P1.175 (holotype); MNA P1.1752 (paratype); UCMP 130580, 130581, 170829, 175166, 175167, 175168 (referred specimens).
- Stegosauria** Marsh, 1877*a*: Gilmore (1914), Galton (1982*a, b*, 1985, 1988, 1990, 1991), Dong *et al.* (1983), Sereno & Dong (1992), Galton & Upchurch (2004*b*); Cast of IVPP V6728 (holotype skull of *Huayangosaurus taibaii*); ZDM 7001 (*Huayangosaurus taibaii*); BMNH 46013, R5902 (holotype and referred specimen, *Dacentrurus armatus*); BMNH R1989, R3167 (holotype and referred specimen, *Lexovisaurus durobrivensis*); MB, *Kentrosaurus aethiopicus* syntypes and referred material (see Galton 1982*b*, 1988); IVPP V2300, CV 202, 203 (all *Chialingosaurus kuani*); CV 205, 206 (*Chungkingosaurus jiangbeiensis*); CV 209, 210 (*Tuojiangosaurus multispinus*).
- Stenopelix valdensis** Meyer, 1857: Sues & Galton (1982), Sereno (1987); GZG 741/2 (holotype).
- Stormbergia dangershoeki** Butler, 2005: Butler (2005); SAM-PK-K1105 (holotype); BMNH R11000 (paratype); BP/1/4885 (referred).
- Talenkauen santacrucensis** Novas *et al.*, 2004: Novas *et al.* (2004).
- Tenontosaurus tilletti** Ostrom, 1970: Ostrom (1970), Forster (1990).
- Tenontosaurus dossi** Winkler *et al.*, 1997: Winkler *et al.* (1997).
- Thescelosaurus neglectus** Gilmore, 1913: Gilmore (1915), Sternberg (1940), Galton (1974*b*, 1995, 1997).
- Unnamed taxon (Coronosauria + Leptoceratopsidae)**: Brown & Schlaikjer (1940, 1942), Maryańska & Osmólska (1975), Sereno (2000), You & Dodson (2004); MOR 542 (*Montanoceratops*, referred specimen).
- Wannanosaurus yansiensis** Hou, 1977: Hou (1977), Sereno (2000); IVPP V4447 (holotype), IVPP V4447.1 (paratype).
- Yandusaurus hongheensis** He, 1979: He & Cai (1984); GCC V20501 (holotype).
- Zephyrosaurus schaffi** Sues, 1980: Sues (1980); MCZ 4392 (holotype).

APPENDIX 2: CHARACTER LIST

The following references were used for compiling previously used characters: Maryańska & Osmólska (1984, 1985), Milner & Norman (1984), Norman (1984, 1990, 1998, 2004), Sereno (1984, 1986, 1987, 1999*a*, 2000), Cooper (1985), Gauthier (1986), Forster (1990), Sereno & Dong (1992), Weishampel & Heinrich (1992), Novas (1993, 1996), Sereno & Novas (1993), Coria & Salgado (1996), Winkler *et al.* (1997), Zhao *et al.* (1999), Carpenter (2001), Makovicky (2001), Williamson & Carr (2002), Xu *et al.* (2002), Rauhut (2003), Yates (2003), Weishampel *et al.* (2003), You *et al.* (2003), Langer (2004), Norman *et al.* (2004*b, c*), Novas *et al.* (2004), Butler (2005).

1. Skull proportions: 0, preorbital skull length more than 45% of basal skull length; 1, preorbital length less than 40% of basal skull length.
2. Skull length (rostral–quadrate): 0, 15% or less of body length; 1, 20–30% of body length.
3. Neomorphic rostral bone, anterior to premaxilla: 0, absent; 1, present.
4. Rostral bone, anteriorly keeled and ventrally pointed: 0, absent; 1, present.
5. Rostral bone, ventrolateral processes: 0, rudimentary; 1, well-developed.
6. Premaxilla, edentulous anterior region: 0, absent, first premaxillary tooth is positioned adjacent to the symphysis; 1, present, first premaxillary tooth is inset the width of one or more crowns.
7. Premaxilla, posterolateral process, length: 0, does not contact lacrimal; 1, contacts the lacrimal, excludes maxilla–nasal contact.
8. Oral margin of the premaxilla: 0, narial portion of the body of the premaxilla slopes steeply from the external naris to the oral margin; 1, ventral premaxilla flares laterally to form a partial floor of the narial fossa.
9. Position of the ventral (oral) margin of the premaxilla: 0, level with the maxillary tooth row; 1, deflected ventral to maxillary tooth row.
10. Premaxillary foramen: 0, absent; 1, present.
11. Premaxillary palate: 0, strongly arched, forming a deep, concave palate; 1, horizontal or only gently arched.
12. Overlap of the dorsal process of the premaxilla onto the nasal: 0, present; 1, absent.
13. Fossa-like depression positioned on the premaxilla–maxilla boundary: 0, absent; 1, present.
14. Premaxilla–maxilla diastema: 0, absent, maxillary teeth continue to anterior end of maxilla; 1, present, substantial diastema of at least one crown's length between maxillary and premaxillary teeth.
15. Form of diastema; 0, flat; 1, arched 'subnarial gap' between the premaxilla and maxilla.

16. Narial fossa surrounding external nares on lateral surface of premaxilla, position of ventral margin of fossa relative to the ventral margin of the premaxilla: 0, closely approaches the ventral margin of the premaxilla; 1, separated by a broad flat margin from the ventral margin of the premaxilla.
17. External nares, position of the ventral margin: 0, below the ventral margin of the orbits; 1, above the ventral margin of the orbits.
18. External naris size: 0, small, entirely overlies the premaxilla; 1, enlarged, extends posteriorly to overlie the maxilla.
19. Deep elliptical fossa present along sutural line of the nasals: 0, absent; 1, present.
20. Internal antorbital fenestra size: 0, large, generally at least 15% of the skull length; 1, very much reduced, less than 10% of skull length, or absent.
21. External antorbital fenestra: 0, present; 1, absent.
22. External antorbital fenestra, shape: 0, triangular; 1, oval or circular.
23. Additional opening(s) anteriorly within the antorbital fossa: 0, absent; 1, present.
24. Maxilla, prominent anterolateral boss articulates with the medial premaxilla: 0, absent; 1, present.
25. Maxilla, accessory anterior process: 0, absent; 1, present.
26. Maxilla, buccal emargination: 0, absent; 1, present.
27. Eminence on the rim of the buccal emargination of the maxilla near the junction with the jugal: 0, absent; 1, present.
28. Slot in maxilla for lacrimal: 0, absent; 1, present.
29. Accessory ossification(s) in the orbit (palpebral/supraorbital): 0, absent; 1, present.
30. Palpebral/supraorbital: 0, free, projects into orbit from contact with lacrimal/prefrontal; 1, incorporated into orbital margin.
31. Palpebral, shape in dorsal view: 0, rod-shaped; 1, plate-like with wide base.
32. Palpebral/supraorbital, number: 0, one; 1, two; 2, three.
33. Free palpebral, length, relative to anteroposterior width of orbit: 0, does not traverse entire width of orbit; 1, traverses entire width of orbit.
34. Exclusion of the jugal from the posteroventral margin of the external antorbital fenestra by lacrimal-maxilla contact: 0, absent; 1, present.
35. Anterior ramus of jugal, proportions: 0, deeper than wide, but not as deep as the posterior ramus of the jugal; 1, wider than deep; 2, deeper than the posterior ramus of the jugal.
36. Widening of the skull across the jugals, chord from frontal orbital margin to extremity of jugal is more than minimum interorbital width: 0, absent; 1, present, skull has a triangular shape in dorsal view.
37. Position of maximum widening of the skull: 0, beneath the jugal-postorbital bar; 1, posteriorly, beneath the infratemporal fenestra.
38. Jugal (or jugal-epijugal) ridge dividing the lateral surface of the jugal into two planes: 0, absent; 1, present.
39. Epijugal: 0, absent; 1, present.
40. Jugal boss: 0, absent; 1, present.
41. Node-like ornamentation on jugal, mostly on, or ventral to, the jugal-postorbital bar: 0, absent; 1, present.
42. Jugal-postorbital bar, width broader than laterotemporal fenestra: 0, absent; 1, present.
43. Jugal-postorbital joint: 0, elongate scarf joint; 1, short butt joint.
44. Jugal, form of postorbital process: 0, not expanded dorsally; 1, dorsal portion of postorbital process is expanded posteriorly.
45. Jugal-squamosal contact above infratemporal fenestra: 0, absent; 1, present.
46. Jugal posterior ramus, forked: 0, absent; 1, present.
47. Jugal, posterior ramus: 0, forms anterior and ventral margin of infratemporal fenestra; 1, forms part of posterior margin, expands towards squamosal.
48. Jugal-quadratojugal contact: 0, overlapping; 1, tongue-and-groove.
49. Postorbital, orbital margin: 0, relatively smooth curve; 1, prominent and distinct projection into orbit.
50. Postorbital: 0, T-shaped; 1, triangular and plate-like.
51. Postorbital-parietal contact: 0, absent, or very narrow; 1, broad.
52. Contact between dorsal process of quadratojugal and descending process of the squamosal: 0, present; 1, absent.
53. Quadratojugal, shape: 0, L-shaped, with elongate anterior process; 1, subrectangular with long axis vertical, short, deep anterior process.
54. Quadratojugal, ventral margin: 0, approaches the mandibular condyle of the quadrate; 1, well-removed from the mandibular condyle of the quadrate.
55. Quadratojugal, orientation: 0, faces laterally; 1, faces posterolaterally.
56. Quadratojugal, transverse width: 0, mediolaterally flattened; 1, transversely expanded and triangular in coronal section.
57. Prominent oval fossa on pterygoid ramus of quadrate: 0, absent; 1, present.
58. Quadrate lateral ramus: 0, present; 1, absent.
59. Quadrate shaft: 0, anteriorly convex in lateral view; 1, reduced in anteroposterior width and straight in lateral view.
60. Paraquadratic foramen or notch, size: 0, absent or small, opens between quadratojugal and quadrate; 1, large.
61. Paraquadratic foramen, orientation: 0, posterolateral aspect of quadrate shaft; 1, lateral aspect of quadrate or quadratojugal.
62. Paraquadratic foramen, position: 0, on quadrate-quadratojugal boundary; 1, located within quadratojugal.
63. Quadrate mandibular articulation: 0, quadrate condyles subequal in size; 1, medial condyle is larger than lateral condyle; 2, lateral condyle is larger than medial.
64. Paired frontals: 0, short and broad; 1, narrow and elongate (more than twice as long as wide).
65. Supratemporal fenestrae: 0, open; 1, closed.
66. Supratemporal fenestrae, anteroposteriorly elongated: 0, absent, fenestrae are subcircular to oval in shape; 1, present.
67. Parietal septum, form: 0, narrow and smooth; 1, broad and rugose.
68. Parietosquamosal shelf: 0, absent; 1, present.
69. Parietosquamosal shelf, extended posteriorly as distinct frill: 0, absent; 1, present.
70. Composition of the posterior margin of the parietosquamosal shelf: 0, parietal contributes only a small

- portion to the posterior margin; 1, parietal makes up at least 50% of the posterior margin.
71. Postorbital–squamosal bar: 0, bar-shaped; 1, broad, flattened.
 72. Postorbital–squamosal tubercle row: 0, absent; 1, present.
 73. Enlarged tubercle row on the posterior squamosal: 0, absent; 1, present.
 74. Frontal and parietal dorsoventral thickness: 0, thin; 1, thick.
 75. Paroccipital processes: 0, extend laterally and are slightly expanded distally; 1, distal end pendent and ventrally extending.
 76. Paroccipital processes, proportions: 0, short and deep (height \geq 1/2 length); 1, elongate and narrow.
 77. Posttemporal foramen/fossa, position: 0, totally enclosed with the paroccipital process; 1, forms a notch in the dorsal margin of the paroccipital process, enclosed dorsally by the squamosal.
 78. Supraoccipital, contribution to dorsal margin of foramen magnum: 0, forms entire dorsal margin of foramen magnum; 1, exoccipital with medial process that restricts the contribution of the supraoccipital.
 79. Basioccipital, contribution to the border of the foramen magnum: 0, present; 1, absent, excluded by exoccipitals.
 80. Basisphenoid: 0, longer than, or subequal in length to, basioccipital; 1, shorter than basioccipital.
 81. Prootic–basisphenoid plate: 0, absent; 1, present.
 82. Basal tubera, shape: 0, knob-shaped; 1, plate-shaped.
 83. Basipterygoid processes, orientation: 0, anteroventral; 1, ventral; 2, posteroventral.
 84. Premaxilla–vomeral contact: 0, present; 1, absent, excluded by midline contact between maxillae.
 85. Dorsoventrally deep (deeper than 50% of snout depth) median palatal keel formed of the vomers, pterygoids and palatines: 0, absent; 1, present.
 86. Pterygovomerine keel, length: 0, less than 50% of palate length; 1, more than 50% of palate length.
 87. Pterygoid–maxilla contact at posterior end of tooth row: 0, absent; 1, present.
 88. Pterygoquadrate rami, posterior projection of ventral margin: 0, weak; 1, pronounced.
 89. Cortical remodeling of surface of skull dermal bone: 0, absent; 1, present.
 90. Prementary: 0, absent; 1, present.
 91. Prementary size: 0, short, posterior premaxillary teeth oppose anterior dentary teeth; 1, roughly equal in length to the premaxilla, premaxillary teeth only oppose prementary.
 92. Prementary, rostral end in dorsal view: 0, rounded; 1, pointed.
 93. Prementary, oral margin: 0, relatively smooth; 1, denticulate.
 94. Tip of prementary in lateral view: 0, does not project above the main body of prementary; 1, strongly upturned relative to main body of prementary.
 95. Prementary, ventral process: 0, single; 1, bilobate.
 96. Prementary, ventral process: 0, present, well-developed; 1, very reduced or absent.
 97. Dentary symphysis: 0, V-shaped; 1, spout shaped.
 98. Dentary tooth row (and edentulous anterior portion) in lateral view: 0, straight; 1, anterior end downturned.
 99. Dorsal and ventral margins of the dentary: 0, converge anteriorly; 1, subparallel.
 100. Ventral flange on dentary: 0, absent; 1, present.
 101. Coronoid process: 0, absent or weak, posterodorsally oblique, depth of mandible at coronoid is less than 140% depth of mandible beneath tooth row; 1, well-developed, distinctly elevated, depth of mandible at coronoid is more than 180% depth of mandible beneath tooth row.
 102. Anterodorsal margin of coronoid process formed by posterodorsal process of dentary: 0, absent; 1, present.
 103. Coronoid process, position: 0, posterior to dentition; 1, lateral to dentition.
 104. External mandibular fenestra, situated on dentary–surangular–angular boundary: 0, present; 1, absent.
 105. Small fenestra positioned dorsally on the surangular–dentary joint: 0, absent; 1, present.
 106. Ridge or process on lateral surface of surangular, anterior to jaw suture: 0, absent; 1, present, strong antero-posteriorly extended ridge; 2, present, dorsally directed finger-like process.
 107. Retroarticular process: 0, elongate; 1, rudimentary or absent.
 108. Node-like ornamentation of the dentary and angular: 0, absent; 1, present.
 109. Level of jaw joint: 0, level with tooth row, or weakly depressed ventrally; 1, strongly depressed ventrally, more than 40% of the height of the quadrate is below the level of the maxilla.
 110. Mandibular osteoderm: 0, absent; 1, present.
 111. Premaxillary teeth: 0, present; 1, absent, premaxilla edentulous.
 112. Premaxillary teeth, number: 0, six; 1, five; 2, four; 3, three; 4, two.
 113. Premaxillary teeth, crown expanded above root: 0, crown is unexpanded mesiodistally above root, no distinction between root and crown is observable; 1, crown is at least moderately expanded above root.
 114. Premaxillary teeth increase in size posteriorly: 0, absent, all premaxillary teeth subequal in size; 1, present, posterior premaxillary teeth are significantly larger in size than anterior teeth.
 115. Maxillary and dentary crowns, shape: 0, apicobasally tall and blade-like; 1, apicobasally short and subtriangular; 2, diamond-shaped.
 116. Maxillary/dentary teeth, marginal ornamentations: 0, fine serrations set at right angles to the margin of the tooth; 1, coarse serrations (denticles) angle upwards at 45° from the margin of the tooth.
 117. Enamel on maxillary/dentary teeth: 0, symmetrical; 1, asymmetrical.
 118. Apicobasally extending ridges on maxillary/dentary teeth: 0, absent; 1, present.
 119. Apicobasally extending ridges on lingual/labial surfaces of maxillary/dentary crowns confluent with marginal denticles: 0, absent; 1, present.
 120. Prominent primary ridge on labial side of maxillary teeth: 0, absent; 1, present.
 121. Prominent primary ridge on lingual side of dentary teeth: 0, absent; 1, present.
 122. Position of maxillary/dentary primary ridge: 0, centre of the crown surface, giving the crown a relatively symmetrical shape in lingual/labial view; 1, offset, giving crown asymmetrical appearance.

123. At least moderately developed labiolingual expansion of crown ('cingulum') on maxillary/dentary teeth: 0, present; 1, absent.
124. Heterodont dentary dentition: 0, no substantial heterodonty is present in dentary dentition; 1, single, enlarged, caniform anterior dentary tooth, crown is not mesiodistally expanded above root; 2, anterior dentary teeth are strongly recurved and caniform, but have crowns expanded mesiodistally above their roots and are not enlarged relative to other dentary teeth.
125. Peg-like tooth located anteriorly within dentary, lacks denticles, strongly reduced in size: 0, absent; 1, present.
126. Alveolar foramina ('special foramina') medial to maxillary/dentary tooth rows: 0, present; 1, absent.
127. Recurvature in maxillary and dentary teeth: 0, present; 1, absent.
128. Overlap of adjacent crowns in maxillary and dentary teeth: 0, absent; 1, present.
129. Crown is mesiodistally expanded above root in cheek teeth: 0, absent; 1, present.
130. Position of maximum apicobasal crown height in dentary/maxillary tooth rows: 0, anterior portion of tooth row; 1, central portion of tooth rows.
131. Close-packing and quicker replacement eliminates spaces between alveolar border and crowns of adjacent functional teeth: 0, absent; 1, present.
132. Fusion between the intercentum of the atlas and the neural arches: 0, absent; 1, present.
133. Epiphyses on anterior (postaxial) cervicals: 0, present; 1, absent.
134. Cervicals 4–9, form of central surfaces: 0, amphicoelous; 1, at least slightly opisthocoelous.
135. Cervical number: 0, seven/eight; 1, nine; 2, ten or more.
136. Articulation between the zygapophyses of dorsal vertebrae: 0, flat; 1, tongue-and-groove.
137. Dorsals, number: 0, 12–13; 1, 15; 2, 16 or more.
138. Sacrals, number: 0, two; 1, three; 2, four/five; 3, six or more.
139. Sacrum, accessory articulation with pubis: 0, absent; 1, present.
140. Posterior sacral ribs are considerably longer than anterior sacral ribs: 0, absent; 1, present.
141. Anterior caudal vertebrae, length of transverse processes relative to neural spine height: 0, subequal; 1, longer than neural spine.
142. Proximal caudal neural spines: 0, height the same or up to 50% taller than the centrum; 1, more than 50% taller than the centrum.
143. Elongate tail (59 or more caudals): 0, absent; 1, present.
144. Chevron shape: 0, rod-shaped, often with slight distal expansion; 1, strongly asymmetrically expanded distally, width greater than length in mid caudals.
145. Sternal segments of the anterior dorsal ribs: 0, unossified; 1, ossified.
146. Gastralia: 0, present; 1, absent.
147. Ossified clavicles: 0, absent; 1, present.
148. Sternal plates, shape: 0, absent; 1, kidney-shaped; 2, shafted or hatchet-shaped (rod-like posterolateral process, expanded anterior end).
149. Proportions of humerus and scapula: 0, scapula longer or subequal to the humerus; 1, humerus substantially longer than the scapula.
150. Scapula blade, length relative to minimum width: 0, relatively short and broad, length is 5–8 times minimum width; 1, elongate and strap-like, length is at least 9 times the minimum width.
151. Scapula acromion shape: 0, weakly developed or absent; 1, well-developed spine-like.
152. Scapula, blade-shape: 0, strongly expanded distally; 1, weakly expanded, near parallel-sided.
153. Humeral length: 0, more than 60% of femoral length; 1, less than 60% of femoral length.
154. Deltpectoral crest development: 0, well-developed, projects anteriorly as a distinct flange; 1, rudimentary, is at most a thickening on the anterolateral margin of the humerus.
155. Humeral shaft form, in anterior or posterior view: 0, relatively straight; 1, strongly bowed laterally along length.
156. Manual length (measured along digit ii or iii, whichever is longest) as a percentage of the combined length of the humerus and radius: 0, less than 40%; 1, more than 40%.
157. Metacarpals with block-like proximal ends: 0, absent; 1, present.
158. Metacarpals 1 and 5: 0, substantially shorter in length than metacarpal 3; 1, subequal in length to metacarpal 3.
159. Penultimate phalanx of the second and third fingers: 0, shorter than first phalanx; 1, longer than the first phalanx.
160. Manual digit 3, number of phalanges: 0, four; 1, three or fewer.
161. Manual digits 2–4: 0, first phalanx relatively short compared to second phalanx; 1, first phalanx more than twice the length of the second phalanx.
162. Extensor pits on the dorsal surface of the distal end of metacarpals and manual phalanges: 0, absent or poorly developed; 1, deep, well-developed.
163. Manual unguis strongly recurved with prominent flexor tubercle: 0, absent; 1, present.
164. Acetabulum: 0, at least a small perforation; 1, completely closed.
165. Preacetabular process, shape/length: 0, short, tab-shaped, distal end is posterior to pubic peduncle; 1, elongate, strap-shaped, distal end is anterior to pubic peduncle.
166. Preacetabular process, length: 0, less than 50% of the length of the ilium; 1, more than 50% of the length of the ilium.
167. Preacetabular process, lateral deflection: 0, 10–20° from midline; 1, more than 30°.
168. Dorsal margin of preacetabular process and dorsal margin of ilium above acetabulum: 0, narrow, not transversely expanded; 1, dorsal margin is transversely expanded to form a narrow shelf.
169. In dorsal view preacetabular process of the ilium expands mediolaterally towards its distal end: 0, absent; 1, present.
170. Dorsal margin of the ilium in lateral view: 0, relatively straight or slightly convex; 1, sinuous, postacetabular process is strongly upturned.
171. Subtriangular process extending medially from the dorsal margin of the iliac blade: 0, absent; 1, present.
172. Subtriangular process, form and position: 0, short and tab-like, above acetabulum; 1, elongate and flange-like, on postacetabular process.

173. Brevis shelf and fossa: 0, fossa faces ventrolaterally and shelf is near vertical and visible in lateral view along entire length, creating a deep postacetabular portion; 1, fossa faces ventrally and posterior of shelf portion cannot be seen in lateral view.
174. Length of the postacetabular process as a percentage of the total length of the ilium: 0, 20% or less; 1, 25–35%; 2, more than 35%.
175. Medioventral acetabular flange of ilium, partially closes the acetabulum: 0, present; 1, absent.
176. Supra-acetabular ‘crest’ or ‘flange’: 0, present; 1, absent.
177. Ischial peduncle of the ilium: 0, projects ventrally; 1, broadly swollen, projects ventrolaterally.
178. Pubic peduncle of ilium: 0, large, elongate, robust; 1, reduced in size, shorter in length than ischial peduncle.
179. Pubic process of ischium, shape: 0, transversely compressed; 1, dorsoventrally compressed.
180. Ischium, shape of shaft: 0, relatively straight; 1, gently curved along length.
181. Ischial shaft, cross-section: 0, compressed mediolaterally; 1, subcircular and bar-like.
182. Ischial shaft: 0, expands weakly, or is parallel-sided, distally; 1, distally expanded into a distinct ‘foot’; 2, tapers distally.
183. Groove on the dorsal margin of the ischium: 0, absent; 1, present.
184. Tab-shaped obturator process on ischium: 0, absent; 1, present.
185. Ischial symphysis, length: 0, ischium forms a median symphysis with the opposing blade along at least 50% of its length; 1, ischial symphysis present distally only.
186. Pubis, orientation: 0, anteroventral; 1, rotated posteroventrally to lie alongside the ischium (opisthopubic).
187. Shaft of pubis (postpubis), shape in cross-section: 0, blade-shaped; 1, rod-shaped.
188. Shaft of pubis (postpubis), length: 0, approximately equal in length to the ischium; 1, reduced, extends for half or less the length of the ischium.
189. Reduction of postpubic shaft: 0, postpubic shaft extends for around half the length of ischium; 1, postpubic shaft is very short or absent.
190. Body of pubis, size: 0, relatively large, makes substantial contribution to the margin of the acetabulum; 1, reduced in size, rudimentary, nearly excluded from the acetabulum.
191. Body of the pubis, massive and dorsolaterally rotated so that obturator foramen is obscured in lateral view: 0, absent; 1, present.
192. Prepubic process: 0, absent; 1, present.
193. Prepubic process: 0, compressed mediolaterally, dorsoventral height exceeds mediolateral width; 1, rod-like, mediolateral width exceeds dorsoventral height.
194. Prepubic process, length: 0, stub-like and poorly developed, extends only a short distance anterior to the pubic peduncle of the ilium; 1, elongated into distinct anterior process.
195. Prepubic process, extends beyond distal end of preacetabular process of ilium: 0, absent; 1, present.
196. Extent of pubic symphysis: 0, elongate; 1, restricted to distal end of pubic blade, or absent.
197. Femoral shape in medial/lateral view: 0, bowed anteriorly along length; 1, straight.
198. Femoral head: 0, confluent with greater trochanter, *fossa trochanteris* is groove-like; 1, *fossa trochanteris* is modified into distinct constriction separating head and greater trochanter.
199. ‘Anterior’ or ‘lesser’ trochanter, morphology: 0, absent; 1, trochanteric shelf ending in a small, pointed, spike; 2, broadened, prominent, ‘wing’ or ‘blade’ shaped, subequal in anteroposterior width to greater trochanter; 3, reduced anteroposterior width, closely appressed to the expanded greater trochanter.
200. Level of most proximal point of anterior trochanter relative to level of proximal femoral head: 0, anterior trochanter is positioned distally on the shaft, and separated from ‘dorsolateral’ trochanter/greater trochanter by deep notch visible in medial view; 1, anterior trochanter positioned proximally, approaches level of proximal surface of femoral head, closely appressed to ‘dorsolateral’/greater trochanter (no notch visible in medial view).
201. Fourth trochanter of femur, shape: 0, low eminence, or absent; 1, prominent ridge; 2, pendent.
202. Fourth trochanter, position: 0, located entirely on proximal half of femur; 1, positioned at midlength, or distal to midlength.
203. Anterior (extensor) intercondylar groove on distal end of femur: 0, absent; 1, present.
204. Posterior (flexor) intercondylar groove of the femur: 0, fully open; 1, medial condyle inflated laterally, partially covers opening of flexor groove.
205. Lateral condyle of distal femur, position and size in ventral view: 0, positioned relatively laterally, and slightly narrower in width than the medial condyle; 1, strongly inset medially, reduced in width relative to medial condyle.
206. Distal tibia: 0, subquadrate, posterolateral process is not substantially developed; 1, elongate posterolateral process, backs fibula.
207. Fibular facet on the lateral margin of the proximal surface of the astragalus: 0, large; 1, reduced to small articulation.
208. Calcaneum, proximal surface: 0, facet for tibia absent; 1, well-developed facet for tibia present.
209. Medial distal tarsal: 0, articulates distally with metatarsal 3 only; 1, articulates distally with metatarsals 2 and 3.
210. Metatarsal arrangement: 0, compact, closely appressed to one another along 50–70% of their length, spread distally; 1, contact each other only at proximal ends, spread strongly outwards distally.
211. Digit 1: 0, metatarsal 1 robust and well-developed, distal end of phalanx 1–1 projects beyond the distal end of metatarsal 2; 1, metatarsal 1 reduced and proximally splint-like, end of phalanx 1–1 does not extend beyond the end of metatarsal 2; 2, metatarsal 1 reduced to a vestigial splint or absent, does not bear digits.
212. Pedal digit 4 phalangeal number: 0, five; 1, four or fewer.
213. Metatarsal 5, length: 0, more than 50% of metatarsal 3; 1, less than 25% of metatarsal 3.
214. Metatarsal 5: 0, bears digits; 1, lacks digits.
215. Pedal unguals, shape: 0, tapering, narrow pointed, claw-like; 1, wide, blunt, hoof-like.

- 216. Epaxial ossified tendons present along vertebral column: 0, absent; 1, present.
- 217. Ossified hypaxial tendons, present on caudal vertebrae: 0, absent; 1, present.
- 218. Ossified tendons, arrangement: 0, longitudinally arranged; 1, basket-like arrangement of fusiform tendons in caudal region; 2, double-layered lattice.
- 219. Parasagittal row of dermal osteoderms on the dorsum of the body: 0, absent; 1, present.
- 220. Lateral row of keeled dermal osteoderms on the dorsum of the body: 0, absent; 1, present.
- 221. U-shaped cervical/pectoral collars composed of contiguous keeled osteoderms: 0, absent; 1, present.

APPENDIX 3: DATA MATRIX

(a = 0/1; b = 1/2; c = 2/3; d = 3/4; e = 0/2)

	10 /	20 /	30 /	40 /	50 /	60 /
<i>Euparkeria</i>	000- - 00000	0000- 00000	000000000-	- - - 000- 000	0000000000	0000000000
<i>Marasuchus</i>	? 0????????	???????????	???????????	???????????	???????????	???????????
<i>Herrerasaurus</i>	000- - 00000	0000- 11010	010000000-	- - - 000- 000	0000010000	0000000000
<i>Abriotosaurus</i>	000- - 10011	? ? 011000? 1	00?? 010010	0000? 0- ???	???????????	???? 0?????
<i>Agilisaurus</i>	000- - 10001	1000- 00011	000? 010? 10	111000- 000	0000000000	0? 10001000
<i>Anabisetia</i>	???????????	???????????	?????? 1????	???????????	???????????	???????????
<i>Ankylopollexia</i>	000- - 11110	100- - 00101	0100110010	000000- 000	0000001000	011100000a
<i>Ankylosauria</i>	000- - 10001	1000- 00001	1- 00010011	- 2- - 10- 000	0110000000	0? 1? 100100
<i>Archaeoceratops</i>	0111110000	? 001010001	000?? 10010	1000211110	1101? 00001	0? 1011? 010
<i>BMNH A100</i>	? ? 0- - 1? 0??	1? 01100? ? 1	00? 00100??	????? 0- 0??	00? 00? ????	???????????
<i>Bugenasaura</i>	? ? 0- - 0? 0??	1???? 00001	0100010010	000100- 000	000000? 00	011000? 000
<i>Chaoyangsaurus</i>	1? 1001? 00?	0? 00- 110? 1	????? 011???	????? 210000	1???? 000??	? ? 1000? 0? 0
<i>Coronosauria + Leptoceratopsidae</i>	0111110000	0001010001	0100010010	1000211110	0101100001	0110110010
<i>Dryosauridae</i>	000- - 11110	110- - 00101	0100110110	001000- 000	0000001000	0111000001
<i>Echinodon</i>	? ? 0- - ? ? 0??	????? 0????	????? 01????	???????????	???????????	???????????
<i>Emausaurus</i>	0? 0- - ? 000?	1000- 000? 1	0000010010	100010- 000	0000010000	001000? 000
<i>Gasparinisaura</i>	00?????????	????10?????	010?? 10010	000100- 000	0000000000	? 01100? 000
<i>Goyocephale</i>	? 00- - ? 001?	1001100001	????? 010011	- 1- ? 00- ? 00	111000000-	1? 1? 00????
<i>Heterodontosaurus</i>	000- - 11011	1101100011	0010010010	000000- 001	00100- 0000	0010000000
<i>Hexinlusaurus</i>	? 00- - ? 0???	????????? 011	000?? 10? 10	000100- 000	0000000000	0? 1000? 000
<i>Homalocephale</i>	? 00- - ? ? ? ? ?	????????? ? 1	1- - ? ? 10011	- 1- - 00- 000	111000000-	1110000000
<i>Hypsilophodon</i>	000- - 10011	1011000011	0010010010	000100- 000	0000000000	0110000001
<i>Jeholosaurus</i>	000- - ? ? 00?	? 010- 00011	000? 010010	? 0? 100- 000	0000000000	0110000001
<i>Lesothosaurus</i>	000- - 10001	1000- 000? 1	0000010110	000000- 000	0000010000	0010000000
<i>Liaoceratops</i>	0? 10111000	0001010001	000? 0110??	??? 0211100	0101100001	0110000010
<i>Lycorhinus</i>	???????????	? ? 011?????	00?? 010???	???????????	???????????	???????????
<i>Micropachycephalosaurus</i>	???????????	???????????	???????????	???????????	???????????	???????????
<i>Orodromeus</i>	000- - 10001	1? 10- 00011	0101010010	000000- 001	0000000010	0110000000
<i>Othnielia</i>	???????????	???????????	???????????	???????????	???????????	???????????
<i>Pachycephalosauridae</i>	000- - 10011	1001a00001	1- - ? 010011	- 1- - 00- 000	111000000-	1110000000
<i>Parksosaurus</i>	00????? 0???	??? 10?? ? 01	010?? 10010	? 0? 100- 000	0001? 00? 00	0? 1100? 000
<i>Pisanosaurus</i>	? 0?????????	???????????	?????? 1????	???????????	???????????	???????????
<i>Psittacosauridae</i>	1010011001	000- - 11001	? ? 00011010	100? 210100	0000010000	0110000000
<i>Rhabdodontidae</i>	000- - 10010	100- - 00001	01000100??	??? 100- 000	0000001100	0111000000
<i>Scelidosaurus</i>	000- - 100??	? 0? 0- ??? 01	0100010011	- 2- 010- 000	0100010000	0010000000
<i>Scutellosaurus</i>	? 00- - ? ? 0? 1	1???? 00?? ?	????? 10?? ?	????? 10- 000	00000100??	????? 0? ? 0??
<i>Stegosauria</i>	000- - 10001	10a0- 00001	0000010011	- 2- 010- 000	0000000000	0110001100
<i>Stenopelix</i>	???????????	???????????	???????????	???????????	???????????	???????????
<i>Stormbergia</i>	???????????	???????????	???????????	???????????	???????????	???????????
<i>Talenkauen</i>	? 00- - 101??	1? 010000? 1	0?? ? 0100??	???????????	???????????	???????????
<i>Tenontosaurus dossi</i>	000- - ? 1110	1001000101	0100110010	000100- 000	0000000100	0111000001
<i>Tenontosaurus tilletti</i>	000- - 11110	100- - 00101	0100110010	000100- 000	0000000100	0111000001
<i>Thescelosaurus</i>	? 0?????????	??? 10?????	???? 001?? 10	000? 00- 000	000000? 00	0???????????
<i>Wannanosaurus</i>	? 0?????????	???????????	?????????? 11	- 1- ? 00- 000	101000000-	0? 1? 0?????
<i>Yandusaurus</i>	???????????	???????????	00000100??	????? 00- 000	0000000???	????????? 0??
<i>Zephyrosaurus</i>	? ? 0- - 1? 011	10? 10000? 1	0?? 1010? 10	100? 00- 001	00000? 0? 10	0? ? 0? ? 100?

Appendix 3 Continued.

	70	80	90	100	110	120
	/	/	/	/	/	/
<i>Euparkeria</i>	00100000--	0000001000	00000-0000	-----0000	0000000000	02000000-0
<i>Marasuchus</i>	??????????	??????????0	0?0???????	???????????	???????????	???????????
<i>Herrerasaurus</i>	00100000--	000000100?	000?0-0000	-----0000	0000000000	02000000-0
<i>Abriotasaurus</i>	???????????	???????????	??????????01	1000-10000	11000?00?0	030011?0-0
<i>Agilisaurus</i>	00100000--	000010?000	00?0-0001	0?00001000	1101000000	01101100-0
<i>Anabisetia</i>	???????????	???????????	???????????	?????????010	1?????????0	?????11?110
<i>Ankylopollexia</i>	10000000--	0000101100	00200-0001	1010101010	1111100010	1--211101
<i>Ankylosauria</i>	00101-10--	100000?001	0000110011	0000-11100	0101000001	0?101100-0
<i>Archaeoceratops</i>	0020010111	000001?01?	?01?0-??01	1101001000	1111011100	031011???1
<i>BMNH A100</i>	????000???	???0???????	??????????0?	????????0000	???????????	030111?0-0
<i>Bugenasaura</i>	-0000000--	0000???????	??????????0?	?????????000	11011200?0	0110111110
<i>Chaoyangsaurus</i>	002???????	??????????0?	?0??0-0?01	1101?01000	?101001100	04101110-0
<i>Coronosauria +</i>	0020010111	000001?010	00b10-1001	11011010?0	11110111000	a410111111
Leptoceratopsidae						
<i>Dryosauridae</i>	1?000000--	0000101100	00100-0001	1010101000	1111000000	1--211101
<i>Echinodon</i>	???????????	???????????	???????????	?????10000	?0?0??0?0	od??1100-0
<i>Emausaurus</i>	00?00000--	0000?????00	?00??????1?	0?????1100	0100010000	01101100-0
<i>Gasparinisaura</i>	?0?00?00--	000000000?	??????????0?	?????????000	1101100010	????111111
<i>Goyocephale</i>	???0000100	111110?0???	?1?????0?0?	0?????0000	11010?01?0	0311111aa0
<i>Heterodontosaurus</i>	00200000--	0000000000	00000-0001	1000-10000	1100000010	0301111101
<i>Hexinlusaurus</i>	00?00000--	00001??????	??????????0?	????????1000	110????000	????110100
<i>Homalocephale</i>	0000001100	111110?000	110?0-?10?	???????????	??????????0?	????11?110
<i>Hypsilophodon</i>	11010000--	0000100000	00100-0001	1100001000	1101100010	01101111a0
<i>Jeholosaurus</i>	11010000--	000010????0	?0010-??01	1100001000	1101000000	00?011?110
<i>Lesothosaurus</i>	00000000--	0000000000	000?0-0001	0000001000	0100010000	00101100-0
<i>Liaoceratops</i>	0020010111	000001?010	001?0-0001	1001001001	1111001100	0310111111
<i>Lycorhinus</i>	???????????	???????????	???????????	???????????	???????????	????11?0-0
<i>Micropachycephalosaurus</i>	??2???????	???????????	???????????	?????????000	110???????	????1110-?
<i>Orodromeus</i>	00010000--	0000100000	000?????01	???0?01000	1101100000	01101100-0
<i>Othnielia</i>	???????????	???????????	???????????	?????????00	?????????0?	????1110-0
<i>Pachycephalosauridae</i>	00001-1100	111110?a00	11010-a101	0?????0000	1101000100	03aa11?aa0
<i>Parksosaurus</i>	-00?0000--	??00???????	?0????????0?	?????????000	110????0010	????111?10
<i>Pisanosaurus</i>	???????????	???????????	???????????	?????????000	?10?000000	????1?0-0
<i>Psittacosauridae</i>	0020000101	00000a0000	00010-1001	1a00001001	111aa00000	1--111111
<i>Rhabdodontidae</i>	-0200000--	0000101000	?01?????01	1000101010	111??00000	1--211110
<i>Scelidosaurus</i>	00100000--	000000?001	001?10001?	0?????1100	0101010001	01101100-0
<i>Scutellosaurus</i>	??1100????	???????????	???????????	?????????000	0?????1?0?	00?01100-0
<i>Stegosauria</i>	00100000--	0000a01001	00001?0001	0000001100	1100000000	a?101100-0
<i>Stenopelix</i>	???????????	???????????	???????????	???????????	???????????	???????????
<i>Stormbergia</i>	???????????	???????????	???????????	???????????	???????????	???????????
<i>Talenkauen</i>	???????????	???????????	???????????	110?101000	11?????0?	01????1??10
<i>Tenontosaurus dossi</i>	11000000--	000010110?	?0?0-0?01	1010001010	111??00000	0???211100
<i>Tenontosaurus tilletti</i>	11000000--	0000101100	001?0-0001	1010001010	1111120000	1--211100
<i>Thescelosaurus</i>	???00000--	0000?01100	001?????01	??????1000	11011200?0	0?1?110?10
<i>Wannanosaurus</i>	????000100	110110?????	??????????0?	?????????000	11010000?0	????1110-?
<i>Yandusaurus</i>	???????????	???????????	??????????0?	???????????	???????????	????111?10
<i>Zephyrosaurus</i>	??010000--	00?0100000	001?????0?	???????????	???????????	0110111?10

Appendix 3 Continued.

	130	140	150	160	170	180
	/	/	/	/	/	/
<i>Euparkeria</i>	0-10010000	0010001000	00000?1000	11000?00??	?0?1000000	0--2010000
<i>Marasuchus</i>	??????????	?010?0?000	00?0?0???	??000?0???	???1000001	0--2000000
<i>Herrerasaurus</i>	0-10010000	0000201000	00000?0???	1100011010	0110000000	0-01000000
<i>Abriostosaurus</i>	??001?1111	0??????2?0	?????????0?	10000?10??	01?0100000	0-11?100??
<i>Agilisaurus</i>	0-02001111	0010101200	0000010?10	10100?0???	???0100000	0-01000100
<i>Anabisetia</i>	?????111?	??????????	?????????00	100100000?	?000110000	0-11111100
<i>Ankylopollexia</i>	1010001111	1011b02c?0	0100010b00	a000000001	100010000a	0-11111110
<i>Ankylosauria</i>	0-00001111	011000?b00	0000010100	?1000?0101	0001111100	0-00000010
<i>Archaeoceratops</i>	?1000?1111	1????10310	0??0?1????	???????????	???0100000	0-1211110?
<i>BMNH A100</i>	??01111111	0?????????	???????????	???????????	???????????	???????????
<i>Bugenasaura</i>	1000001111	0?????????	???????????	???????????	???????????	???????????
<i>Chaoyangsaurus</i>	0-00001111	0??0???????	???????????	1???????????	???????????	???????????
<i>Coronosauria + Leptoceratopsidae</i>	1100001111	1-102?03?0	0?00011101	1000000000	1000100001	0-12111110
<i>Dryosauridae</i>	1010001111	0?11101310	0100010100	00000?????	???0100001	0-11111110
<i>Echinodon</i>	0-00?11111	0?????????	???????????	???????????	???????????	???????????
<i>Emausaurus</i>	0-00001111	0?????????	???????????	????????01??	???????????	???????????
<i>Gasparinisaura</i>	??000?1111	00?0????310	0??1?10???	00?00?????	???0100001	0-11111100
<i>Goyocephale</i>	0-01??111?	00????1?3?1	????01?2??	??111?????	???0101110	101211????
<i>Heterodontosaurus</i>	1a1111101	1?001?03?0	0000010?01	1000011010	0110100000	0-11110000
<i>Hexinlusaurus</i>	0-0?001111	0010101200	0000010?10	1000000000	0000100000	0-11010100
<i>Homalocephale</i>	??0????1111	0?????1?311	1??001?2??	???????????	???0101110	1112111111
<i>Hypsilophodon</i>	1000001111	0010101310	0000110100	1000000000	0000100000	0-12111100
<i>Jeholosaurus</i>	0-000?1111	001010????	0??0?1????	???????????	???????????	???????????
<i>Lesothosaurus</i>	0-00001111	0000?0?20?	?????????00	101000000?	0000100000	0-01000000
<i>Liaoceratops</i>	1100001111	0?????????	???????????	???????????	???????????	???????????
<i>Lycorhinus</i>	??0??11111	0?????????	???????????	???????????	???????????	???????????
<i>Micropachycephalosaurus</i>	0-00001111	0?????????	???0???????	???????????	???010000?	?????1?????
<i>Orodromeus</i>	0-00001111	0010101310	00?0?10100	10?0000000	0000100000	0-12111100
<i>Othnielia</i>	0-0????1?1?	0??0?013?0	00?0110100	10000?????	???0100000	0-11111100
<i>Pachycephalosauridae</i>	0-ob?0a111	0?????1?3?1	1??001?201	10111?????	???0101110	1112111111
<i>Parkosaurus</i>	0-00001111	0?????023?0	0?0111?100	00000?0???	???0100000	0-???1????00
<i>Pisanosaurus</i>	0-?00?1111	0??0???????	???????????	???????????	???????????	???????????
<i>Psittacosauridae</i>	1000001111	0010a00310	0?0001110a	1000000000	0000100000	0-12111100
<i>Rhabdodontidae</i>	1010001111	0?11?0?3?0	01?0?10?2?0	00?00?????	???0100100	0-?1110110
<i>Scelidosaurus</i>	0-00001111	0000002200	0000010?00	10000?????	???0100100	0-00000000
<i>Scutellosaurus</i>	0-0?001111	00?01012??	0?1???????	1?000?00??	0000100000	0-?1?0?0?00
<i>Stegosauria</i>	0-00001111	0110e0e200	0100010?00	11000?0101	0000111100	0-00000000
<i>Stenopelix</i>	???????????	?????????3??	0??0?1????	?0?????????	???0100100	0-11110110
<i>Stormbergia</i>	???????????	?0?0?01200	00????????00	10??0?????	???0100000	0-01000000
<i>Talenkauen</i>	???0??1111	0?00102???	?????10?00	10010?????	???0100001	0-1111?1??
<i>Tenontosaurus dossi</i>	1010001111	0?0120?3?0	0110?10100	00000000??	?000100001	0-11111100
<i>Tenontosaurus tilletti</i>	1010001111	0001202310	0110010100	0000000001	1000100001	0-11111100
<i>Thescelosaurus</i>	100000111?	???0?02310	01?0110?00	1000000000	0000100001	0-11110100
<i>Wannanosaurus</i>	0-010?1111	0??0???????	???????????	??111?????	???????????	???????????
<i>Yandusaurus</i>	??0????1111	0??0?0?????	?????????00	10?00?????	???????????	???????????
<i>Zephyrosaurus</i>	0-00?01111	0???????????	???????????	???????????	???????????	???????????

Appendix 3 Continued.

	190	200	210	220	
	/	/	/	/	
<i>Euparkeria</i>	00000000-0	00--0000-	0000000000	0000000-1?	0
<i>Marasuchus</i>	00000000-0	00--00010	1000000010	1001000-0?	0
<i>Herrerasaurus</i>	10000000-0	00--00010	1000000000	0000000-00	0
<i>Abriotosaurus</i>	???????????	??????0?2?	200??1?????	10110????00	0
<i>Agilisaurus</i>	00110110-0	0101010020	2000011100	1011010000	0
<i>Anabisetia</i>	01011110-0	0101110131	20101111?0	1?1101?000	0
<i>Ankylopollexia</i>	1101111100	01011111C1	2111111100	0011010200	0
<i>Ankylosauria</i>	0e001111a1	11000110--	01000111-1	2111110011	1
<i>Archaeoceratops</i>	0000111110	011101?131	?????11110	0011010000	0
<i>BMNH Aoo</i>	???????????	???????????	???????????	???????????	?
<i>Bugenasaura</i>	???????????	???????????	???????????	???????????	?
<i>Chaoyangsaurus</i>	???????????	???????????	???????????	???????????	?
<i>Coronosauria +</i>	0000111110	0100010131	2010011110	0011a10000	0
<i>Leptoceratopsidae</i>					
<i>Dryosauridae</i>	11011110-0	0101110131	2011111110	2011010000	0
<i>Echinodon</i>	???????????	???????????	???????????	???????????	?
<i>Emausaurus</i>	???????????	???????????	???????????	?????0????11	?
<i>Gasparinisaura</i>	00011110-0	0111110131	2000011110	2011011000	0
<i>Goyocephale</i>	???????????	???????????	?????1??1?	?????011100	0
<i>Heterodontosaurus</i>	0000?110-0	0100010021	200001??00	1011010000	0
<i>Hexinlusaurus</i>	00011110-0	0111110020	2000011110	1011010000	0
<i>Homalocephale</i>	0000111111	0111110131	10?0?11?10	?????11100	0
<i>Hypsilophodon</i>	00011110-0	0111110131	2000011110	0011011000	0
<i>Jeholosaurus</i>	???????????	??????0131	2000011110	10110???00	0
<i>Lesothosaurus</i>	00100110-0	0100010020	2000011100	1?11010000	0
<i>Liaoceratops</i>	???????????	???????????	???????????	???????????	?
<i>Lycorhinus</i>	???????????	???????????	???????????	???????????	?
<i>Micropachycephalosaurus</i>	???????????	??????0131	?0???1?????	???????????	?
<i>Orodromeus</i>	00011110-0	0111110131	2000a11110	001101?000	0
<i>Othnielia</i>	00011110-0	0111110131	2000011110	101101?000	0
<i>Pachycephalosauridae</i>	0000111111	0111110131	10?0???????	?????11100	0
<i>Parksosaurus</i>	0001111??0	0111110131	2100?1?????	0011011000	0
<i>Pisanosaurus</i>	???????????	???????????	?????0?0?0	?????0????00	0
<i>Psittacosauridae</i>	0000111110	0111010131	2010011100	0011010000	0
<i>Rhabdodontidae</i>	10001?????	??????1131	2111?111??	?????11?00	0
<i>Scelidosaurus</i>	00001110-0	1100010020	2100011100	0011110011	1
<i>Scutellosaurus</i>	00000110-0	010??10020	200001?????	?????01??11	0
<i>Stegosauria</i>	02001110-0	a1010110--	01000111-1	21111a0011	0
<i>Stenopelix</i>	000011???	0111a101C1	?????1?????	0011010000	0
<i>Stormbergia</i>	00a11110-0	0100010020	20000111?0	1?1101??00	0
<i>Talenkauen</i>	?????11???	010111?131	2????111?0	00?101?000	0
<i>Tenontosaurus dossi</i>	01011110-0	010111?131	21111111?0	0011011000	0
<i>Tenontosaurus tilletti</i>	0101111100	0101111131	2111111110	0011011000	0
<i>Thescelosaurus</i>	00011110-0	0111110131	2100011110	0011011000	0
<i>Wannanosaurus</i>	???????????	??????0???	10?0?1?????	?????????00	0
<i>Yandusaurus</i>	???????????	???????????	??000?????	?????0?????	?
<i>Zephyrosaurus</i>	???????????	???????????	???????????	???????????	?

APPENDIX 4: TREE DESCRIPTIONS

The 'describrees' option of PAUP* was used to interpret character state transformations. All transformations are based upon the derivative strict reduced consensus tree (see Fig. 4). Transformation was evaluated under accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) options; unambiguous synapomorphies are those that diagnose a node under both ACCTRAN and DELTRAN optimisation. Node numbers refer to Fig. 4. For simple 0–1 state changes only the character number is given; for other state changes the type of change is specified in parentheses.

Node 1 (Ornithischia): Unambiguous: 26, 102, 115, 127, 128, 129, 130; ACCTRAN: 6, 10, 11, 20, 29, 53, 77 (1 to 0), 90, 101, 112 (2 to 0), 116, 123 (1 to 0), 138 (0 to 2), 152 (1 to 0), 165, 186, 187, 192, 196, 199 (1 to 2), 201 (1 to 2), 207, 211, 213, 214, 216.

Node 2 (Heterodontosauridae + Genasauria): Unambiguous: 206; ACCTRAN: 208; DELTRAN: 6, 10, 11, 20, 29, 53, 77 (1 to 0), 90, 116, 123 (1 to 0), 135, 138 (0 to 2), 152 (1 to 0), 165, 186, 187, 192, 196, 199 (1 to 2), 201 (1 to 2), 206, 211, 213, 214, 216.

Node 3 (Heterodontosauridae): Unambiguous: 9, 14, 15, 91, 96, 125, 173, 176; ACCTRAN: 12, 23, 40, 43, 6 3 (1 to 2), 109, 112 (0 to 3), 117, 121, 137 (1 to 0), 175, 200; DELTRAN: 101, 112 (2 to 3), 157, 162.

Node 4: Unambiguous: 114, 124; ACCTRAN: 7, 138 (2 to 3).

Node 5 (Genasauria): Unambiguous: 97, 113, 126 (1 to 0), 156 (1 to 0), 159 (1 to 0), 163 (1 to 0); ACCTRAN: 150 (1 to 0), 157 (1 to 0), 162 (1 to 0); DELTRAN: 148, 207, 208.

Node 6 (Thyreophora): Unambiguous: 106; ACCTRAN: 19 (1 to 0), 101 (1 to 0), 160, DELTRAN: 46, 112 (2 to 0).

Node 7: Unambiguous: 35, 89, 219, 220; ACCTRAN: 31, 77, 85, 211 (1 to 0).

Node 8: Unambiguous: 98, 112, 158; ACCTRAN: 135 (1 to 0), 137 (1 to 2), 168, 174 (1 to 0), 185, 191, 202, 221.

Node 9: Unambiguous: 30, 32 (0 to 2), 80, 215; ACCTRAN: 42, 104, 110; DELTRAN: 19 (1 to 0), 85, 135 (1 to 0), 137 (1 to 2), 168, 174 (1 to 0), 185, 191, 202.

Node 10 (Eurypoda): Unambiguous: 46 (1 to 0), 58, 106 (1 to 0), 132, 133, 152, 166, 167, 197, 201 (2 to 0), 210, 211, 212; ACCTRAN: 52, 86, 182 (0 to 2); DELTRAN: 160.

Node 11 (Neornithischia): Unambiguous: 184; ACCTRAN: 46, 52, 75, 92, 104, 112, 133, 185.

Node 12: Unambiguous: 178, 194; ACCTRAN: 149; DELTRAN: 75, 101, 104, 112 (2 to 1), 133.

Node 13: Unambiguous: 173, 176, 193, 195, 209; ACCTRAN: 14, 63 (1 to 0), 91; DELTRAN: 185.

Node 14: Unambiguous: 117, 138 (2 to 3), 175, 177, 198, 199 (2 to 3), 200; ACCTRAN: 119, 139, 145, 149 (1 to 0).

Node 15 (Cerapoda): Unambiguous: 174 (1 to 2), 211 (1 to 0); DELTRAN: 52, 63 (1 to 0), 92, 119, 139.

Node 16 (Ornithopoda): Unambiguous: 13, 64, 105; ACCTRAN: 217.

Node 17: Unambiguous: 34, 6 1, 118; ACCTRAN: 9, 60, 62, 83, 121; DELTRAN: 91, 145, 217.

Node 18: Unambiguous: 19 (1 to 0), 22, 64 (1 to 0), 137 (1 to 2), 142, 174 (2 to 1); ACCTRAN: 10 (1 to 0), 13 (1 to 0), 54, 60 (1 to 0), 62 (1 to 0), 77, 92 (1 to 0), 95, 202; DELTRAN: 14, 83, 121.

Node 19: Unambiguous: 99, 193 (1 to 0), 203, 205; ACCTRAN: 47, 48, 103, 111, 123, 134, 145 (1 to 0), 160, 161, 182.

Node 20: Unambiguous: 115 (1 to 2), 151 (1 to 0), 197, 204; ACCTRAN: 179, 181; DELTRAN: 9, 10 (1 to 0), 13 (1 to 0), 54, 77, 92 (1 to 0), 103, 111, 123, 134, 202.

Node 21: Unambiguous: 7, 8, 18, 25, 6 0, 78, 93, 119 (1 to 0), 170; DELTRAN: 145 (1 to 0), 160, 161, 182.

Node 22: Unambiguous: 62, 133 (1 to 0), 135 (1 to 2), 143; ACCTRAN: 47 (1 to 0), 95 (1 to 0), 106 (0 to 2), 179 (1 to 0), 181 (1 to 0); DELTRAN: 48

Node 23: Unambiguous: 34 (1 to 0), 120, 217 (1 to 0); ACCTRAN: 48 (1 to 0); DELTRAN: 47, 95, 179, 181.

Node 24: Unambiguous: 109, 144, 151 (1 to 0); ACCTRAN: 52 (1 to 0), 75 (1 to 0), 77 (1 to 0), 121 (1 to 0); DELTRAN: 54.

Node 25 (Marginocephalia): Unambiguous: 19 (1 to 0), 68, 84, 112 (1 to 3), 150, 184 (1 to 0), 188, 189; ACCTRAN: 31, 41, 94, 108, 136, 137 (1 to 0), 145 (1 to 0), 147, 203.

Node 26 (Ceratopsia): Unambiguous: 3, 11 (1 to 0), 16, 27, 35 (0 to 2), 36, 63 (0 to 2); ACCTRAN: 1, 7, 17, 70, 75 (1 to 0), 76, 107, 195 (1 to 0); DELTRAN: 91.

Node 27: Unambiguous: 38, 103, 118, 120, 121; ACCTRAN: 38, 41 (1 to 0), 87, 100; DELTRAN: 31, 70, 75 (1 to 0), 137 (1 to 0), 147, 195 (1 to 0), 203.

Node 28 (Neoceratopsia): Unambiguous: 5, 10 (1 to 0), 37, 42, 44, 45, 50, 59, 66, 69, 79, 83, 122; ACCTRAN: 1 (1 to 0), 2, 17 (1 to 0), 135 (1 to 2), 16 1, DELTRAN: 14, 76, 94, 107.

Node 29: Unambiguous: 4, 39, 55, 56, 106, 131; ACCTRAN: 4, 7 (1 to 0), 100 (1 to 0); DELTRAN: 2, 27 (1 to 0).

Node 30 (Pachycephalosauria): Unambiguous: 30, 32, 43, 71, 72, 74, 124, 153, 154, 155, 168, 179, 201; ACCTRAN: 9, 15, 21, 81, 82, 88, 91 (1 to 0), 114, 140, 148 (1 to 2); DELTRAN: 41, 97 (1 to 0).

Node 31: Unambiguous: 42, 51, 73, 167, 169, 171, 217, 218; ACCTRAN: 118, 141, 180, 190; DELTRAN: 9, 14, 82, 108, 136, 140, 148 (1 to 2).

Node 32: Unambiguous: 67, 172; DELTRAN: 21, 81, 88, 141, 180, 190.