Lower limits of ornithischian dinosaur body size inferred from a new Upper Jurassic heterodontosaurid from North America

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1. Institutional Abbreviations

LACM, Dinosaur Institute of the Natural History Museum of Los Angeles County, Los Angeles, USA; MNA, Museum of Northern Arizona, Flagstaff, USA; NHM, Natural History Museum, London, UK; SAM-PK, Iziko South African Museum, Cape Town, South Africa.

2. Geological Context and Previous Work

(a) Locality

The specimens that make up the hypodigm of *Fruitadens haagarorum* were collected at the LACM Fruita Paleontological Area (FPA), west of Fruita, 19 km northwest of Grand Junction, Mesa County, Colorado, USA (Fig. 1). The approximate latitude and longitude of the FPA is 39.2° N, 108.8° W.

LACM 115747 and LACM 128258 are listed on the LACM catalogue as having been collected from locality 4684, which is a “General locality for specimens from FPA with poor specific locality data” (Kirkand 2006:95). LACM 115727 is from locality 5576, “George’s ‘Coelurosaur’ Site” (Kirkland 2006:93), while LACM 120478 is from locality 5572, the “Main Callison Quarry” (Kirkland 2006:94). Kirkland (2006:fig. 4) provided a map showing the positions of these sites within the FPA.

Specimens were collected in the late 1970s and early 1980s by teams led by George Callison. The specimens were collected from crevasse splay sandstones of the “drab floodplain facies” at the base of the Brushy Basin Member of the Morrison Formation (Kirkland 2006), immediately above the “clay change” horizon (Fig. S1). The “clay change” horizon is commonly used for regional correlation of the Morrison Formation (e.g., Turner & Peterson 1999). Turner & Peterson (1999:fig. 7) placed the localities (listed as CO-33 in their
stratigraphic sections and their Appendix 3) yielding *Fruitadens haagarorum* within the Kimmeridgian, and within their “Dinosaur Zone 2” and charophyte-ostracode Zone 4. Stratigraphic horizons closely equivalent to the Fruita quarries yield $^{40}$Ar/$^{39}$Ar isotopic dates of $150.3 \pm 0.3$ Ma and $150.2$ and $\pm 0.5$ Ma (Kowallis *et al.* 1998; Turner & Peterson 1999:fig. 7). This would suggest an early Tithonian age for the Fruita quarries based upon the most recent geological time scales (Gradstein *et al.* 2004; Walker & Geissman 2009) that places the Tithonian at 150.8–145.5 Ma.

The Brushy Basin Member resulted from deposition on a complex flood plain influenced by a low sinuosity anastomosing river system (Kirkland 2006).

(b) Notes on associations of specimens

No data on the original field associations of the holotype and referred specimens is currently available at the LACM. Within each of the specimens, the preserved material is consistent (in terms of size, morphology, lack of duplication of elements, and preservation) with belonging to a single individual. All elements in the holotype and referred specimens compare closely to the anatomy of *Heterodontosaurus tucki* (Santa Luca 1980), and we see no reasons to doubt their associations.

(c) FPA fauna

General accounts of the FPA, including the history of discovery, geology, taphonomy and paleoenvironments, and fauna, are given by Callison (1987), Kirkland (1997, 2006), and Foster (2007). Snails, clams and crayfish are the principal invertebrates occurring in the FPA; trace fossils include fossil caddisfly cases, termite nests, soil bug burrows and beetle burrows (Hasiotis *et al.* 1998a, b; Kirkland 2006). Dipnoan fish are represented by scales and rare tooth plates (*Ceratodus guentheri*). Osteichthyes are also represented by scales, the vertebrae
of an amioid (Kirkland 1998), and the actinopterygian *Hulettia hawesi* (Neopterygii, Halecostomi: Kirkland 1998). Described reptilian taxa include shell fragments of the chelonian *Glyptops*, the rhynchocephalians *Opisthias* and *Eilenodon robustus* (Rasmussen & Callison 1981a; Evans 1996; Foster 2003a), lizards including the anguimorphs *Parviraptor gilmorei* and *Dorsetisaurus*, and the scincomorphs *Paramacelodus* and *Saurillodon* (Evans 1996), and a small (1 m long) cursorial mesosuchian crocodile (Clark 1985; Kirkland 1994). Callison (1987) also listed a pterosaur and a goniopholid crocodile, but his small *Compsognathus*-like coelurosaurian dinosaur is the cursorial sphenosuchian crocodile *Macelognathus vagans* (Göhlich et al. 2005). Dinosaur eggshell has been found associated with microvertebrate sites in the FPA (Hirsch 1994).

Described mammals include the eutriconodontid *Priacodon fruitaensis* and the multituberculate *Glirodon grandis* (Rasmussen & Callison 1981b; Rougier et al. 1996; Engelmann & Callison 1998, 1999), as well as a burrowing form, *Fruitafossor windsheffeli* (Luo & Wible 2005) which apparently represents a previously unknown mammalian group. Several undescribed mammals were also listed by Callison (1987).

The general FPA area is rich in disarticulated to semiarticulated dinosaur remains (Kirkland 1997), including the theropods *Ceratosaurus magnicornis* (Madsen & Welles 2000; holotype) and *Allosaurus*, the sauropods *Camarasaurus* and *Apatosaurus*, and the large-bodied ornithischians *Stegosaurus* and *Dryosaurus*. Remains of the latter include juvenile and hatchling-sized bones and shell fragments plus bones of small mesosuchian crocodilians; the site is interpreted as being close to a nesting area that was preyed upon by the crocodilians (Kirkland 1994).
(d) Previous work

Several of the specimens of *Fruitadens* have been mentioned, figured or briefly described in the literature previously. Callison & Quimby (1984: figs 3B, C) figured a femoral shaft and a distal tibia with an associated astragalus and calcaneum (LACM 120478, 115727) as those of a small “fabrosaurid” ornithischian dinosaur, and discussed the ontogenetic stage of this material. Subsequently, on the basis of an initial assessment of the morphology of another specimen, consisting of associated jaws with teeth, this material was identified as *Echinodon* sp. (Callison 1987; Olshevsky & Ford 1994). In a conference abstract, Galton (2002) proposed several autapomorphies for *Echinodon* based upon material from England and Fruita, including the form of the dentary symphysis and the presence of an anteromedially directed edge on the distal part of the tibia. In addition, he listed several cranial and postcranial character synapomorphies shared by *Echinodon* (postcranial characters based on Fruita material) and *Heterodontosaurus*. Galton (2006), as part of a review of the dentition of ornithischian dinosaurs from the Morrison Formation, made an initial comparison of the morphology of the dentition of the Fruita material to *Echinodon*, noted several differences, and figured parts of two specimens (Galton 2006: fig. 2.7; LACM 128258, 115747).
Figure S1. Stratigraphic section exposed in the area of the Fruita Paleontological Area showing the level at which material of *Fruitadens haagarorum* has been collected. Image modified from Kirkland (2006:fig. 6) and used courtesy of JI Kirkland.
3. Selected measurements

Anteroposterior lengths of centra of sacral vertebrae 1–6 (LACM 115747, holotype): 10.1 mm, 9.1 mm, 8 mm, 8 mm, 7.9 mm, 8.1 mm

Humerus (LACM 120478): length = 36.7 mm; maximum anteroposterior width, proximal end = 4.3 mm; maximum mediolateral width, proximal end = 8 mm; maximum anteroposterior width, distal end = 4.1 mm; maximum mediolateral width, distal end = 6.6 mm; midshaft diameter = 2.7 mm

Femur (LACM 115727), right: maximum mediolateral width, proximal end = 13.3 mm; maximum anteroposterior width, proximal end = 10.4 mm

Femur (LACM 115727), left: maximum anteroposterior width, proximal end = 10.5 mm

Femur (LACM 115747), right: maximum mediolateral width, proximal end = 13.2 mm; maximum anteroposterior width, proximal end = 10.1 mm

Femur (LACM 120478), left: length of preserved shaft = 42.2 mm; maximum anteroposterior width, distal end = 9 mm; maximum mediolateral width, distal end = 9.6 mm; thickness of shaft proximal to fourth trochanter = 4.2 mm; diameter of hollow medullary cavity at same point = 2.6 mm

Tibia (LACM 120478), left: length (tibia and attached astragalus/calcaneum) = 74.1 mm; length (tibia only) = 71.8 mm; maximum anteroposterior width, proximal end = 12.2 mm; maximum mediolateral width, proximal end = 7.3 mm; maximum anteroposterior width, distal end = 7 mm; maximum mediolateral width, distal end = 8.6 mm; midshaft, anteroposterior width = 3.6 mm; midshaft, mediolateral width = 4.3 mm

Tibia (LACM 115747), left: proximal end: maximum anteroposterior width, proximal end (incomplete) = 8 mm; maximum mediolateral width, proximal end = 9.2 mm
Tibia (LACM 115747), right and left (measurements identical): maximum anteroposterior width, distal end (incomplete) = 8 mm; maximum mediolateral width, distal end = 10.6 mm

Fibula (LACM 120478), left: length = 61 mm; maximum anteroposterior width, proximal end = 6.9 mm; maximum mediolateral width, proximal end = 2.7 mm; maximum anteroposterior width, distal end = 1.4 mm; maximum mediolateral width, distal end = 2.2 mm; midshaft, diameter = 1 mm

Fused astragalus/calcaneum (LACM 120478): transverse width = 9.1 mm

Fused astragalus/calcaneum (LACM 115727): transverse width = 11.3 mm
4. CT Methodology

Specimens were scanned at the NHM (London) by SA Walsh using a HMX-ST CT 225 System (Metris X-Tek, Tring, UK) in February 2009. Data was reconstructed using CT-PRO software version 2.0 (Metris X-Tek). 2000 transverse slices were taken of the left maxilla and left dentary of LACM 115747, and the left maxilla and both dentaries of LACM 128258. Image size and resolution are variable; average voxel size is 0.013 mm. Contrast between fossil material and matrix is excellent. CT data was segmented (to extract bones, teeth, and cavities) and visualized by L.B.P. using Amira 5.2.0 (Visage Imaging, Berlin, Germany; www.amiravis.com). Some additional visualization was carried out using VG Studio MAX 2.0 (Volume Graphics, Heidelberg, Germany).

5. Histological Analysis

An analysis seeking to determine the developmental status of the Fruitadens haagarorum specimens was conducted by G.M.E. using gross anatomical and osteohistological features of two representative femora. These included a 42.32 mm distal section from LACM 120478, one of the smaller individuals, and a 47.22 mm proximal section from LACM 115727, one of the larger individuals.

(a) Gross anatomical features

Both elements were examined using dissecting microscopy. Developmentally pertinent attributes were described. The periosteal surfaces spanning the entire length of the distal metaphysis of LACM 120478 (Fig. S2A) show coarse endochondral bone trabeculae that are, for the most part, longitudinally oriented. The condyles are capped by a thin layer of calcified
cartilage. This morphology is consistent with a juvenile that is undergoing extensive longitudinal growth at the time of death (Haines 1969). By contrast, the proximal femur from LACM 115727 has a metaphysis that is capped by a well-formed periosteal bone collar (Fig. S2B). The femoral head and trochanters are capped by a layer of calcified cartilage that is relatively and absolutely thinner than that of LACM 120478. These characteristics of LACM 115727 are consistent with a sub-adult or young adult whose longitudinal growth is nearing completion.

![Figure S2](image)

**Figure S2.** Femoral metaphyses of small and larger *Fruitadens haagarorum*. A. Distal femur of LACM 120478. B. Proximal femur of LACM 115727.

**(b) Osteohistological features**

A mid-diaphyseal transverse plane thin section was made for each of the two specimens. These were viewed using polarizing microscopy with crossed nicols. The microstructural attributes were described (Francillon-Vieillot et al. 1990).
The femoral cortex of LACM 120478 is almost entirely (~70% by area) composed of primary parallel-fibered bone with radial vascularization. This peculiar vascular pattern is similar to that reported by Erickson & Tumanova (2000) in *Psittacosaurus mongoliensis*. An isolated portion where the cortex is thickest shows a woven fabric. This does not extend around the cortex and is not representative of the earliest formed tissue-type. Where the cortex is thinnest, the inner two-thirds of the element is composed of longitudinally vascularized, compacted trabecular bone. The outer cortex on the other hand shows longitudinal vascularization and a parallel-fibered matrix. A single line of arrested growth (LAG) extends around three-quarters of the periphery of the specimen. A thin layer of endosteal bone lines the medullar cavity. No Haversian bone is present. The specimen fits almost entirely within the medullar cavity of the larger specimen, LACM 115727. These results suggest that the smaller individual, and other specimens of similar size from the assemblage (i.e. LACM 128258), were in their second year of life when they perished and are juveniles.

The cortex of the larger specimen is entirely composed of parallel-fibered and lamellar bone with longitudinal vascularization (Fig. 3F). Four growth lines are present and these delineate five growth zones. A LAG is present locally very near to the endosteal border of the element. The deep cortex shows two more growth lines in the form of annuli that locally become LAGs. Near the periosteal border a single annulus is present. The vascularization pattern shows diminishing primary vascular canal density and size moving from the endosteal to periosteal surfaces. The outermost zone is composed of a conspicuous layer of avascular parallel-fibered bone. The endosteal border shows a thin layer of endosteal bone. These findings suggest that this individual was four years old and its growth (in terms of body mass) was slowing at the time of death. This represents an absolute, rather than minimum, age, because remnants of all growth lines are present, i.e. Haversian remodelling
did not efface all signs of the growth lines in the deepest cortex. This specimen and others of similar size from the assemblage (LACM 115747, holotype) appear to have been young adults with the potential to grow somewhat larger but not appreciably so.

(c) Body size implications
Collectively all evidence points to *Fruitadens haagarorum* being a very small non-avian dinosaur. The growth signatures at the metaphyses and diaphyses of the bones of the larger individual (LACM 115727) show it to be nearing somatic maturity at a very small size. Furthermore, other very small non-avian dinosaurs (all of which are theropods) reached adult size in no less than three years (Erickson 2005); therefore, the longevity estimate of four years for *F. haagarorum* is consistent with an animal growing like such diminutive animals, if not more slowly. The fact that *F. haagarorum* possessed long bones that formed using histological types with very slow appositional rates is also consistent with this deduction (Castanet *et al.* 1996, 2000). Finally, very small vertebrates including birds, mammals, and extinct ornithodirans show slow forming parallel-fibered bone at very small sizes (Foote 1916; Enlow & Brown 1956, 1957, 1958; Enlow 1969; Klevezal 1996; Padian *et al.* 2004). Therefore, the discovery of this bone type in *F. haagarorum* femora is not entirely unexpected (i.e., fibro-lamellar bone does not compose the long bone cortices in all non-avian dinosaurs). For example, the small theropod *Mahakala*, with a femoral circumference of 19.93 mm as compared to 19.6 mm in *F. haagarorum* (LACM 115727), shows nearly identical osteohistology (Turner *et al.* 2007).
6. Body Size Estimates

(a) Estimation of body size in Fruitadens haagarorum

The incomplete nature of the material of *F. haagarorum* complicates attempts to assess the body size of this taxon. The tibia (excluding the attached proximal tarsals) of LACM 120478, one of the smaller individuals, is 71.8 mm in length. By comparison, the tibia of SAM-PK-K1332, the nearly complete skeleton of the largest described individual of *Heterodontosaurus tucki*, is 145 mm, with an estimated complete body length of 1.1 m (Santa Luca 1980).

Assuming that the scaling relationship between tibial length and body length is the same for *F. haagarorum* and *H. tucki*, this suggests a body length of approximately 0.55 m for LACM 120478. Based upon relative sizes of the proximal and distal ends of the bones of the hindlimb, LACM 120478 was approximately 80% of the size of the holotype LACM 115747 and the large referred specimen LACM 115727; this would suggest a body length for these latter two larger specimens of approximately 0.70 m. Because of the inexactness of this approach, we report an adult body length estimate of 0.65–0.75 m in the text and use this range of estimates for calculation of body mass estimates (see below). It should be noted, however, that neurocentral sutures are not fused in cervical and dorsal vertebrae of LACM 115747 and that the osteohistological analysis suggests that LACM 115727 is not completely full-grown, suggesting that the maximum adult body size would have been somewhat larger.

For comparison of body size with other small-bodied dinosaurs (see below) we additionally reconstructed femoral length of the largest known individuals of *F. haagarorum*. We estimate the largest known individuals of *F. haagarorum* to be approximately 64% of the size of SAM-PK-K1332, the referred specimen of *H. tucki* (Santa Luca 1980), suggesting a femoral length of approximately 72 mm for the largest known individuals of *F. haagarorum*. 
Body mass estimates for the largest known individuals (LACM 115747, LACM 115727) were calculated by D.M.H. using the approach outlined by Henderson (1999), and were obtained by using lateral and frontal outlines of a skeletal reconstruction of *H. tucki*, scaled to the size of the *F. haagarorum* individuals. Such an approach assumes geometric similarity – i.e., that body shape does not change with body size. This may therefore overestimate the mass of *F. haagarorum* because the appendicular skeleton of this taxon appears to be slightly more lightly built than that of *H. tucki*, and the values provided for *F. haagarorum* in the text (0.48–0.74 kg) probably represent maximum estimates. These estimates are substantially lighter than that provided previously (5 kg: Foster 2003b, 2007), but are similar to mass estimates generated for similar sized theropod dinosaurs using alternative approaches (Turner et al. 2007: supporting online material).

(b) Minimum body sizes in other dinosaurian taxa

(i) *Ornithischia*. A large number of relatively small ornithischian taxa are known, but nearly all of these are more than 1 m in length. As discussed above, the largest published specimen of *Heterodontosaurus tucki* (SAM-PK-K1332) has a femoral length of 112 mm and an estimated body length of 1.0–1.1 m (Santa Luca 1980), with mass estimated at 1.8 kg (Seebacher 2001; based upon a reconstructed body length of 1.0 m) or 2.59 kg (D.M.H. unpublished data; based upon a reconstructed body length of 1.12 m). The holotype specimen of *Tianyulong confuciusi* is 0.7 m in length, and is reported to represent a subadult individual (Zheng et al. 2009) based upon the absence of neurocentral fusion, although osteohistological analysis has not been carried out and so ontogenetic stage has not been precisely established. The holotype specimen (NHM RU B.54) of the heterodontosaurid *Abrictosaurus consors* has a femoral length of 77.5 mm, but this individual is often considered a juvenile based upon the relatively short preorbital region (e.g., Norman et al. 2004b) and independent evidence of
ontogenetic stage is lacking. Other heterodontosaurids (*Lycorhinus angustidens*: Gow 1990; *Echinodon becklesii*: Norman & Barrett 2002) are only known from cranial material and assessing their ontogenetic stage is highly problematic. *Lycorhinus angustidens* was probably similar in size to *Heterodontosaurus tucki* (based upon cranial dimensions).

The femur is unknown in the small Triassic ornithischian *Pisanosaurus mertii*, but the tibia (160.7 mm: Casamiquela 1967) is substantially longer than in *F. haagarorum*. Butler et al. (2007) reconstructed a body length of approximately 1.0 m for the holotype specimen of *Eocursor parvus*, with a femoral length of 109 mm, but the ontogenetic stage of this specimen is uncertain. Among small-bodied Early and Middle Jurassic non-heterodontosaurid ornithischians the femoral length is 199 mm in *Agilisaurus louderbacki* (Peng 1992), 103 mm in *Lesothosaurus diagnosticus* (Butler 2005), 83.5–114 mm in *Scutellosaurus lawleri* (MNA P1.175, P1.1752), and 147–202 mm in *Stormbergia dangershoeki* (Butler 2005). Estimated body masses are: *Hexinlusaurus multidens*, 6.6 kg (Seebacher 2001); *Lesothosaurus diagnosticus*, 1.76 kg (DMH unpublished data). Moreover, in most cases the ontogenetic status of the specimens comprising the hypodigms of these taxa is uncertain. For example, individuals of *Lesothosaurus diagnosticus* are probably juveniles (e.g., Norman et al. 2004a) although this has yet to be unambiguously demonstrated.

Amongst Late Jurassic and Cretaceous ornithischians, the smallest pachycephalosaur, *Wannanosaurus yansiensis*, has a femoral length of at least 92.5 mm, and is known only from probable sub-adult specimens (Butler & Zhao 2009). The basal margonopelican *Stenopelix valdensis* is known from a single sub-adult specimen with a femoral length of 144 mm (Sues & Galton 1982; Butler & Sullivan 2009). The early ceratopsian *Yinlong downsi* is based upon a sub-adult holotype with a body length of 1.2 m (Xu et al. 2006), and the femoral length of *Psittacosaurus* typically ranges from 100–160 mm (Sereno 1987). Amongst basal ornithopods, the femur of *Hypsilophodon foxii* ranges from 101–202 mm (Galton 1974);
moreover, many individuals referred to this taxon are believed to be sub-adults. Mass estimates for *Hypsilophodon foxii* are 7.0 kg (Seebacher 2001; based upon a 1.4 m reconstructed body length) and 15.6 kg (DM Henderson unpublished data; based upon a reconstructed body length of 2.07 m). Larger individuals of *Orodromeus makelai* have femoral lengths of 106–118 mm (Horner & Weishampel 1988), while a specimen of *Othnielosaurus consors* has a femoral length of 151 mm (Galton & Jensen 1973). Other small ornithopods are of similar sizes to *Hypsilophodon, Orodromeus*, and *Othnielosaurus*.

(ii) *Saurischia*. Nearly all known sauropodomorphs are substantially larger than *F. haagarorum*, even the very earliest taxa such as *Panphagia protos* (body length of 1.2 m; Martinez & Alcobar 2009) and *Saturnalia tupiniquim* (body length of 1.5 m; Langer *et al.* 1999). *Pantydraco caducus* has an estimated femoral length of 72 mm, but this is based upon juvenile material (Yates 2003). Most theropods are larger in size than *F. haagarorum* (Carrano 2006); however, a small number of deinonychosaurian theropods closely related to birds are of similar or possibly smaller size. These taxa include *Mahakala omnogovae* (0.65 m body length, 0.7 kg body mass; Turner *et al.* 2007), *Mei long* (0.53 m body length, 0.7 kg body mass; Turner *et al.* 2007; however, this taxon is based upon a sub-adult specimen), and *Microraptor* spp. (0.63–0.77 m body length, 0.6–1.4 kg body mass; Turner *et al.* 2007).

(iii) *Summary*. The largest known adult specimens of *Fruitadens haagarorum* are substantially smaller than any other known ornithischian dinosaur, with the possible exception of the closely related heterodontosaurids *Echinodon becklesii* and *Tianyulong confuciusi*. The currently known individuals of *E. becklesii* may have been similar in size to *F. haagarorum*, but their ontogenetic stage is completely unknown at present; likewise, the ontogenetic stage of the holotype of *T. confuciusi* remains unconfirmed. The only saurischian
dinosaurs of similar or smaller body size to *F. haagarorum* are deinonychosaurian theropods closely related to birds and characterised as having undergone “extreme miniaturisation” (Turner *et al.* 2007:1378). Indeed, *F. haagarorum* was only slightly larger than the earliest bird, *Archaeopteryx* (0.58 m body length, 0.5 kg body mass; Turner *et al.* 2007).

7. Phylogenetic Analysis

(a) Methods

*Fruitadens haagarorum* was added to the data matrix of Butler *et al.* (2008), which focuses on relationships among basal ornithischians. The recently described taxa *Eocursor parvus* (Butler *et al.* 2007), *Tianyulong confuciusi* (Zheng *et al.* 2009), and *Yinlong downsi* (Xu *et al.* 2006) were also added, as well as six new characters (numbers 222–227), creating a data matrix of 50 taxa and 227 characters. Several corrections were made to the scores for *Echinodon becklesii* (see character list, below), character 2 was reworded following Xu *et al.* (2006), and character 156 was reworded following Butler *et al.* (2007). The data matrix was constructed using Mesquite v.2.6 (Maddison & Maddison 2009). Analyses were carried out using PAUP* v.4.0b10 (Swofford 2002); search settings used included collapsing branches with a minimum length of zero (the ‘-amb’ option), treating five characters (characters 112, 135, 137, 138, 174) as ordered, treating all characters as equally weighted, and treating multistate taxa as polymorphisms. Analysis was conducted using a heuristic search with 1000 replicates, each starting tree being produced by random stepwise addition. The resulting set of trees was filtered to ensure that only minimum length trees (most parsimonious trees: MPTs) were retained. 1137 MPTs (length = 578 steps, CI = 0.51, RI = 0.72, RC = 0.37) were recovered, and a strict component consensus tree (SCC) is shown in Figure S3. A monophyletic Heterodontosauridae is recovered; however, relationships within the clade are
unresolved. There is little resolution of relationships at the base of the neornithischian clade Cerapoda, with the exception of the recovery of a monophyletic Iguanodontia and Marginocephalia. In order to better assess the underlying structure of the MPT set we used REDCON 3.0 (Wilkinson 2001) to generate a reduced consensus tree profile, containing six reduced component consensus (RCC) trees. The first RCC is identical to the SCC. The second RCC excludes *Abrechtosaurus consors*, and reveals that *Fruitadens haagarorum*, *Echinodon becklesii*, and *Tianyulong confuciusi* are placed in a polytomy basal to a clade of *Heterodontosaurus tucki* + *Lycorhinus consors* + NHM RU A100. Other RCC trees exclude varying combinations of ‘hypsilophodontid’ and iguanodontid taxa, providing increased resolution within Cerapoda. Finally, we *a posteriori* pruned the wildcard taxon *Abrechtosaurus consors* from the MPT set and calculated a maximum agreement subtree based upon the remaining topologies (Figs 4, S4) that contains a monophyletic but taxonomically limited Ornithopoda.

Contra to some previous hypotheses that hypothesized that the Fruita specimens represented a new species of *Echinodon* (Callison 1987; Galton 2002), a sister group relationship between *Fruitadens haagarorum* and *Echinodon becklesii* cannot be demonstrated on the basis of available material. Characters supporting the position of *Fruitadens haagarorum* within Heterodontosauridae include the presence of three premaxillary teeth, the presence of an arched and recessed diastema between the premaxillary and maxillary tooth rows, the dentary caniniform, a reduced and peg-like post-caniniform dentary tooth, a groove on the proximal surface of the humerus separating the head from the medial tubercle, a rod-like fourth trochanter, reduction of the distal end of the fibula, and the fusion of the astragalus and calcaneum.
Figure S3. Strict component consensus (SCC) of 1137 MPTs (see above).
Figure S4. Maximum agreement subtree following deletion of the wildcard taxon *Abrictosaurus consors*. Note increased resolution of relationships within Heterodontosauridae and the presence of a monophyletic (but taxonomically restricted) Ornithopoda.
(b) Character list

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. 10% or less of body length; 1. 13% or more of body length (modified following Xu et al. 2006).


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.


11. Premaxillary palate: 0. Strongly arched, forming a deep, concave palate; 1. Horizontal or only gently arched.

Coding changed from ‘?’ to 1 for Echinodon becklesii

12. Overlap of the dorsal process of the premaxilla onto the nasal: 0. Present; 1. Absent.

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.


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.


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.


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.


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.


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.


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.


49. Postorbital, orbital margin: 0. Relatively smooth curve; 1. Prominent and distinct projection into orbit.


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. Paraquadrtic foramen or notch, size: 0. Absent or small, opens between quadratojugal and quadrate; 1. Large.

61. Paraquadrtic foramen, orientation: 0. Posterolateral aspect of quadrate shaft; 1. Lateral aspect of quadrate or 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.


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.


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.


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. Predentary: 0. Absent; 1. Present.

91. Predentary size: 0. Short, posterior premaxillary teeth oppose anterior dentary teeth; 1. Roughly equal in length to the premaxilla, premaxillary teeth only oppose predentary.

92. Predentary, rostral end in dorsal view: 0. Rounded; 1. Pointed.

93. Predentary, oral margin: 0. Relatively smooth; 1. Denticulate.

94. Tip of predentary in lateral view: 0. Does not project above the main body of predentary; 1. Strongly upturned relative to main body of predentary.


96. Predentary, ventral process: 0. Present, well-developed; 1. Very reduced or absent.

   Changed from ‘1’ to ‘?’ for *Echinodon becklesii*


98. Dentary tooth row (and edentulous anterior portion) in lateral view: 0. Straight; 1. Anterior end downturned.


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.

106. Ridge or process on lateral surface of surangular, anterior to jaw suture: 0. Absent;
    1. Present, anteroposteriorly extended ridge; 2. Present, dorsally directed finger-like process.


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.
    Changed from ‘0’ to ‘?’ for Echinodon becklessi

111. Premaxillary teeth: 0. Present; 1. Absent, premaxilla edentulous.

112. Premaxillary teeth, number: 0. Six; 1. Five; 2. Four; 3. Three; 4. Two; 5. One.

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 sub-triangular; 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 degrees 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.

    Changed from ‘1’ to ‘0’ for *Echinodon becklessi*

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; 2. Caudal 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. Epipophyses 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.
146. Gastralia: 0. Present; 1. Absent.
147. Ossified clavicles: 0. Absent; 1. Present.
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. Deltopectoral 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. Longest manual phalanx as percentage of length of humerus: 0. Less than 10% ; 1. More than 15%.
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.


164. Acetabulum: 0. At least a small perforation; 1. Completely closed.

165. Preactacetal 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. Preactacetal process, length: 0. Less than 50% of the length of the ilium; 1. More than 50% of the length of the ilium.


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 & 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.


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).


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.


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.

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, sub-equal 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 processs, 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 & proximally splint like, end of phalanx 1-1 does not extend beyond the end of metatarsal 2; 2. Metatarsal 1 reduced to a vestigal 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.


216. Epaxial ossified tendons present along vertebral column: 0. Absent; 1. Present.

217. Ossified hypaxial tendons, present on caudal vertebrae: 0. Absent; 1. Present.


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.


**New characters**

222. Wear facets on teeth: 0. Absent or sporadically developed; 1. Systematic development of wear facets along the entire tooth row.

223. Head of humerus is separated from prominent medial tubercle on proximal surface by a groove: 0. Absent; 1. Present.

224. Pendent fourth trochanter, rod-like with subparallel anterior and posterior surfaces: 0. Absent; 1. Present.

225. Fibula, distal end is strongly reduced and splint-like: 0. Absent; 1. Present.

226. Astragalus and calcaneum are indistinguishably fused to one another: 0. Absent; 1. Present

227. Maximum expansion of distal tibia relative to proximal: Distal tibia is considerably less expanded than proximal (0); Maximum expansion of distal tibia is subequal to that of proximal tibia (1).

(c) Data matrix

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Bugenasaura infernalis

Chaoyangosaurus youngi

Dryosauridae

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| Gasparinisaura cincosaltensis |
Goyocephale lattimorei

Heterodontosaurus tucki

Hexinlusaurus multidens

Homalocephale calathocercos
Hypsilophodon foxii

Jeholosaurus shangyuanensis

Lesothosaurus diagnosticus

Liaoceratops yanzigouensis
Lycorhinus angustidens

Micropachycephalosaurus hongtuyanensis

NHM RU A100 (formerly BMNH RU A100)

Orodromeus makelai
Othnieliosaurus consors

Pachycephalosauridae

Parksosaurus warreni
Pisanosaurus mertii

Psittacosauridae

Rhabdodontidae

Scelidosaurus harrisonii
**Scutellosaurus lawleri**

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**Stegosauria**

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**Stenopelix valdensis**

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**Stormbergia dangershoeki**

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Tenontosaurus tilleti

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**Yinlong downsi**

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**Zephyrosaurus schaffi**

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8. References


Casamiquela, R. M. 1967. Un nuevo dinosaurio ornitisquio Triásico (*Pisanosaurus mertii*;
Ornithopoda) de la Formación Ischigualasto, Argentina. Ameghiniana 4:47–64.


Galton, P. M. 2002. New material of ornithischian (?heterodontosaurid) dinosaur *Echinodon*
(Early Cretaceous, southern England) from the Late Jurassic of Fruita near Grand Junction, Colorado, USA. Journal of Vertebrate Paleontology 22 (3, Suppl.):55–56A.


The Upper Jurassic Morrison Formation: An Interdisciplinary Study. Modern Geology 22.


Carpenter, D. J. Chure, & J. I. Kirkland (eds.), The Upper Jurassic Morrison Formation: An Interdisciplinary Study. Modern Geology 22.


