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ON THE HISTORY, OSTEOLOGY AND SYSTEMATIC POSITION OF THE WEALDEN (HASTINGS GROUP) DINOSAUR *HYPSELOSPINUS FITTONI* (IGUANODONTIA: STYRACOSTERNA)

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ABSTRACT. The history of discovery and interpretation of several dinosaurs collected from quarries near the town of Hastings during the latter half of the 19th century is more complicated than it should be. Samuel Husbands Beckles and Charles Dawson collected several large ornithopod skeletons from this area, but just a few bones from these skeletons were subsequently described and interpreted (principally) by Richard Owen and Richard Lydekker. All these specimens merited recognition because they had the potential to contribute to an on-going debate about the anatomical structure and relationships of the iconic Wealden dinosaur *Iguanodon*. Unfortunately, no detailed description of these important skeletons was published in later years. Furthermore, previously known associations of bones and even provenance information, linked to the specimens that were gradually acquired by the Natural History Museum, are unclear. Confusion may have arisen because Richard Lydekker used the private collector Charles Dawson as a voluntary curatorial assistant. This account documents the past work on the osteology of material that can be attributed to *Hypselospinus fittoni*. Nearly all such material is described here for the first time, and every effort has been made to re-establish associations between bones as well as provenance information. A skeletal reconstruction of *Hypselospinus* is attempted on the basis of the hypodigm. Most of the on-going confusion concerning the affinity of this material with either *H. fittoni* or its sympatric contemporary *Barilium dawsoni* has resolved. *Hypselospinus fittoni* (Lydekker, 1889) is re-diagnosed on the basis of this new and relatively comprehensive anatomical description, and this animal is compared to known contemporary and closely related taxa. Some recently published accounts claiming to be revisions of the taxonomy of Wealden ‘iguanodonts’, including material belonging to the hypodigm of *H. fittoni,* have failed to adhere to basic taxonomic principles and have caused more confusion than was strictly necessary. The systematic position of *Hypselospinus* is reassessed cladistically. The cladistic analysis forms the basis for a revised hierarchical classification of derived ornithopods. The consensus topology generated by the systematic analysis has been used to explore the phylogenetic history of these dinosaurs and create an internally consistent classificatory hierarchy (phylogenetic definitions and Linnaean diagnoses are given for critical positions in the topology). This analysis suggests that there is a fundamental split among the more derived (clypeodontan) ornithopod ornithischians into the clades Hypsilophodontia and Iguanodontia. There is evidence for anatomical parallelism and convergence (homoplasy) particularly between large-bodied representatives of both clades. *Hypselospinus* is one of the earliest known styracosternan iguanodontians and displays anatomical characteristics that presage the evolution of the extraordinarily abundant and diverse hadrosaurs of the latest Cretaceous (Campanian-Maastrichtian). These observations cast fresh light on the phylogeny, classification, diversity and biology of derived ornithopods. There is little doubt that *Hypselospinus fittoni* could have been understood far better more than a century ago. That this statement is undoubtedly true is reflected in the century of doubt and confusion that has surrounded this taxon and its original incarnation as *Iguanodon fittoni*.

Institutional Abbreviations.

CEUM – College of Eastern Utah Prehistoric Museum (Price, Utah, USA)
NHMUK – The Natural History Museum (London, UK)
RBINS (formerly IRSNB) – Royal Belgian Institute of Natural Sciences, (Brussels, Belgium)
USNM – The Smithsonian Institution, National Museum of Natural History (Washington, DC, USA)

INTRODUCTION AND HISTORY OF ACQUISITIONS

Richard Lydekker named *Iguanodon fittoni* and *I. hollingtoniensis* on the basis of some incomplete skeletal remains collected by the St Leonards-based fossil collector Charles Dawson (1864-1916). Dawson (Woodward, 1916) was able to collect abundant dinosaur remains from several sites in the surrounding area (Norman, 2011a; Brooks, 2011): these ranged from larger and more traditional quarries to a variety of smaller, temporary excavations. The remains referred to above were found at two localities (named 'Shornden' and 'Hollington') that were situated close together on the northern edge of the town of Hastings, which is located on the East Sussex coast (Fig. 1). There is doubt about the exact location of the Hollington quarry referred to by Lydekker because a number of small sites were excavated in and around the district known as Hollington and unfortunately Dawson failed to keep (or pass on) records of his discoveries. These long-since abandoned quarries contained exposures of the Wadhurst Clay Formation (Hastings Group: Fig. 2). A number of other sites scattered across this area yielded similar dinosaur remains in a restricted area to the southwest of the minor NW-SE orientated Ore-Fairlight Anticline (Kirkaldy, 1975); the road labelled 'The Ridge B2093' in Figure 1 more or less follows the axis of the anticline.

<< INSERT FIGURE 1 NEAR HERE>>

Samuel Husbands Beckles (1814-1890), an experienced fossil collector who had retired to St Leonards (9 Grand Parade) obtained a partial skeleton (NHMUK R1831) with the assistance of a team of labourers (Owen, 1872:1), during the spring of 1871. The skeleton was discovered on the intertidal foreshore west of St Leonards (Fig. 1). This collection of bones was accessioned, by the Natural History Museum after Beckles' death, in batches using the numbers NHMUK R1831, R1832, R1833 and R1835. Some of this material was described after viewing Beckles' private collection and was referred to as '*Iguanodon Mantelli'* by Owen (1872, 1874: NHMUK R1831-1833) or as '*Iguanodon'* by Hulke (1885: NHMUK R1835). Beckles also supervised the collection of a partial skeleton (NHMUK R1834) later in 1871 at 'Silverhill-Tivoli' (Fig. 1); this skeleton was unearthed during the excavation of footings for Silverlands House (in what is now Silverlands Road) according to records held by Hastings Museum. This latter discovery was made within a quarter of a mile [400 metres] of the Shornden locality (Fig. 1).

The comparatively young fossil collector Charles Dawson was encouraged by Beckles to collect more dinosaur bones from the area. By 1884 Dawson had amassed an important collection of dinosaur remains (Woodward, 1916), which were added in batches to what became known as the Dawson Collection at the Natural History Museum (formerly the British Museum [Natural History]). The early material, purchased between 1884 and 1887 (Lydekker, 1888b: 196), became the subject of study by Richard Lydekker (1849-1915) who held a purely voluntary position at the Natural History Museum (Stearn, 1981:184). Under the guidance of the Keeper of Geology (Henry Woodward), who also had a keen interest in *Iguanodon* (Woodward, 1885), Lydekker was engaged in documenting and publishing a series of systematic catalogues of the fossil vertebrate collections (1885-1891). Lydekker was assisted in this task by Charles Dawson who became involved, in a similarly voluntary capacity, in the documentation of his own collection as well as that of his mentor Samuel Beckles. The bulk of the Beckles collection was donated to the Natural History Museum in 1890, following Beckles' death.

<< INSERT FIGURE 2 NEAR HERE>>

Lydekker, 1889: I. fittoni *and* I. hollingtoniensis

Iguanodon fittoni was first announced in a short article that reported a series of (allegedly associated) specimens comprising a "…left ilium, part of a pubis [*sic* = ischium], and the imperfect sacrum (B.M. No. R.1635), which appear to indicate a distinct species" (Lydekker, 1889: 354).

These specimens were all collected from a site named Shornden or Shornden Quarry (Fig. 1 – Norman, 2011a; Brooks, 2011). This site probably derived its name from Shornden Forest, the southern edge of which contained early settlements in medieval times and was little more than a mile (1.6 km) north of what was later to become the coastal town of Hastings. Today, one street name and Shornden Reservoir appear to be the last reminders of Shornden as an actual location. Areas of land were routinely surface-quarried: stone (Tilgate Stone) was used for road mending, walling and simple building work, while clay (Wadhurst Clay) was fired to make bricks, roofing tiles and chimney pots. The remnants of much older quarries seem also to have pock-marked the district, reflecting the widespread extraction of Weald ironstone for an iron industry that had its origin in Elizabethan times (Topley, 1875).

During the period 1850-1880 this area became the focus of considerable development as Hastings' population expanded rapidly. One particular problem created by population growth was the need to provide an adequate water supply; this led to the conversion of the large, but probably long-exhausted, Shornden and Buckshole quarries into reservoirs (Fig. 1). Abundant Wadhurst Clay would have been available to line these two sites and it seems that while these earthworks were being undertaken Dawson was on-hand to collect dinosaur remains. Other earthworks, associated with the construction of cuttings and embankments for the railway lines that extended to the coast from London; and, somewhat later, the creation of civic parkland during the 1880s (notably Alexandra Park, Coronation Wood and Old Roar Ghyll [Gill] – Norman, 2011a) provided further opportunities for fossil collection. Digging at the nearby Old Roar Quarry and Little Ridge Farm Quarry, as well as house building in and around the adjoining areas known as Hollington and Silverhill-Tivoli (Fig. 1) created further opportunities for collecting. It is a source of considerable regret that no correspondence or notes (particularly between the key players: Dawson, Beckles, Owen and Lydekker) detailing the excavation of these dinosaurs, have been discovered to date. Indirect comments by Richard Lydekker (originating from discussions with Dawson) hint at details of some excavations, and the direct quotation from a letter from Beckles to Richard Owen (Owen, 1872) offer tantalizing snippets of information.

It was stated in Lydekker's (1889) original article that the sacrum and ilium of *Iguanodon fittoni* were found on the same horizon, but separated by a distance of about 50 yards (~45m) and that the ilium represented part of an animal that was smaller in size than *I. dawsoni* (=*Barilium dawsoni* – Norman 2010, 2011a,b, 2012). The latter species included an ilium that had been found at a slightly lower stratigraphic level in the same quarry. The ilium of *I. fittoni* was distinguished from the type-specimen of *I. dawsoni* because it had a preacetabular process that was transversely compressed and lacked the pronounced medial ridge seen in the latter species (Figs 3, 9, mr). The postacetabular portion of the ilium also differed significantly in shape: that of *I. dawsoni* having a deeper and more rounded profile, whereas in the new species the blade tapered to a rounded end that was expanded transversely, creating a pronounced brevis fossa (Figs 3, 9, brf). Differences of proportion included the depth of the iliac blade above the acetabulum and the shape of the acetabulum; these, though mentioned as being “distinctive”, were ill-defined.

<< INSERT FIGURE 3 NEAR HERE>>

The preserved fragment of the sacrum exhibited transverse compression and fusion (both features found, according to Lydekker, in *Iguanodon mantelli* – based on comparison with NHMUK OR37685 – Owen 1855, tabs 3-6) but the latter species was reported to have a shallower iliac blade and to lack the pronounced brevis fossa seen in *I. fittoni*. The only other form to which this new species might be compared was *Sphenospondylus gracilis* Lydekker, 1888a (the generic name *Sphenospondylus* was originally proposed by Seeley [1883], Lydekker subsequently added the species name). *Sphenospondylus gracilis* was based upon a series of dorsal vertebrae, so objective comparison was not possible, not that that fact inhibited Lydekker (1889: 354). In passing, Lydekker also noted that the ilium of *I. fittoni* bore some resemblance to those described as *Camptonotus (=Camptosaurus)* from the Late Jurassic of North America (Marsh, 1879); however, Lydekker also noted that the sacrum of *I. fittoni* could be distinguished from that of *Camptosaurus* because, unlike the latter, it had vertebrae that were fused together and bore ventral midline keels.

Iguanodon hollingtoniensis was briefly named and described in addition to *I. fittoni*. Lydekker established *I. hollingtoniensis*, using a partial skeleton recovered from the Wadhurst Clay at a site referred to as Hollington Quarry (Fig. 1). He noted that some of this material had earlier been referred to either *Iguanodon dawsoni,* or as probable juvenile material of *I. bernissartensis* (Lydekker 1888a,b). The type material of this new species was regarded as "[NHMUK] R.1148 together with others belonging to the same individual numbered R.1629, and also certain vertebrae numbered R.1632, which are also believed to belong to the same individual" (Lydekker, 1889: 355). Additional material (NHMUK R811 and R604 – previously assigned by Lydekker to *I. dawsoni*) was also transferred to this new species and another specimen, comprising a portion of a skeleton collected also at Hollington (NHMUK R33) was also mentioned as being referable to either *I. fittoni* or *I. hollingtoniensis* (but he, perhaps tellingly, was unable to confirm its specific identity).

<< INSERT FIGURE 4 NEAR HERE>>

Iguanodon hollingtoniensis was distinguished from *I. mantelli* by having a curved femoral shaft (Fig. 4) and a pendant [incorrect] "inner" (=fourth) trochanter. Both of these anatomical features had been reported as present in the femur of the smaller Late Jurassic *Camptosaurus* (Marsh 1879, 1885). The femur of *I. hollingtoniensis* was also described as "smaller and of different contour" (Lydekker 1889: 355) compared to a femur associated with a partial skeleton that he attributed to *I. dawsoni* (by inference he appears to be referring to NHMUK R1627, a partial skeleton, collected from Brede a small village north of the Ore-Fairlight Anticline: see Fig. 1). The sacral vertebrae of NHMUK R811 (originally referred to *I. dawsoni*), and those of NHMUK R1632 were described as "not anchylosed together" (=unfused) and having flattened haemal (=ventral) surfaces; both of these features echoed those that had been described in *Camptosaurus*. An associated fragmentary ilium (NHMUK R811b) was described as having a preacetabular process of "the thin type of *I. Fittoni*, and therefore different from that of *I. Dawsoni*, while this ilium is decidedly different from that of *I. Fittoni*" (Lydekker, 1889: 355).

[N.B. The evidence used by Lydekker to support such a definite statement was never revealed.] While alleged similarities with *Camptosaurus* were being over-emphasized, the presence of the "peculiar pollex of *Iguanodon*" was used to support Lydekker's reference of this new taxon to the genus *Iguanodon*.

Lydekker, 1890a

Lydekker's preliminary description of both *Iguanodon fittoni* and *I. hollingtoniensis* was supplemented by additional information that was included in a slightly longer article (Lydekker, 1890a).

Iguanodon fittoni. The holotype left ilium (NHMUK R1635) was illustrated diagrammatically in lateral and ventral views (Lydekker 1890a: Fig. 5A, B) and this indicated that a significant portion of the preacetabular process was present (compare Figs 3, 5 and 9). Unfortunately, the preacetabular portion (prp) has been either misplaced or lost [this portion was not found when the holotype was first examined by the author in 1975 and is still missing today]. The illustration emphasized its general shape and the presence of the large brevis fossa (brf). In addition, mention was made of a proximal portion of a left ischium (see Fig. 10: previously identified as a pubis) and an anterior caudal vertebral centrum (Fig. 8) found some 25 yards [~23m] west of the ilium; and also that the sacral fragment (Fig. 7) was found a further 25 yards west of the two latter specimens. The association of these specimens was justified on the evidence of two theropod dinosaur metatarsals having been found five years apart and on the same bedding plane in a nearby quarry (Hollington) and separated by a greater distance (180 yards [~165m]); these latter were reckoned to be associated bones of the same individual (Lydekker, 1890a: 38). The specimens of *I. fittoni* were all found in "a three-foot [~1m] bed of ferruginous sand, which is separated by a stone band of two feet [~0.6m] in thickness from the underlying clay bed, four feet thick [~1.3m], which yielded the type specimens of *I. Dawsoni*" (Lydekker 1890a: 38).

<< INSERT FIGURE 5 NEAR HERE>>

Comparative comments emphasizing the differences between the ilia of *I. fittoni* and *I. dawsoni* repeat those in his first paper (Lydekker, 1889), although he also noted that the anterior tip of the pubic process was missing and that the preacetabular process of *I. fittoni* was not twisted axially along its length (in contrast to the condition described in *Iguanodon dawsoni*). Lydekker also reported that the preacetabular process was shorter than that of *I. dawsoni*; how this latter point could be established is not clear, given that both are incomplete and that of *I. fittoni* was apparently missing its mid-section. Additional "minor features" indicated that in *I. fittoni* the preacetabular notch was shallower, that the pubic peduncle was deflected downward more strongly (this is a visual distortion created by the erosion of the anterodorsal edge of the peduncle), the distance between pre- and postacetabular notches was smaller, and the edge of the preacetabular notch was "rounded off" (Lydekker, 1890a: 39). This latter feature is not correct: the edge of the embayment (notch) is not rounded but has a distinct ridge that marks the junction between the rounded lateral surface and the flattened medial surface. The ischial fragment was described as having a "hammer-shaped head", which is of no diagnostic value, and the specimen is in anycase clearly water-rolled and polished (Fig. 10). The sacrum description repeated that which was given in the original paper and no further mention was made of the caudal vertebra.

This new species was differentiated from other described taxa: *Sphenospondylus gracilis*, *Iguanodon mantelli* and *I. bernissartensis*, all of which come from younger "Upper Wealden" deposits; and, again, some general similarities to the anatomy of *Camptosaurus* were mentioned. The new taxon was referred neither to the latter genus nor to the closely allied English Kimmeridgian taxon *Iguanodon [=Cumnoria] prestwichii* Hulke, 1880, because of the fused and laterally compressed form of the sacral vertebrae. There was an additional taxonomic note concerning "the so-called *Iguanodon Prestwichii*, which I am unable to separate from *Camptosaurus*." (Lydekker, 1890a: 40). Seeley (1888) had already created the new name *Cumnoria prestwichii* on the basis of perceived differences of geological age, and its osteology compared to that of

Iguanodon [sensu lato]. However, in the supplement to part IV of the catalogue it is clear that Lydekker regarded this species as referable to *Camptosaurus* and catalogued it provisionally as such (Lydekker, 1890b: 258).

Iguanodon hollingtoniensis. No complete ilium of this taxon had been recovered, so its diagnosis was not so clear-cut. The type material was evidently collected in batches at the same Hollington quarry (Fig. 1): "one moiety of which (B.M. No. R.1148) was obtained in 1887, while the others (B.M. No. R.1629), were collected in 1889" (Lydekker, 1890a: 40). Another associated series of sacral and caudal vertebrae from the same quarry (NHMUK R1632) was also referred to the same individual. The right femur (NHMUK R1148), though slightly crushed and distorted, was illustrated (Lydekker, 1890a: fig. 2, see Fig. 4A); it displays some curvature of the shaft, angular sides and a prominent fourth trochanter with a very slightly pendant tip (but this is morphologically unlike the tapering, finger-like pendant trochanter seen in camptosaurs). While distinguishing the form of this femur from those described as *I. mantelli* and *I. bernissartensis* by Dollo (1888), Lydekker (1890a: 42) also separated it from a femur associated with a partial skeleton from Brede (NHMUK R1627) that he had referred to *Iguanodon (=Barilium) dawsoni*. The Brede femur was described as poorly preserved but of larger size and with a straighter shaft. The dorsal vertebrae associated with NHMUK R1148 were also distinguished as being smaller than those of *I. dawsoni*. General similarities in the form of the femora of *I. hollingtoniensis* and *Camptosaurus* were noted, but these glossed over a considerable number of genuine anatomical differences.

The sacral and caudal vertebrae (NHMUK R1632) identified with the type specimen were reported as having flat ventral surfaces and lacking fusion between the vertebrae. These characters were described as resembling the condition of the sacrals reported in *Camptosaurus*, and seemed generally indistinguishable from those found with NHMUK R811 (collected by Dawson at Hollington in 1884). Lydekker (1888a,b) had referred this latter material to his new taxon *I. (=Barilium) dawsoni*; these specimens were associated with dorsal vertebrae accessioned as

NHMUK R604 (also collected at Hollington). An "imperfect left ilium (No. R.811b)" (see Norman 2010: fig. 8C,D, see Fig. 30B, C) associated with the remainder of NHMUK R811 was also mentioned. The ilium was referred to as "much flattened" and was supposedly illustrated (reversed) by Lydekker (1890a: fig. 1E). It is obvious from the outline drawing in the figure that the ilium illustrated by Lydekker is that of another specimen entirely (NHMUK R1636 – an isolated partial right ilium collected at Shornden – Fig. 35B). Lydekker reported that precisely similar features were to be found in the right ilium of "another imperfect skeleton collected by Mr. Dawson (No. R.1636)" that Lydekker also referred to *I. hollingtoniensis*. These referrals had been transposed and the mistake was corrected (Lydekker, 1890b: 264).

In summary, Lydekker concluded that *I. hollingtoniensis* was anatomically distinct from all other described species, bore similarities to *Camptosaurus* but, because of its possession of a conical thumb-spike, should be referred to the genus *Iguanodon*. Lydekker regarded this taxon as representative of the "proiguanodonts": an informal grouping of more primitive taxa first proposed by Lydekker (1888b: 196). Proiguanodonts "connect[ed] the typical forms of *Iguanodon* [euiguanodonts] with the less specialized genus *Camptosaurus*" (Lydekker, 1890a: 43). Lydekker mentioned that the skeleton of NHMUK R1636 had a long and slender scapula. This attribution is incorrect, the partial skeleton he is actually referring to is NHMUK R2357 and this was collected from the West Marina locality (Fig. 1). Furthermore, the scapula of the latter is extremely poorly preserved and incomplete but very massive proximally and is part of an associated partial skeleton that has more recently been referred to *Barilium dawsoni* (Norman, 2011a). Lydekker claimed that this anatomical feature (the long slender scapula) was shared with another partial skeleton (NHMUK R33 – also collected at Hollington) that he claimed was also referable to *Iguanodon hollingtoniensis*.

Lydekker (1890a) also mentioned that another associated skeleton of smaller size (and presumed to be juvenile) had been collected from Wadhurst Clay exposures at Hastings by Samuel Beckles and [lately, 1890] presented to the Museum. The material included a right ilium, left pubis, left femur and several vertebrae. The ilium (though smaller than that of the holotype NHMUK R1835) was claimed to resemble that of *I. fittoni*. The skeleton being referred to is certainly NHMUK R1834, which had been collected at Silverhill-Tivoli (Fig. 1) in 1871. The femur was singled out for particular mention because it was reported as displaying a 'crested' fourth trochanter, rather than the slightly pendant form of this structure that had been illustrated in the holotype of *I. hollingtoniensis* (Fig. 4, Lydekker 1890a). Unfortunately no femur exists among the material allocated with the number NHMUK R1834. However an almost complete but very poorly preserved and partially plaster-jacketed femur (NHMUK R1831 [R1833]), belonging to a partial skeleton collected (also by Beckles) from the foreshore locality west of St Leonards (Fig. 1) is most probably the one to which Lydekker is referring. The latter femur possesses a large (clearly 'crested') but eroded fourth trochanter; this specimen may well have been the source of Lydekker's reference because all of these specimens would have arrived at the same time in the museum following Beckles' death in 1890. Although smaller, what can be discerned of the structure of the femur in NHMUK R1831 differs in no significant way from the femora of the holotype (NHMUK R1148/R1629). Other material associated with the Beckles skeleton collected at Silverhill-Tivoli (NHMUK R1834) was reported as showing fused caudal vertebrae as well as some caudals with procoelous articular surfaces. Two small blocks of fused caudals are still preserved with this specimen and these, as interpreted by Lydekker, are probably pathological. However, the procoelous caudal centrum belongs to a (rare) sauropod dinosaur.

It is interesting to note today that inspection of the collections in the Natural History Museum has revealed the presence of three teeth: one is an eroded stump of a probable dentary tooth and two worn maxillary tooth crowns (Fig. 5C) that bear the registered number of the holotype of *I. fittoni* (NHMUK R1635). While these teeth are not diagnostic beyond the level of ankylopollexian ornithopod: the maxillary crowns display the prominent primary ridge (p), subsidiary ridges (r) and the vertical channels marking the positions occupied by successional tooth crowns, it is slightly surprising that Lydekker made no mention of such *Iguanodon*-like teeth in either his reports or his catalogues.

Lydekker, 1890b

The last contribution by Lydekker on the subject of these Wadhurst Clay species is found in the supplement to Part IV of his catalogue of the *Fossil Reptilia and Amphibia of the British Museum [Natural History]* (Lydekker, 1890b). This offered Lydekker's definitive list of material referable to *Iguanodon dawsoni, I. fittoni* and *I. hollingtoniensis* with, where appropriate, reassignments and corrections. It also allowed Lydekker to reaffirmed his concept of these taxa as representatives of an intermediate (proiguanodont) morphological stage that was intermediate between that seen in the stratigraphically older Late Jurassic camptosaurs and the stratigraphically younger Early Cretaceous (euiguanodonts) from the Weald District and the Isle of Wight (Fig. 2).

Recent work

Since the work of Lydekker (1888-1890) little critical attention has been given to Hastings Group, Wadhurst Clay Formation (Valanginian) ornithopod taxa. The taxa were mentioned briefly by Hooley (1925), and also appear in taxonomic checklists (Romer, 1956; Steel, 1969; Weishampel, Dodson & Osmólska, 1990, 2004). Norman (1977) re-described and illustrated some of this material. Norman (1987) illustrated a few characteristic skeletal elements of *Iguanodon dawsoni* and *I. fittoni* as representative of taxa associated with a Hastings Group palaeofauna. These dinosaurs had potential biostratigraphic utility because they could be distinguished osteologically from the younger ornithopod taxa (*Iguanodon bernissartensis* and *I.* [*Mantellisaurus*] *atherfieldensis*) associated with a Weald Clay Group palaeofauna. Norman (2010, 2011a) began a study of all the known material in order to clarify its osteology, the association of skeletal material and the appropriate nomenclature of all these taxa. Two taxa of Hastings Group (Valanginian) ornithopods were recognised and formally diagnosed (Norman, 2010) and new nomenclatural combinations *Barilium dawsoni* (Lydekker, 1888a) and *Hypselospinus fittoni* (Lydekker, 1889) were proposed. *Barilium dawsoni* was described more fully (Norman, 2011a).

Blows (1998), Naish & Martill (2008), Paul (2007, 2008, 2012), Galton (2009) and Carpenter & Ishida (2010) have reviewed this and other material. Naish & Martill (2008) and Galton (2009) surveyed the material and observed that these taxa would benefit from detailed analysis. In marked contrast, Paul (2007, 2008, 2012) as well as Carpenter & Ishida (2010) proposed a number of taxonomic changes. The new taxonomic proposals have been criticised by Norman (2011a,b, 2012, 2013) and McDonald (2012a).

McDonald, Barrett & Chapman (2010a) examined Wealden material and diagnosed the new taxon *Kukufeldia tilgatensis,* which had earlier been referred to *Barilium dawsoni* (Norman, 2010), using an isolated dentary (NHMUK OR28660) collected from the Whiteman's Green Quarries at Cuckfield (West Sussex – Fig. 1). The holotype of *Kukufeldia* is presently diagnosed upon a single apomorphy (the pattern of vascular openings on the external surface of the dentary) but is considered to be most probably referable to *Barilium dawsoni* (Norman, 2011a,b, 2013). It may be noted, in passing, that McDonald now considers that the material originally assigned to *Kukufeldia* can be referred to the genus *Barilium* (McDonald, pers. comm. 5 October 2013). McDonald, et al. (2010a) also assigned a partial skeleton (NHMUK R1834) to *Barilium dawsoni*; this had previously been referred to the taxon *Hypselospinus fittoni* by Norman (2010). It will be demonstrated below that NHMUK R1834 can be referred to *H. fittoni* (this latter referral has also been accepted (McDonald, pers. comm., 5 October 2013).

This contribution

Hastings Group (Valanginian) beds form outcrops in south-east England and are enclosed by a belt of Weald Clay in an area of countryside known locally as *The Weald* (Fig. 6); this geographic area encompasses the counties of East and West Sussex as well as adjacent parts of Surrey, Kent and Hampshire. Iguanodontian remains that are considered here have been recovered from a narrow stratigraphic range within the Valanginian (Fig. 2).

<< INSERT FIGURE 6 NEAR HERE>>

This contribution offers:

1. A historical review of the material that was collected from Wadhurst Clay Formation localities near Hastings.
2. An osteological description and taxonomic assessment of this material (with detailed consideration of the assignment of all presently known material).
3. A first attempted reconstruction of *Hypselospinus fittoni*.
4. A systematic analysis of large-bodied ornithopod taxa, which incorporates new evidence from *H. fittoni* and its sympatric contemporary *Barilium dawsoni* and has generated a new phylogeny that prompts a revised taxonomy of derived ornithopod dinosaurs.
5. A brief phylogenetically derived narrative of pre-euhadrosaurian ornithopod evolution.

Institutional abbreviations

NHMUK – The Natural History Museum, London
RBINS [IRSNB] – The Royal Belgian Institute of Natural Sciences [formerly the Institut Royal des Sciences Naturelles de Belgique]
USNM – United States National Museum (Smithsonian Institution) Washington, DC.

SYSTEMATIC PALAEONTOLOGY

Linnaean classification

Superorder DINOSAURIA Owen, 1842
Order ORNITHISCHIA Seeley, 1887
Suborder ORNITHOPODA Marsh, 1881
Infraorder CLYPEODONTA novum
Division IGUANODONTIA Sereno, 1986 (emended)
Subdivision ANKYLOPOLLEXIA Sereno, 1986
Infradivision STYRACOSTERNA Sereno, 1986

Genus *HYPSELOSPINUS* Norman, 2010

Hypselospinus fittoni (Lydekker, 1889)

Figures 3-5, 7-10

*1889	*Iguanodon Fittoni* Lydekker: 354.
v*1889	*Iguanodon hollingtoniensis*: 355.
v 1890	*Iguanodon Fittoni* Lydekker: 38, fig. 1C.
v 1890	*Iguanodon hollingtoniensis*: 40, figs 1E, 2.
v*2010	*Hypselospinus fittoni* (Lydekker, 1889); Norman, figs 5-9.
v.2010	*Wadhurstia fittoni* (Lydekker, 1889); Carpenter and Ishida, fig. 2.31.
v.2012	*Huxleysaurus hollingtoniensis* (Lydekker, 1889); Paul
v.2012	*Huxleysaurus fittoni* (Lydekker, 1889); Paul
v.2012	*Darwinsaurus evolutionis* (Lydekker, 1889); Paul, fig. 1B,b.

Holotype. NHMUK R1635 (Figs 3-5, 7-10): incomplete left ilium, partial sacrum, mid-caudal centrum, the eroded proximal end of an ischium [very dubious association]. In addition three isolated teeth (1 stump of a dentary crown and 2 worn and rootless maxillary crowns) have the same registered number and may well have been part of the original accession.

Referred material. NHMUK R1148 (incorporating material registered as R1629 and R1632), R604, R604a (including bones registered as R811, R811a, R811b), NHMUK R33, R966, R1636 (ilium only), R1831 (incorporating specimens registered separately as R1832, R1833 and R1835), R1834, R4743 (scapula). N.B. NHMUK R1627 (a fragmentary skeleton collected from the village of Brede – see Fig. 1) is tentatively associated with the hypodigm of *H. fittoni*, pending further study. The specimens registered as NHMUK R2848 (an isolated femur and an associated scapula-coracoid), which were referred to *Barilium dawsoni* (Norman, 2011a) may eventually prove to be referable to *H. fittoni*.

Stratigraphical horizon, age and type locality. Lower Cretaceous, Hastings

Group, Wadhurst Clay Formation (Fig. 2). Age: Valanginian: 139-137Ma (Allen & Wimbledon, 1991; Rawson, 2006; Gradstein, Ogg & Smith, 2004). Type locality: Shornden Quarry, Hastings (Fig. 1): originally an open-cast quarry site, the area where this quarry was located was landscaped and part converted into a reservoir in Alexandra Park during the late 19th century, East Sussex, UK (Norman, 2011a; Brooks, 2011).

Diagnosis. Asterisks* signify apomorphies. Other characters listed below form a unique combination of characters that are apomorphic when considered together, even though they may occur sporadically within a plexus of morphologically similar ornithopods.

Holotype diagnosis

Ilium (Figs 3, 9). Preacetabular process (prp) with medial and lateral surfaces that are vertical, laterally compressed and shows little evidence of long-axis torsion*; ventral edge of the proximal portion of the preacetabular process thicker than dorsal edge, and its dorsal edge is narrow and flat-topped*; low-relief, curved, medial ridge on the medioventral surface of the preacetabular process associated with a shallow, irregular facet marking the area for attachment of the distal end of the first sacral rib*; central portion of iliac blade above the acetabulum is flat and stands more or less vertically (rather than having its lateral surface concave vertically and leaning outward so that it faces ventrolaterally); straight, narrow, transversely compressed and flat-topped dorsal edge to the central portion of the iliac blade*; postacetabular process with an inflection point dorsally, after which the dorsal margin slopes posteroventrally before terminating at a transversely expanded and thick bar*; medial deflection of the ventral half of the postacetabular process creates an elongate, broad, low-arched, brevis fossa; brevis fossa bordered laterally by a thick horizontal ridge; the postacetabular process displays sacral rib facets that track the ventral margin of the postacetabular blade and rise obliquely toward the posterior tip, and merge with the dorsally positioned 'transverse process' facets that run horizontally along the mid-section of the iliac blade.

Vertebrae (Fig. 7). Ventral surfaces of posterior sacral centra are keeled; anterior-middle caudal sub-cylindrical with a transversely convex ventral surface.

Supplementary diagnostic characters based on the hypodigm

Cranial. Dentary ramus elongate and gently arched anteriorly; diastema comparatively short: 2-3 crown widths; coronoid process short and orientated at an oblique angle to the long axis of the dentary (N.B. This latter feature may be the consequence of breakage and subsequent restoration of the original specimen).

Dental. Dentary crowns are large, shield-shaped and thickly enamelled on the lingual surface; marginal denticles on the mesial and distal margins of the crown form curved, oblique ledges that are mammillated; well-defined primary ridge off-set distally on the lingual surface; the mesial sector of the crown has a low, broad mound that runs parallel to the primary ridge and is traversed by numerous, irregular and strand-like accessory (tertiary) ridges*.

Axial. Dorsal and anterior caudal vertebrae have narrow, very elongate and obliquely inclined neural spines; the bases of anterior caudal neural spines are flanked by buttresses on either side of median anterior and posterior ridges*; dorsal centra have unusually thickened articular rims*; mid-caudal vertebrae exhibit a ventral midline sulcus*.

Appendicular. Sternal plates have a broad, apron-like posterior edge to the 'blade'*; the 'handle' portion of the sternal plate is robust and dorsoventrally flattened; calcification of the intersternal cartilage (leading to co-ossification of the sternal bones) occurred in ontogenetically mature specimens*; pollex ungual large, pointed, triangular in lateral profile, laterally compressed (rather than conical) and curved slightly palmwards along its length*; pollex claw grooves present; pubic shaft has a circular cross-section; lateral surface of the proximal end of the ischial shaft (adjacent to the obturator process) forms an elongate flattened facet*; ischial shaft comparatively short, stout, J-shaped and terminates in an anteriorly expanded ischial boot.

THE HOLOTYPE OF *HYPSELOSPINUS FITTONI* (LYDEKKER, 1889)

Dentition

Three partial teeth are included in the material registered as NHMUK R1635 (Fig. 5C). One appears to be a very heavily worn (shed and subsequently eroded) dentary tooth stump (Fig. 5C,1) while the other two were functional (worn) maxillary crowns of differing size. Figure 5C,2 appears to be a shed left crown in a state of advanced wear. The smaller right maxillary crown (Fig. 5C,3) probably comes from either the mesial or distal ends of the maxillary 'magazine' (where teeth are normally smaller than those positioned nearer to the centre of the array). The maxillary crowns offer little morphological information beyond a similarity to that seen in ankylopollexians generally (Norman 1986: fig. 22): crowns are narrow and lozenge-shaped, very prominent distally off-set primary ridge (p), mesial sector of the labially enamelled face marked by a small number of narrow, sub-parallel accessory (tertiary) ridges (r); transversely thickened mesial and distal edges to the crown; and longitudinally channelled roots (ch).

Axial skeleton

Sacrum. The eroded remains of three fused posterior sacral centra including portions of their sacral ribs (Fig. 7A-C). The specimen is iron-stained, poorly consolidated and appears not to be heavily permineralized. The most posterior sacral centrum has a smooth, shallow, rounded and concave posterior articular face; the main body of the centrum is spool-like, being mildly contracted around its mid-length while its ventral surface is pinched transversely to form a smoothly rounded ventral keel. The keel, in lateral view, appears to be slightly arched. The base of the sacral rib is fused at mid-height on the centrum alone, rather than having it base encroaching on the sutured articulation with the preceding centrum (as seen in more anterior sacral ribs). The neural arch is similarly confined to the dorsal surface of the centrum and the sacral rib is fused to the lateral wall of the neural arch as well as the centrum. These features:

smooth posterior articular surface, positioning of the neural arch and sacral rib relative to the centrum, confirm that this was the last in the sacral series. The penultimate sacral is badly eroded but similarly spool-shaped and it is clear that the sacral rib was more anteriorly positioned so that its base was fused across the junction between its own vertebra and that of the preceding vertebra; the base of the neural arch also overlaps the dorsal edge of the preceding centrum. The preceding vertebra displays the spool-shape of the centrum, a keel and the eroded portions of the sacral rib and neural arch (which are similarly intervertebrally positioned). The three fused sacrals diminish progressively in overall dimensions anteriorly.

<< INSERT FIGURE 7 NEAR HERE>>

Although difficult to interpret, this sacral block differs from a specimen attributed to *Barilium dawsoni* (NHMUK R3789 – Norman 2011a) in the following characters: substantially smaller size, positioning of the last sacral rib on the side of the centrum rather than intervertebrally, reduced prominence of the ventral keel, lack of arching of the keel and less pronounced thickening at the fused intervertebral junctions.

Caudal vertebra. The anterior caudal centrum (Fig. 8A-C) is approximately commensurate with those of the sacrum (allowing for its more posterior position along the tail) and its general preservational state is similar. The vertebra is almost cylindrical and its sides only slightly contracted between the articular margins. The centrum is very slightly forwardly inclined and there is a prominent posterior haemapophysis (chevron facet), with little development of a discrete anterior facet (although such anterior facets are, as a general rule, less prominent). The ventral surface of the centrum is broadly convex, with no indication of either a midline keel or sulcus. The articular faces of the centrum display a swollen rim that encloses a very shallow central concavity. The caudal ribs (cr), broken at their bases on both sides, are positioned along the line of the neurocentral suture and appear to have been well developed: a feature seen specifically in anterior caudal vertebrae.

<< INSERT FIGURE 8 NEAR HERE>>

This caudal cannot be identified and compared to the direct serial equivalent of one of the caudals of the sympatric contemporary *Barilium dawsoni*, but it differs substantially in size, structure and proportions from those of the latter taxon (Norman, 2011a).

Appendicular skeleton

Ilium. Though somewhat eroded and broken in places, and apparently lacking most of the preacetabular process that was illustrated by Lydekker (1890a: reproduced in Figure 5), it appears to be relatively little distorted (Figs 3A,B, 9). The general preservation is very similar to that described in the sacrum and caudal. The preacetabular process (prp) is laterally compressed and its dorsal edge is flattened, while the ventral border is slightly thicker and smoothly rounded transversely. The lateral surface of the preacetabular process is shallowly concave dorsoventrally, while the medial surface is equivalently convex and there is a low, oblique ridge (mr) medioventrally that is associated with a shallow rugose depression; this indicates a probable area of contact with the distal end of the ‘free’ rib of the sacrodorsal vertebra (not preserved). Compared with *Barilium dawsoni,* the preacetabular process differs substantially in size, shape and proportions (Figs 3, 9). The main portion of the iliac blade stands essentially vertically and its lateral surface is shallowly concave, the dorsal edge is narrow and flattened (Fig. 9B, fdm). The dorsal edge and its muscle scar may have expanded slightly in the region above and behind the ischiadic peduncle, but this area is broken (Fig. 9A, cross-hatching) and is interpreted by reference to NHMUK R1834 (Fig. 46). Posteriorly, the dorsal edge inclines posteroventrally before merging with a transversely thickened shelf at the posterior end of the iliac blade (Fig. 9C). This shelf reflects the abrupt medial deflection of the ventral portion of the iliac blade, which forms a shallow arched brevis fossa (brf) bounded by a distinct lateral ridge (lr). The medial edge of the brevis fossa curves ventrally and forms a thin sheet of bone that is visible lateral view (Fig. 9A).

<< INSERT FIGURE 9 NEAR HERE>>

The ventral margin of the postacetabular process is sinuous and oblique, merging with the expanded ischiadic peduncle anteriorly. The latter, though somewhat eroded, expands laterally to form a stepped boss: having a prominent posterodorsal eminence that is separated – step-wise – from a flatter bevelled area adjacent to the acetabulum. The ischiadic sutural surface is obliquely offset (facing posteroventrally – Fig. 9A). The dorsal margin of the acetabulum curves smoothly into the lateral surface of the iliac blade, although the remnant of the pubic peduncle (pp) shows that there was a distinct supra-acetabular crest (sac) developed as a ledge along the margin of that peduncle. The pubic peduncle has been sheared off, thereby obscuring its overall appearance and orientation. The medial surface of the ilium (Fig. 9D) has a mid-height horizontal ridge punctuated by a line of thumbprint-like depressions; these mark the attachment points for the sacral transverse processes and dorsal parts of the sacral ribs. Beneath this ridge the surface is smooth before developing into a broader and more continuously scarred area (sy) for attachment of the sacral yoke (formed by the coalesced ventral portions of the sacral ribs). The posterior sacral rib scars are conjoined (srf) indicating the region where the sacral yoke and ventral portions of the sacral ribs have coalesced.

The orientation of the articular surface for the ischium (posteroventral) and the positioning of the supra-acetabular crest (restricted almost exclusively to the pubic peduncle) suggests that 'in life' the ilium was articulated against the sacrum and orientated such that its dorsal edge was inclined posterodorsally so that the pubic peduncle, supported medially by a very robust first sacral rib, formed the dorsal rim of the acetabulum.

<< INSERT FIGURE 10 NEAR HERE>>

Ischium. Comprising the proximal end only of a (comparatively) small left ischium (Fig. 10), it is missing almost all its features, both peduncles have been broken off and worn smooth, the obturator process (obt) can be inferred only from the curvature of the preserved bone, and the shaft is almost entirely missing and its stump is worn smooth. The preservation of this specimen is such that it is permineralized, appears not to be strongly iron-stained and has been very water-rolled. The suggested association of this specimen with the earlier-described specimens is regarded as conjectural at best, but since it contributes nothing to the determination of this taxon it can be disregarded safely.

IGUANODON HOLLINGTONIENSIS **LYDEKKER, 1889**

Norman (2010) described, albeit briefly, the anatomical basis upon which Lydekker established the Wadhurst Clay Formation taxon (*Iguanodon hollingtoniensis* Lydekker, 1889) whose remains were collected from the same geographic area and horizon as *B. dawsoni* and *H. fittoni*. It was concluded that *I. hollingtoniensis* was a nomen dubium and its skeletal material could be assigned to *H. fittoni*. A detailed review and description of the original type and referred material of the latter species is now necessary. Norman's proposal that a single taxon (incorporating *I. fittoni* and *I. hollingtoniensis*) be recognized under the binomial *Hypselospinus fittoni* (Lydekker, 1889) has been challenged firstly by Paul (2008) who later made specific taxonomic proposals (2012), and secondly when an alternative set of taxonomic proposals were made by Carpenter & Ishida (2010).

History. Between 1884 and 1889 Charles Dawson collected the major portion of an associated partial skeleton of at least one *Iguanodon*-like from Ridge Farm Quarry near Hastings (Brooks, 2011); this location was referred to as either 'Hollington' or 'Holllington Quarry' (Fig. 1). The circumstances surrounding the original discovery of this material – its apparent piecemeal collection, as well as its phased acquisition by the

Natural History Museum – add unwanted uncertainty to claimed associations. The brief formal descriptions and catalogue notes of Lydekker (1889, 1890a,b) help to clarify some of these matters, but errors and inconsistencies (even in Lydekker's accounts) confirm to readers in the present day that an air of confusion must have been created by non-systematic collecting procedures and [possibly] anecdotal recollections. As alluded to above, it was also the case that Dawson was taken on by Lydekker, to assist with the documentation of the remains from Hastings. The archives of the Natural History Museum contain no letters, site maps or notes pertaining to the original excavations by Charles Dawson. Similar problems pertain in the case of *Barilium dawsoni* (Norman, 2011a).

<< INSERT FIGURE 11 NEAR HERE>>

The holotype NHMUK R1148 includes specimens allocated with the registered numbers R1629 and R1632, which were collected from the same quarry. As evidence of association some specimens, for example the metatarsals of the left pes (MtIII: NHMUK R1148 and MtII: NHMUK R1629) fit together perfectly (Fig. 11A-H). Additional material assigned to registered numbers NHMUK R811, R811a,b (including sacral and pelvic bones) as well as NHMUK R604 (cervical, dorsal and caudal vertebrae, some imperfectly preserved ribs and some broken tooth fragments) were also collected from this quarry and are, if not part of the type series, commensurate, show the same preservational characteristics and there is *almost* no duplication of elements. It must be noted, however, that an ischial shaft fragment of NHUMUK R1629 (Fig. 17) duplicates one of the two ischia associated with NHMUK R811 (Fig. 31B). The ischium fragment alone suggests that two commensurate and osteologically identical ornithopod skeletons must have been collected from a site that Dawson recorded as the same locality.

A very flattened and broken left ilium NHMUK R811(b) (figured by Norman, 2010: fig. 8C, D – but as a reversed image – see Fig. 30B, C) was claimed to be associated with material assigned to NHMUK R811 and R604 (Lydekker, 1890b: 263) and this duplicates a small portion of the preacetabular process preserved in NHMUK R1629 (Fig. 15). However, the association of the material referred to as NHMUK R811, R811(a) and R811(b) is compromised because: i. R811(a) – a partial right pubis was formerly assigned to *'I'. dawsoni* (Lydekker, 1888b: 199-200); and ii. The flattened ilium (NHMUK R811b) was not mentioned in Lydekker's first catalogue (1888b) but was later recorded as having been purchased separately in 1884 (Lydekker, 1890a: 264).

NHMUK R1148

Note. This specimen comprises four vertebral fragments from the dorsal column, a right femur, proximal right tibia and right metatarsal III. This material was assigned to *Iguanodon bernissartensis* originally (Lydekker, 1888b: 217), with the cautionary note that "these specimens might belong to *I. dawsoni*."

Vertebral column (Fig. 12). Two incomplete neural arches, each of which comprises a well-preserved platform and the sheared-off base of the neural spine. The first neural arch (Fig. 12, A1, A2) shows details of the rib articulation and the transverse process. The capitular facet (parapophysis – par) is large and positioned on the anterior half of the pedicel (adjacent to the prezygapophysis); its facet extends posterolaterally along the edge of the transverse process. The latter is elongate, robust and obliquely orientated when compared to the other example; its distal tip bears a diapophyseal facet. The postzygapophyses overhang the posterior margin of the neural arch and the neural spine is positioned posteriorly on the neural arch platform. All these features suggest that this neural arch comes from a relatively anterior position in the dorsal series (d4-d6) because the combination of features (position and size of parapophysis, robust and oblique transverse process and backward extension of the posterior zygapophyses) echoes the morphology in the posterior cervical-anterior dorsal section of the column.

<< INSERT FIGURE 12 NEAR HERE>>

The other neural arch (Fig. 12B) has a more discrete, almost circular, parapophysis tucked into the recess between the prezygapophysis (prz) and the base of the transverse process. The posterior margin of the parapophysis stands clear of the sidewall of the neural arch because there is a recess between it and the adjacent buttress for the transverse process. The transverse process is elongate, moderately robust and projects less obliquely from the neural platform; its distal tip forms a large, rugose facet (diapophysis - dia) for the tuberculum of its rib. The posterior edge of the transverse process forms a shelf that curves toward the base of the neural spine and merges with the anterolateral margin of the postzygapophysis (poz). The base of the neural spine rises from the midline and the anterior and posterior edges converge slightly before being abruptly truncated by breakage. The position of the parapophysis on the neural arch suggests that this was probably from a mid-dorsal vertebra (d7-d9).

The centra (Fig. 12A, B) have had their neural arches sheared away, rather than their being separated along an imperfectly fused neurocentral suture. The centra are generally spool-shaped, but the sides are compressed and distorted. The ventral edge of the centrum forms a narrow keel (k). The articular faces are flattened with a central concavity; the margins of the articular surfaces are everted, thickened and rugose as if for the attachment of powerful collateral ligaments. These centra appear, from their proportions, to have come from the anterior half of the dorsal series but probably never attached to the neural arches as shown here.

Femur. The majority of the right femur (Fig. 4B,C) is well-preserved, although it is damaged proximally and shows evidence of having been crushed along the length of the shaft and there is a depressed fracture on the shaft above the medial condyle (cr). The proximal end preserves part of a large, medially offset, globular, femoral condyle. The anterior trochanter (at) is notably thickened along its anterior edge and has a bevelled, rugose, anterolateral facet that extends distally on to the base of a prominent ridge that runs diagonally across the shaft of the femur to merge with the medial side of the distal condyle (Fig. 4B). The thickness of the anterior trochanter suggests that it would have masked the anterolateral portion of the greater trochanter. The shaft of the femur is angular and bowed along its length. There is a very large, heavily muscle-scarred, fourth trochanter (4t); the distal tip of the trochanter is slightly eroded and may originally have been very slightly pendant (but not as suggested in Lydekker's sketch (Fig. 4A). The overall shape of the femur and position on the shaft of the fourth trochanter is unlike that seen in camptosaur femora (Galton, 2009; pers. obs. USNM November 2010). The distal end of the femur is marked by a large extensor intercondylar groove (icg) that is nearly enclosed by overgrowth from the adjacent buttresses on the tibial condyles of the femur; again this morphology differs markedly from that seen in camptosaurs, in which the extensor intercondylar groove is deep, but broadly open (pers. obs. USNM November 2010).

So far as it can be compared to NHMUK R2848 (a femur that has been tentatively referred to *B. dawsoni* – Norman, 2011a) these femora appear similar in their shape and proportions and it is considered possible that NHMUK R2848 (femur and scapula – Norman, 2011a) may be referable to *H. fittoni*.

Tibia. This bone is represented by its proximal portion only. It shows an expanded articular region with two asymmetric condyles posteriorly, and the base of a robust (but broken) cnemial crest projecting anterolaterally. The shaft is stout and angular-sided and bears a large rugosity on its lateral surface that probably represents anchorage for ligaments that stabilized the proximal end of the fibula.

Metatarsal III (Fig. 11A-D). Is well preserved and large (310mm long), its proximal surface is very rugose, planar and triangular in proximal view (Fig. 11C): the apex of the triangle is directed posteriorly. The proximal surface was undoubtedly cartilage covered and probably provided an area for attachment of a flattened distal tarsal. The medial surface of the shaft faces obliquely posteromedially and the upper two-thirds is covered with rugosities (lig) reflecting the presence of powerful ligaments that bound the shaft of metatarsal II (NHMUK R1629: Fig. 11E, F). Approximately half way along the length of the metatarsal there is a distinct indentation (tab.sc) on its anteromedial edge for the attachment of a tab of bone that projects from the anterolateral edge of metatarsal II (Fig. 11E,tab). The proximal end of the shaft is also rugose laterally (for ligament attachment), and has a wedge-like form that fitted into a complementary recess that ran down the medial surface of the shaft of metatarsal IV. The anterior surface of the shaft of mtIII is concave along its length, and there is a distinct anterolaterally positioned thumbprint-shaped scar (sc). The distal portion of this metatarsal lacks ligament scars, which suggests that the metatarsal shafts diverged distally, allowing the toes to diverge when in extension. There is a smooth, slightly asymmetrical, pulley-like, articular surface (Fig. 11D), with depressed areas laterally and medially that are pitted and rugose from the attachment of collateral ligaments.

NHMUK R1148 (R1629)

Note. “An associated series of bones belonging to the same individual as the preceding [NHMUK R1148]; from the Wadhurst Clay of Hollington quarry” (Lydekker, 1890b: 262). All elements are commensurate and none are duplicates; the femur is a good match for that of NHMUK R1148, and metatarsal II fits neatly against metatarsal III of NHMUK R1148.

Pectoral girdle and forelimb

Scapula. Portions of left and right scapulae are preserved. The right scapula comprises just part of the blade, the proximal and distal ends having been sheared away. The left scapula (Fig.13) is reasonably well preserved, although the proximal (coraco-glenoid) end is damaged and the distal portion of the blade is missing. The blade is curved posteriorly and bowed medially (following the contour of the ribcage). The preserved part of the acromial buttress (ar) is a thick ridge, which is rugose along its apex and clearly curved forward into the base of the acromion. The external surface of the proximal end of the blade is concave between the acromial buttress and a portion of another thickened buttress above the scapular glenoid. There is also shallow depression (hr) adjacent to the margin of the glenoid (gl) that represents a ‘stop’ to limit the excursion of the lateral tuberosity of the humerus. The medial surface of the scapula is marked with ligament and muscle attachment scars (m/l.sc). The development of much of this scarring is probably related to the necessity for anchoring the shoulder girdle against the rib-cage in a facultatively quadrupedal animal. Along the scapulocoracoid suture (co.s) there is a well-marked notch that represents the mediodorsal continuation of the channel associated with the coracoid foramen. The overall similarity in morphology of this partial scapula to that described in the near complete scapula (NHMUK R2848) formerly referred to *B. dawsoni* (Norman, 2011a) is noted.

<< INSERT FIGURE 13 NEAR HERE>>

Radius and *Ulna* (Fig. 14). These two bones are nearly complete, although the ulna is crushed proximally. Both are similar in shape (although smaller and less robust) to those described in *Barilium dawsoni* (Norman 2011). The radius (Fig. 14A,RA) is 380 mm long and the element is expanded at both ends and tapers in the middle. The proximal articular surface is sub-circular, slightly concave and has thickened margins. The ventral edge of the shaft, adjacent to this articular surface, has a distinct channel (seen also in the associated forelimb of NHMUK R1831: Figs 38 & 40 which was first described and figured by Owen [1872:pl.I]). The main part of the shaft of the radius is roughly circular in cross-section and narrow, but becomes deeper and laterally compressed distally, where it articulates against the carpometacarpal block. The distal articular surface is convex and rugose. The adjacent surfaces of the shaft, particularly medially, are prominently ridged (rug). The ventral edge of the distal radius has an elongate facet (ul.f) for attachment to the dorsal edge of the ulna. There is another distinct rugose facet (m.sc) on the dorsal surface of the radial shaft about a third of the way from its proximal end and there is another distinct tubercle positioned more proximally on the medial surface of the shaft. The former tubercle may be the insertion site for *m. biceps* but, if so, it would be unusually distal in its location.

<< INSERT FIGURE 14 NEAR HERE>>

The ulna (Fig. 14A,UL) is 480 mm long, crushed and distorted, so the olecranon and associated articular areas for the humerus and radius are indistinct. A vertical 'flange' projects from the dorsolateral margin of the shaft proximally; this represents a displaced lateral shelf that formed the ventral part of an articular facet for the proximal end of the radius (ra.f). The originally medially positioned vertical wall of the ulna associated with this articular region has been crushed into the shaft of the ulna. Distally, a lateral ridge strengthens the ulnar shaft. The shaft tapers distally before re-expanding to contact the radius dorsomedially (part of this sutural surface is visible in Fig. 14C), and developing a convex distal surface that would have articulated against a recess in the proximal surface of the carpometacarpal block.

Phalanges. An almost perfect and large (160 mm from base to apex) right pollex (Fig. 15) displays what might be termed a classic 'Iguanodon' morphology, in the sense that it is similar to the 'nasal horn' first identified and illustrated by Mantell (1827: pl. XX, fig. 8).

Though generally conical in lateral/medial aspects (Fig. 15A,B), the anterior/posterior views (Fig. 15D,E) show that it was laterally flattened, although the extent of this may be exaggerated a little by post-mortem crushing. This morphology is unlike the more regularly conical pollexes reported in the geologically younger taxa *Iguanodon bernissartensis* (Norman, 1980) and *Mantellisaurus atherfieldensis* (Norman, 1986). It is also morphologically distinct from the abraded, but apparently truncated, pollex seen in the sympatric contemporary taxon *Barilium dawsoni* (Norman, 2011a: text-figs 18 & 19). The base of the pollex has a sinuous edge (Fig. 15A,B,C,F). The proximal 'articular' surface is concave and probably accommodated a disc-shaped proximal phalanx. Above its base, the sides of the pollex converge toward the tip; however, the posterior margin is longer than the anterior and the pollex was therefore naturally tilted forward, a feature that would have been exaggerated further by the oblique orientation of the distal articular surface of metacarpal I. The pollex is curved, slightly medially, along its length (Fig. 15D,E). An ungual (claw) groove is present along almost the entire length of its posterior margin (Fig. 15D c.gr) and although a similar groove is present along its anterior edge (Fig. 15F, c.gr), the latter is not so clearly defined.

<< INSERT FIGURE 15 NEAR HERE>>

A partial ungual phalanx of manus digit III is preserved in this collection. It is small (compared to the pollex), relatively more symmetrical and more laterally compressed than the corresponding phalanx in the manuses of *I. bernissartensis* and *M. atherfieldensis*, but is identified as a potential manus digit III ungual because of the longer and more twisted form of a very similar-sized ungual (probably from manus digit II) associated with NHMUK R1632.

A small phalanx possibly of digit II (ph. 2) is strongly asymmetric, as is typically of this phalanx (taking for comparison the general form of manus phalanges seen in *M. atherfieldensis*: Norman, 1986, 2011b, and in prep.) and might well be associated with this individual.

Pelvic girdle and hindlimb

Ilium. Represented by a small (230 mm long) fragment from the base of the preacetabular process of the left ilium (Fig. 16). This portion is transversely compressed, curves laterally and there is a shallow rugose indentation (srf) for the presumed articulation of the sacrodorsal rib, and a low-relief, curved medial ridge (mr). The dorsal edge of the ilium is laterally compressed, flat-topped, and has a band of blister-like rugae (m.sc) along its dorsolateral edge. Though extremely incomplete, this resembles the corresponding part of NHMUK R1635 (the holotype ilium of *H. fittoni* – Figs 3A,B; 9) and contrasts markedly with the corresponding region of the ilium of the sympatric contemporary *Barilium dawsoni* (Fig. 3C,D)

<< INSERT FIGURE 16 NEAR HERE>>

Ischium. The ischium is represented by a part of the shaft (Fig. 17). This shows the broken base of the obturator process (obt) and an associated curved ridge (ri) that extends distally on the medial side of the shaft (creating the characteristic 'twist' to the shaft). The lateral surface of the ischial shaft is marked by some roughened areas (m.sc) that probably represent muscle scars.

<< INSERT FIGURE 17 NEAR HERE>>

Hindlimb elements. Include the undoubted counterpart left femur (Fig. 18) to that of NHMUK R1148 (cf. Fig. 4). The differences in length (NHMUK R1148: 900 mm, NHMUK R1629: 860 mm) reflect the effects of breakage and compression in both specimens. The robust anterior trochanter (at), large, crested 4th trochanter (4t) curved, angular shaft and enlarged distal condyles are well-displayed. A poorly preserved proximal portion of the left tibia similarly complements that belonging to NHMUK R1148. A distal end of the right fibula is also preserved.

A well-preserved right metatarsal II (Fig. 11E-H) is transversely compressed proximally; it has a tab-like flap on its dorsolateral edge (tab) and has an obliquely offset distal articular surface that is slightly bicondylar (pulley-like) ventrally (Fig. 11H). It fits snugly against the corresponding surface of the third metatarsal (NHMUK R1148). A well-preserved proximal pedal phalanx (probably pedal digit II – Fig. 11I-N) resembles that of left pedal digit II (in comparison with *I. bernissartensis* and *M. atherfieldensis* – Norman, 1980, 1986) and articulates snugly with the metatarsal just described.

<< INSERT FIGURE 18 NEAR HERE>>

Some rib fragments are preserved in this collection; these include proximal portions that exhibit the wide separation or neck (n) between capitulum (cap) and tuberculum (tub) and angulation between the articular portion and the main shaft of the rib typical of anterior dorsal ribs (Fig. 25A,B). More posterior members of the series (Fig. 25C,D) gradually lose the distinct neck region as the capitulum and tuberculum begin to merge, and the shaft of the rib does not show the strong curvature seen in the anterior dorsal series.

NHMUK R1148 (R1632)

Note. Lydekker (1889) incorrectly identified broken cervical centra as sacrals. No specimens duplicate the holotype and these specimens were collected from the same quarry at “a short distance from [NHMUK R1148 and R1629], and almost certainly belong to the same individual” (Lydekker 1890a: 263).

Vertebrae. Cervical vertebrae (Fig. 19) are mostly badly crushed and sheared, and their neural arches are separated and broken. Individually they retain some characteristic cervical features: strong opisthocoely; thick and rugose ventral keels (k); anteroposteriorly expanded parapophyses (par) close to the margin of the anterior articular condyle and positioned on a lateral ridge on the side of the centrum; broad neural canal; neural arches with no obvious neural spine and long, hooked, divergent postzygapophyses (poz). The prezygapophyses (prz) are widely separated from the midline and the diapophyseal facets (dia) lie above and lateral to the parapophyses.

<< INSERT FIGURE 19 NEAR HERE>>

The dorsal vertebra is a crushed centrum that resembles in size and shape those associated with NHMUK R1148. The sacral vertebra comprises just a centrum (sheared off dorsally) and somewhat crushed dorsoventrally. It was clearly a sacral, judged by its general shape and remnants of intervertebral sacral rib attachments, but little else can be gleaned. The caudal vertebrae are similarly poorly preserved, having been crushed, distorted and broken (resulting in loss of the caudal ribs and neural arches). The more anterior in the series tend to have tall centra with sub-parallel sides, prominent haemal arch facets and caudal ribs placed adjacent to the neurocentral suture. More posterior caudal centra have a lower profile and more angular sides, with a slight ridge dividing the external surface horizontally, just above mid-height. Beneath this ridge, the sides converge upon a keeled area between the haemapophyses (chevron bone facets) that has a midline sulcus. The articular facets are oval and slightly depressed in their upper centre and the posterior haemapophysis is more prominent than the anterior. The posterior caudals are low, angular-sided cylinders with a prominent midline ridge laterally and the ventral surface is flattened, rather than sulcate.

Metatarsal III (right) is well preserved, but lacks its proximal half. It closely resembles the left metatarsal III of NHMUK R1148. This specimen is just slightly smaller than the latter (the width of the distal articular surface being 115 mm vs 120 mm in R1148) but the details of the surface features are identical.

Phalanges. A manus ungual closely resembles in shape that of digit II of the manus of late Wealden taxa such as *Iguanodon* (Norman, 1980) and *Mantellisaurus* (Norman, 1986, 2012) in being elongate, but flattened and twisted distally.

SKELETAL MATERIAL REFERABLE TO *HYPSELOSPINUS FITTONI*

*1. **NHMUK R604 & R604a***

A partial skeleton collected by Dawson from Hollington quarry (old specimen cards associated with this collection of bones indicate that it was collected at Ridge Farm quarry). Most of this collection represents the vertebral column: 1 cervical centrum and fragments of a neural arch, 12 dorsal vertebrae, 16 caudal vertebra, several fragmentary ribs and the proximal end of a chevron bone. Other associated remains include: 3 worn and somewhat damaged maxillary crowns, a well-preserved pollex ungual, a partial ulna and some bones of the pes. The specimen was initially referred to *Iguanodon dawsoni* by Lydekker (1888a,b), but a little later Lydekker (1889: 355) transferred it, without explanation, to *I. hollingtoniensis*.

Axial skeleton

The cervical fragments exhibit typical features such as opisthocoely of the centrum, a thick ventral keel and a parapophysis located, just posterior to the margin of the convex anterior articular surface, at mid-centrum height on a raised ridge located.

<< INSERT FIGURE 20 NEAR HERE>>

Dorsal vertebrae. The dorsal vertebrae are mostly well-preserved and comprise a series of 12 (close to a complete dorsal vertebral count of 16). The numbering system adopted here is for guidance only.

The most anterior of the preserved series is probably a 1st or 2nd dorsal [d1/2] (Fig. 20A-C). It retains a number of cervical morphological attributes: a low broad centrum, with a thick ventral keel and opisthocoely (and a modest convex anterior articular surface). Crucially (for positioning in the series) it has a large oval parapophysis (par) on the ventrolateral surface of the neural arch pedicel (clearly above the neurocentral suture - ncs). The transverse processes are robust and angled obliquely dorsolaterally. The prezygapophyses (prz) are separated from the midline by a shallow embayment and do not project forward; this is a standard configuration seen in cervicals (Fig. 19A,B). The pedicels that support the postzygapophyses (poz) are elongate and therefore overlap the succeeding vertebra substantially and the neural spine (ns) is posterodorsally inclined. Unfortunately, the spine is broken so its actual length is unknown. Neural spine length may have been substantial, judged by the shape of its base, and the spine length attained by succeeding dorsals).

<< INSERT FIGURE 21 NEAR HERE>>

The next in the series is probably a 3rd dorsal [d3] (Fig. 21). It resembles the former in that the centrum is comparatively low and broad, retains slight opisthocoely, though its anterior face is slightly concave

(Fig. 21C). The ventral keel (k) is thick, albeit narrower than the previous example (Fig. 20). The parapophysis (par) is smaller and positioned higher on the neural arch pedicel above the neurocentral suture (ncs) than in the previous example. The prezygapophyses (prz) project anteriorly, are closer together on either side of the midline and the articular faces are more steeply inclined (Fig. 21C). The transverse processes are robust, elongate and dorsolaterally directed, terminating in a well-developed tubercular facet (dia); the anteroventral surface of the transverse process is scarred (rs) by ligaments that helped to anchor the neck of the dorsal rib. The postzygapophyses (poz) do not overlap the succeeding vertebra so extensively as in the previous example and the neural spine (ns) is little damaged showing it to have been remarkably tall, slender and obliquely inclined (rising to a rugose, slightly expanded, apex).

<< INSERT FIGURE 22 NEAR HERE>>

The 4th dorsal [d4] (Fig.22) is less complete, but continues the morphological transition: the centrum is taller than wide, the ventral keel (k) is narrower (Fig. 22B), the anterior articular surface of the centrum is gently concave (Fig. 22C, the posterior half of the centrum is not preserved). The parapophysis is positioned higher on the pedicel, so that its upper border is now adjacent to the top edge of the prezygapophysis (Fig. 22A) and the transverse processes are massive, ligament scarred (rs) but less upswept than in the previous example.

<< INSERT FIGURE 23 NEAR HERE>>

Dorsals 7th/8th [d7/8] and 9th/10th [d9/10] (Fig. 23) have centra of a more rectangular outline and smaller, more rounded parapophyses (par) compared to previous examples. The parapophysis (par) can also be seen to commence its lateral migration along the transverse process. These centra have a narrow keel and have shallowly concave articular surfaces (and the 7th/8th example [Fig. 23A] is most similar to the dorsals of the holotype NHMUK R1148: Fig. 12). Judged by their shape these centra (particularly d7/8) resemble 'keystones' at the centre of the span of an arched dorsal series. Centrum [d9/10 – Fig. 23B] is leans more posteriorly and has rather thicker and more prominent articular margins.

The 9th/10th dorsal (Fig. 23B) includes a substantial portion of its neural spine. The transversely process is less robust. The centrum is has thickened, rugose articular margins.

<< INSERT FIGURE 24 NEAR HERE>>

The most posterior dorsals (in the range d13-16: Fig. 24) have substantially larger, almost circular, articular faces; the anterior articular face of the centrum is shallowly concave, while the posterior face has become more obviously opisthocoelous. The articular margins of the centra form thickened rims that are more flared than previous examples. The centra also lean posteriorly. The last preserved dorsal (probably d16) has a more regular rectangular profile (Fig. 24C-C3) and is anteroposteriorly compressed compared to the previous two examples and has an almost circular articular face (C1). A ventral keel (k) is present in the first two examples, but is lost in the most posterior in the series (Fig. 24C2). The parapophyses (par) are small, forming something akin to a 'notch' on the leading edge of the transverse processes. The transverse processes are less robust than earlier dorsals, horizontally directed as well as twisted along their length such that the dorsal surface faces anterodorsally (Fig. 24).

<< INSERT FIGURE 25 NEAR HERE>>

Associated dorsal ribs. A few examples of partial dorsal ribs (NHMUK R604a) are illustrated (Fig. 25). The larger examples (Fig. 25A,B) are representative of those from the anterior of the dorsal series. They have robust shafts with a well-marked longitudinal ridge (ar) running down the anterolateral margin; this probably reflects the attachment area for the intercostal ligaments and musculature. The articular rib heads: capitulum (cap) and tuberculum (tub) are prominent and separated by a distinct ligament-scarred neck (n – reflecting the wide separation of parapophyses and diapophyses seen in the anterior dorsal series). Two more posterior dorsal ribs (Fig. 25C,D) are preserved and have more slender rod-shaped shafts and rib heads that are smaller and connected via a ligament-scarred ridge; this shows that the entire articular region (incorporating capitulum, tuberculum and intervening neck) was securely fastened to its transverse process.

<< INSERT FIGURE 26 NEAR HERE>>

Caudal vertebrae. The caudals in this collection include examples from the anterior, middle and posterior sections of the tail, each of which have their own distinctive features that are generally indicative of progressive changes in shape along the length of the tail. The anterior caudals (Figs 26-27) include one with an intact neural spine of considerable height.

The most anterior caudal preserved (c2) has, when compared to others in the series, a relatively elongate centrum (Fig. 26,A), which is slightly anteriorly inclined (more so dorsally). Its anterior articular face (Fig. 26,A1) exhibits a modest convexity dorsally and shallow concavity ventrally (which is similarly reflected in the morphology of the posterior face: Fig. 26,A2). The centrum lacks an obvious haemal arch facet anteriorly, but a slight crease on the posteroventral rim (Fig. 26,A3) may indicate a haemapophysis (articular facet for a diminutive 1st haemal arch). The ventral surface of the centrum displays a pair of shallow sulci separated by a smooth midline keel and flanked laterally by similarly smooth ridges (Fig. 26,A3). The neural spine is broken off, but the prezygapophyses (prz) are anterodorsally directed prongs (Fig. 26,A4). The neural arch is squat and has very thick pedicels that enclose a relatively narrow neural canal. The pedicels flare laterally where they are fused to the bases of robust caudal ribs (cr), which are also sheared off.

<< INSERT FIGURE 27 NEAR HERE>>

Succeeding caudals (Figs 26B-28) show a graduated series of changes: the centra become initially more axially compressed, the chevron facets (cf) become far more prominent on the anterior and posterior ventral rims, and the articular faces of the centrum tend to shift from an almost circular outline to more dorsoventrally elongate (Fig. 27). One of these caudals [?c5] (Fig. 27) is well preserved, apart from relatively minor fracturing, displaying the full development of the caudal rib and structure of the neural spine. The latter is very elongate, slightly sinuous in profile and leans posteriorly; the lower half of the spine has thickened lateral flanks that are separated by grooves from midline ridges anteriorly and posteriorly (asr, psr).

<< INSERT FIGURE 28 NEAR HERE>>

Farther behind the anterior caudals, the centra become more elongate, have less oblique prezygapophyses (Fig. 28) and progressively less prominent caudal ribs. Later caudals become generally more rectangular in form and lose the prominent anterior chevron facet, as they also lose the caudal rib, which becomes reduced to a ridge on the side of the centrum. Posterior caudals (Fig. 29) become lower, lose the elongate neural spine and, in proportion, their centra become more elongate and develop a hexagonal cross-section and a shallow ventral midline sulcus; these features are well displayed in NHMUK R1148 [R1632]: Fig. 29B,C). The middle and posterior caudals of NHMUK R604 are indistinguishable from those attributed to the holotype (NHMUK R1148 [R1632]).

<< INSERT FIGURE 29 NEAR HERE>>

2. ***NHMUK R811*** (incorporating NHMUK R811a & R811b)

Note. Originally assigned to *Iguanodon dawsoni* by Lydekker (1888a,b), these specimens, collected from the Hollington quarry, comprise a dorsoventrally compressed sacrum, two nearly complete ischia, the left ilium (R811b, badly crushed and broken with pieces missing) and an incomplete right pubis (NHMUK R811a). The sacrum (NHMUK R811) and ilium (NHMUK R811b) were illustrated first by Norman (2010: fig. 8).

Sacrum. Comprises a fused row of vertebral centra that have been dorsoventrally crushed (Fig. 30A). The dorsal region (Norman, 2010: fig. 8B) reveals the sheared bases of the neural arch pedicels, the neural canal as well as the position of the bases of the sacral ribs. Ventrally (Fig. 30A) the enlarged sacrodorsal vertebra (sd) has neural pedicels clearly positioned in the middle of the centrum (rather than in the intercentrum position seen in succeeding sacrals) and a smooth articular anterior surface for the preceding dorsal. The centrum seems to have had a broad, un-keeled ventral surface compared to succeeding sacrals.

<< INSERT FIGURE 30 NEAR HERE>>

Five ‘true’ sacrals are firmly fused together behind the sacrodorsal. The junctions between each of the centra are clearly thickened and there appears to have been a modest midline keel (k) present on each centrum. The bases of intervertebrally positioned sacral ribs (sr) can be seen, and the last of the sequence preserved retains an intervertebrally positioned sacral rib. The latter centrum has a posterior articular face that is rugose, indicating that at least one further sacral centrum would have been present originally. This additional (last) sacral did not bear an intervertebrally positioned sacral rib, judged by the absence of rib ossification marks on the posterodorsal margin of the last preserved sacral. Allowing for the effects of crushing, the form and proportions of the posterior sacrals seen in this example appear generally similar to those observed in the holotype (NHMUK R1635: Fig. 7).

Ilium. Though crushed and broken, some diagnostic features can be seen (NHMUK R811b: Fig. 30B,C). As seen in the holotype (NHMUK R1635: Figs 3, 9) the blade of the ilium is narrow dorsally, flat-topped and the preacetabular process (prp) is laterally compressed in cross-section and slightly dorsoventrally bowed axially. There is a low, oblique ridge (mr) on the medial surface of the preacetabular process, which is linked to a small facet for the attachment of the ‘free’ rib of the adjacent sacrodorsal vertebra. The remainder of the blade was relatively flat with a straight dorsal margin. The postacetabular blade is missing. What is preserved is comparable in all respects to that of the holotype of *H. fittoni* (as well as the far better preserved ilium of NHMUK R1834: Fig. 46) and this morphology is entirely distinct from that of the sympatric contemporary *Barilium dawsoni* (Fig. 3C,D). In the latter taxon (Norman, 2011a) the preacetabular process is stout, transversely expanded and has a pronounced medial ridge and an enlarged sacral rib facet (clearly visible laterally within the embayment between the preacetabular process and pubic peduncle). The dorsal edge of the ilium is also considerably thicker and rounded transversely.

Pubis. The right pubis (NHMUK R811a: Fig. 31A) is incomplete but comprises part of the acetabular margin (ac) and iliac peduncle (il.p), a significant portion of the prepubic process (ap) and the base of the pubic shaft (p.pu). The prepubic process is deep and blade-like, with a thick dorsal edge and a thinner ventral edge. The upper edge of the blade, which is more complete than the lower, curves anterodorsally, hinting at the presence of either a dorsoventrally expanded distal tip to the blade (as in *Mantellisaurus*: Norman, 1986), or that the prepubic process is deep but parallel-sided and bowed dorsally (vaguely resembling that of *Camptosaurus*: Dodson, 1980). The pubic shaft is rod-shaped, being roughly circular in cross-section; the preserved portion gives the impression that, when complete, it would have been shorter than the length of the shaft of the ischium. The preserved portion also shows the remnant of a dorsally directed, finger-shaped process; this would have formed, along with the posterior lip of the acetabular margin, the posterodorsal margin of the obturator foramen and its associated channel (obt.c). This structure also provided a sutural surface for the pubic peduncle of the ischium. The proximal portion of the pubic shaft differs markedly from the equivalent area of the pubis of the sympatric contemporary *Barilium dawsoni,* which is dorsoventrally flattened and strap-like.

<< INSERT FIGURE 31 NEAR HERE>>

Ischium. Both ischia are well preserved and virtually complete (NHMUK R811: Fig. 31B). The proximal end is mostly transversely compressed, and broadly Y-shaped where it contributes to the margin of the acetabulum. The anterior portion (pubic peduncle - pp) forms a narrow and abruptly truncated blade that contacts the pubis, and the dorsal edge of the ischium near the articulation forms a small, triangular acetabular facet. The posterior portion of the proximal end of the ischium expands to form a rugose, everted and dorsally flattened, iliac peduncle (il.p). There is a prominent obturator process (obt) projecting from the medial edge of the proximoventral part of the shaft and a ridge originates at the distal base of this process. The latter ridge curves across the medial surface of the shaft, as it extends distally, from the anterior to the posterior edge of the shaft, creating the impression of a twist to the shaft that is only visible medially (*contra* Lydekker, 1888a: 50). The shaft of the ischium is comparatively stout and its proximal portion is flattened laterally (rather than longitudinally ridged as in *Barilium dawsoni*), has a J-shaped profile and its distal tip forms an anteriorly expanded 'boot' (Fig. 31B, ib).

3. ***NHMUK R33***

First noted by Lydekker (1888b: 226) as a partial skeleton collected from Hollington quarry in 1888 (and purchased by the NHM in the same year) pertaining to "*Iguanodon* sp." A year later Lydekker (1889: 356) was unable to decide whether this specimen "belongs to *I. Fittoni* or *I. hollingtoniensis*." However, in 1890 he referred this skeleton to *Iguanodon hollingtoniensis* (Lydekker, 1890a: 43, 1890b: 262).

This skeleton is associated with older specimen cards that record the locality from which it was collected (by Mr Lee) as 'Little Ridge quarry, Hollington'. It comprises two dentary fragments with remnants of several embedded teeth and three well-preserved isolated dentary teeth; ~44 vertebrae, most of which are poorly preserved (4 cervicals, 10 dorsals and approximately 30 caudals); a partial scapula and coracoid, ulna and radius, a partial carpal block, 2 metacarpals and 5 phalanges of the manus; the proximal part of the right preacetabular process of the ilium, a partial femoral shaft, an isolated astragalus, 3 partial metatarsals and 4 phalanges of the pes.

This individual is commensurate with NHMUK R1148 [the holotype of I*. hollingtoniensis*] and its preservational condition is similar to that of the type material and comprises only complementary parts of the appendicular anatomy. The vertebrae resemble those described in the holotype, as well as those in the referred specimen NHMUK R604 (above).

<< INSERT FIGURE 32 NEAR HERE>>

Dentary teeth. Two pieces of dentary ramus (one is narrower and represents a more anterior part of the dentary ramus than the other) display broken fragments of 11 teeth. In addition, three isolated dentary teeth (Fig. 32) comprise two worn crowns (left and right): the right tooth (Fig. 32A) has a long, angular-sided, tapering root and a rather damaged crown, while the other (B) has lost its root but displays more clearly some of the key features; the third tooth (C) is fully-erupted (the root appears to be well mineralized) but not yet worn, tooth that was probably positioned nearer to the front (or possibly the rear) of the dentition because it is smaller than the other two crowns.

Enamel can be seen clearly to be restricted to the lingual surface of the crown, and is distinctively sculpted (Fig. 32B,C). There is a distally offset primary ridge (p), which subdivides the crown into two unequal sectors. The distal sector is shallowly channelled and has a number of narrow, strand-like, ridges (st) of enamel running down this surface and this sector is bordered distally by a coarsely denticulate margin (dm). The marginal denticles on the sides of the crown form ledges that wrap around the edge of the crown and bear small irregular mammillae. Denticles on the occlusal margin are simple cusps. The distal corner of the crown bears a thick 'rolled' structure (inr) that has a cluster of small denticle ridges (Fig. 32B) confirming the impression of the distal corner of the crown having been literally rolled. This structure creates an oblique ledge or 'cingulum' (cin) above an elongate recess on the distal side of the root-crown interface. This recess accommodated the mesial edge of the crown of the adjacent successional tooth.

Mesial to the primary ridge of the crown a broader sector of the crown is again channelled, but partially subdivided by a broader raised area that is traversed numerous narrow, strand-like, enamel ridges. The mesial edge of the crown is coarsely denticulate and produces a thickened, but unrolled, oblique ledge (‘cingulum’) that converges on the central lingual portion of the crown/root junction. The smaller dentary crown has similar general features but there are fewer strand-like enamel ridges and the mesial sector of the crown is less obviously subdivided by a low and broad ridge.

The root to the crown has angular sides that form channels (ch) to accommodate the closely packed replacement crowns. The well-developed root (Fig. 32A) displays an eroded recess (cr) in the area where a replacement crown is positioned as it grew within the alveolus. The morphology of the enamelled surface of dentary crowns (see also NHMUK R1831 – Fig. 37) is distinct from dentary teeth referred to *Barilium dawsoni* (NHMUK R2357: Norman, 2011a)

<< INSERT FIGURE 33 NEAR HERE>>

Vertebrae. Representative vertebrae from the dorsal series include comparatively upright middle dorsal vertebrae (Fig. 33A) similar to those of the holotype, as well as those that show an oblique (parallelogram-like) form, which resemble the range of profiles seen in the dorsal series of NHMUK R604 (Figs 20-24). In addition, some of the anterior caudal vertebrae (Fig. 33B) retain partial neural spines that are axially narrow and exhibit the very characteristic slot-and-ridge (asr) structure on their anterior margin. The ventral surfaces of anterior caudals – those supporting caudal ribs – tend to be transversely convex (though often punctured by numerous vascular foramina: Fig. 34A, vf), while mid-caudals ((Fig. 34B,C, caudal rib absent) bear a midline sulcus (sul) between chevron facets (cf).

<< INSERT FIGURE 34 NEAR HERE>>

Appendicular elements. An imperfect right coracoid shows the presence of an externally discrete coracoid foramen that is separated from the scapulocoracoid articulation. A portion of the left carpal block is preserved and indicates (based on the smooth structure of the distal metacarpal articular surface) that the pollex had the potential to move against the metacarpal block. A portion of the preacetabular process of the ilium is also preserved and exhibits the laterally compressed form, narrow flat-topped dorsal margin, shallow lateral concavity and minor medial ridge that is typical of other examples referred to *H. fittoni*.

*4. **NHMUK R1627***

This specimen comprises a partial scapula, shaft of the left humerus, distal end of an ulna, central portion of a right ilium, an incomplete right femur, distal ends of left and right tibia, a complete right metarsal III, and 3 anterior caudals. These were collected from a quarry at the village of Brede (Fig. 1) northeast of the minor anticline. This specimen was originally referred to *Iguanodon dawsoni* by Lydekker [1888b] because of its large size. The bones are representative of an individual roughly commensurate with *Barilium dawsoni*, the osteology is however more typical of that seen in *H. fittoni*. What can be seen of the femur suggests that it is extremely massive (and comparatively short), but it is unfortunately very broken and eroded both proximally and distally, as well as being still embedded in matrix and is not particularly informative. The femoral shaft is transversely broad and somewhat flattened longitudinally giving it an angular cross-section, and a proximal portion of the extensor intercondylar groove is visible. The caudal vertebrae do not exhibit any of the unique features described in *B. dawsoni* (Norman, 2011a). The forelimb bones are generally large and robust, but do not differ from those seen in large-bodied ornithopods. Perhaps most significantly, the preserved central portion of the ilium (Fig. 35A) has a transversely compressed dorsal margin and the base of the preacetabular process is shallowly concave both vertically and anteroposteriorly. There is also no indication of either a transversely expanded medial ridge or a prominent sacral rib facet at the base of the preacetabular process, as observed in

Barilium dawsoni (NHMUK R802: Fig. 3C,D). This partial ilium appears to represent a larger and more robust version of several ilia referred to *H. fittoni*. It is also quite comparable to, and only slightly larger than, that of NHMUK R1636: Fig. 35B) which similarly comprises just a central portion of the ilium. The other associated bones are not taxonomically diagnostic beyond being clearly referable to a large ornithopod.

<< INSERT FIGURE 35 NEAR HERE>>

5. ***NHMUK R1636***

This specimen is a poorly preserved central portion of a right ilium (Fig. 35B) that has been the source of some confusion. Lydekker (1890a: 42) reported "an imperfect left ilium (No. R.811b), which although much broken and flattened … is represented in fig. 1E." The specimen illustrated as figure 1E, even though only a simple line drawing is clearly NHMUK R1636. Furthermore this specimen, collected from the Shornden locality by Dawson, was incorrectly associated by Lydekker (1890b: 264) with a partial skeleton (NHMUK R2357) collected from the West Marina locality (Norman, 2011a: text-fig. 3). NHMUK R2357 is not associated with NHMUK R1636; it was collected from an entirely different quarry and is itself an important specimen that has been referred to *Barilium dawsoni* (Norman, 2011a).

NHMUK R1636 is the central portion of the ilium, comprising the base of the preacetabular process, the pubic peduncle (pp) and part of the acetabular margin (ac), but lacks the entire postacetabular process. The dorsal margin of the ilium is slightly sinuous in profile, transversely compressed and flat-topped, and its lateral edge bears a strip of blister-like rugosities (m.sc). The preacetabular process is laterally compressed, shallowly concave and its structure suggests that the process when complete would have swung laterally and bowed gently ventrally, but was not notably axially twisted. The medial side of this process bears a small rugose sacral rib facet and a low, oblique medial ridge. The pubic peduncle is nearly complete and bears a prominent supra-acetabular crest (sac).

This specimen is very similar in all respects to other ilia attributed to *Hypselospinus fittoni* and differs significantly from those attributed to the sympatric contemporary taxon *Barilium dawsoni* (NHMUK R802, R4746, R3788 [left]: Norman 2011a) particularly in respect of the morphology of the dorsal margin of the ilium and the base of the preacetabular process.

6. ***NHMUK R1831*** (incorporating NHMUK R1832, R1833 and R1835)

Note on the original discovery. Samuel Beckles collected this important associated skeleton from a small excavation site (~3m x 5m – Fig. 1) on the intertidal seashore 2 miles west of St Leonards (Owen, 1872). The original report of the discovery of a partial skeleton (consolidated in this account under the number NHMUK R1831) by Owen alluded to the difficulties encountered by Beckles when excavating these remains. The material was so poorly consolidated that several bones were destroyed while they were being excavated (Owen, 1872: 1). The remains that were retrieved received immediate, but not necessarily expert, treatment (as reported in an extract of a letter from Beckles to Owen): "The bones were imperfectly mineralized and could only be secured by plaster of Paris … I applied the plaster with my own hands; but as the weather was severe … I was compelled to leave the manipulation of more than one bone to my navvies, and consequently one femur was destroyed, one jaw, one humerus, and one tibia, nearly destroyed." (Owen, 1872: 1). The dentary (NHMUK R1831: "one jaw … nearly destroyed") shows signs of having been damaged during collection (Fig. 36). It is extensively fractured, somewhat crushed and distorted, as well as showing signs of having been repaired.

Note on the registered material. NHMUK R1831 comprises a dentary (right) with several *in-situ* and isolated teeth, 54 vertebrae (comprising 3 cervicals, 14 dorsals, 1 sacrodorsal, 3 sacrals, 33 caudals [registered as R1833]). The appendicular skeleton is represented by a pair of fused sternals [registered as R1835]; the distal end of humerus and a radius fragment [both incorrectly labelled R1836]; a nearly complete right radius and ulna with a partial fused carpometacarpal block and detached pollex spine as well as a left pollex that is completely fused to a partial carpometacarpal block [registered as R1832]. Nine fragments (some complete) of metacarpals II-V, 13 manus phalanges [most of which are labelled R1832]. In addition there are two manus ungual phalanges and one partial phalanx [registered as R1833]; three partial metacarpals and one phalanx, although unlabelled, are of the exact same preservational condition and also bear Beckles' 'blue shield' tag that is seen on several specimens in this collection. An ischium (proximal right), pubis (right) including most of the preacetabular ramus and acetabular margin [registered as R1832]; both of these latter specimens are still embedded in plaster-of-Paris jackets. Two femora [one labelled R1833] both damaged, one is more complete but badly shattered and lies on a bed of plaster-of-Paris and two incomplete tibiae. Three of these hindlimb elements specimens are also incorrectly labelled R1836. The tarsus and pes are represented by an astragalus, calcaneum and a distal tarsal, four incomplete metatarsals, 14 pedal phalanges (including three apparently pathologically distorted unguals [labelled R1833]: see Figure 41).

Sauropod dinosaur. It should also be noted, in passing, that two other angular-sided and elongate shafts of long bones (both incomplete antebrachial elements) are also registered with the associated skeleton NHMUK R1831. The preservational condition differs from that of the ornithopod, and it is not clear whether these specimens were found at the same location.

Dentary (Fig. 36). This specimen was described and illustrated originally by Owen (1874: pl. I, fig. 1). It was recognised as potentially indicative of a new Wealden taxon (Paul, 2008: 192) and was later (Paul, 2012) designated as part of a dubious composite 'holotype' of *Darwinsaurus evolutionis* (see Norman, 2013). Norman (2010: fig. 10B) sketched the specimen and referred it to *Hypselospinus fittoni*. McDonald, et al. (2010: 3) reviewed the taxonomic status of NHMUK R1831. They concluded that this specimen could not be referred to their new taxon *Kukufeldia tilgatensis*, which was also based on a large, tooth-bearing dentary, for detailed anatomical reasons; however, the lack of anatomical overlap with contemporaneous holotypes (*H. fittoni* and "*I. hollingtoniensis"*) made it impossible to refer NHMUK R1831 to *Hypselospinus* with confidence.

<< INSERT FIGURE 36 NEAR HERE>>

Teeth. The remnants of crowns of 15 teeth are preserved in varying states of eruption in the dentary of NHMUK R1831 (Fig. 36A); none are part of the occlusal dentition, which supports the suspicion that significant damage was done to the dentary and its associated dental magazine during excavation. One isolated worn maxillary crown is also preserved (Fig. 37B) and was figured by Owen (1874: pl. I, figs 2-4). Another unworn, but shattered, dentary crown is also preserved (Fig. 37A).

Dentary teeth. In lingual view (Figs 36A, 37A,C-E) the enamelled faces of the crowns preserved in the dentary are bowed labially and slightly recurved, broad and shield-like (all these features are consistent with those seen in the isolated crowns of NHMUK R604). The margins are fringed by curved, tongue-like denticles that are simple conical points along the broad coronal edge of the crown; along the mesial and distal margins of the crown these denticles become labiolingually expanded to form oblique ledges that wrap themselves around edges of the crown. The edges of these denticle ledges are irregularly mammillated (Fig. 37E, m). The base of the distal denticulate edge of the crown is rolled (mesiolingually) creating an oblique cingulum-like ledge (as described in NHMUK R33: Figure 32B) so far as can be judged by the form of the broken base of one, potentially functional, crown.

The large unworn crown is more complete than those seen in NHMUK R33 (Fig. 32) but is similar in morphology (Fig. 37 A, C-E). The enamelled face of the crown is bisected unequally into distal and mesial sectors dominated by a distally offset primary ridge (p). The edge of the primary ridge is characteristically flattened in better-preserved examples. The mesial sector of the crown is divided into two very shallow channels by a broad secondary ridge that runs parallel to the primary ridge. The coronal edge of the enamelled face bears a row of parallel ridges (r) that extend down the crown surface from the small, conical, coronal cusps.

Most of these comparatively minor ridges merge into the crown surface, but a few form longer ridges of enamel (st) that run roughly parallel to the mound-like secondary ridge.

Maxillary teeth referable to this taxon are, to date, only represented by rootless eroded crowns (NHMUK R1635: Fig. 5C; NHMUK R33; and NHMUK R1831: Fig. 37B, and Owen, 1874: pl.1, figs 2-4). These crowns are narrower and more lanceolate than dentary crowns. The labial surface is thickly enamelled, has a very prominent distally offset primary ridge and is framed by thickened mesial and distal edges that bear labiolingually expanded, ledge-like denticles. The distal sector between the primary ridge and distal edge forms a smooth elongate channel with no (or at most one) strand-like enamel ridges. The somewhat broader mesial sector has between two and five well-developed narrow ridges that run sub-parallel to one another, but generally converging as they approach the coronal margin of the crown.

<< INSERT FIGURE 37 NEAR HERE>>

Dentary: form and preservation. In medial view (Fig. 36A) the dentary symphysis (Fig. 36C,ds), though partially crushed and distorted, can be judged to have been essentially horizontal and there is the remnant of a ‘slot-and-lip’ structure toward its posterior end (Fig. 36A,sl) that served to lock adjacent dentaries together. Farther anteriorly (beyond and lateral to the symphyseal surface) there is a short, smooth, finger-like projection (pr) that articulated against the lateral edge of the pedicel of the predentary. The upper surface of this projection curves posterodorsally, and forms a laterally compressed edge that supported and was ligamentously bound to the medial side of the lateral arm of the predentary. Ventromedial to this projection, the ventral surface of the dentary adjacent to the symphysis is shallowly arched for attachment of the flap-like ventrolateral predentary process. In medial view (Fig. 36A) the dentary ramus displays an adductor fossa that is extensive but matrix-plugged (m) posteriorly; anteriorly this narrows to form a shallow Meckelian groove (Fig. 36A, mgr). Part of a sutural facet for the splenial/prearticular (sf) is preserved on the medial wall of the dentary.

The anterolateral edge of the dentary extends posteriorly for a short distance as a transversely compressed broken edge; however, the upper edge of the dentary is sheared off farther posteriorly and this broken zone (br) extends for more than one third of the length of the dentary ramus (Fig. 36B,C). It is nevertheless possible to observe broken remnants of crowns represented by blocks of dentine fabric (tf) embedded in the alveolar bone in this area. Tooth-bearing alveoli extended into this region and this interpretation is confirmed by the presence of a sub-alveolar vascular channel immediately ventral to this area (Fig. 36A,vc). It is clear that there was likely to have been a comparatively modest diastema, which accords with the proportions of this same region in the fragmentary jaw preserved with NHMUK R1834 (cf. Fig. 44). Breakage and shattering (excavation-related) affects the upper part of the dentary to the extent that all of the functional dentition is missing.

The extent of the damage to the dentary and its dentition creates the impression of an elongate edentulous region (analogous to the mammalian diastema) between the presumed location of the posterior margin of the predentary and the onset of the dental magazine, this is an illusion (see the ‘note’ below). The only remnant of the true alveolar margin is found as a short row of scallops (moulded to support the labial sides of fully erupted teeth) that are preserved near the posterior end of the dentition (Fig. 36B, am); these scallops indicate the true level of the upper edge of the dentary. Fracturing and crushing makes it impossible to confirm the author’s suspicion that the dentary ramus was gently arched toward the symphysis, as is the case in an incomplete, less distorted, dentary ramus (Fig. 44) that is also referred to this taxon.

The coronoid process (cp) is positioned off-set laterally and adjacent to the posterior alveoli (Fig. 36A,C). The coronoid process (which is eroded and incomplete dorsally) was probably separated from the body of the dentary at the time of excavation and re-attached by plaster-cement. It may also be noted that the coronoid process, as illustrated in Owen (1874), appears to be substantially taller and also had two dentary crowns attached by matrix. This process (Fig. 36, cp) now appears to be relatively short and oblique (especially by comparison to that seen in NHMUK 28860 – the holotype of *Kukufeldia tilgatensis* McDonald, Barrett

& Chapman, 2010, and referred to *Barilium dawsoni* (Norman, 2010: fig. 10C; 2011a: 188; 2013).

Note on the morphology of the dentary. In the original lithograph (Owen, 1874, pl.1, fig.1) the dentary and dentition of NHMUK R1831 are fully illustrated. A small tooth, structurally atypical and positionally anomalous, is shown projecting from the dentary adjacent to the most anteriorly positioned of the securely embedded replacement crowns. This small tooth (Norman, 2010: fig. 10A, at) resembles those positioned at the extreme ends of the dental magazine: crowns become smaller and more bowed (*e.g.* Norman, 1980: fig. 19; 1986: figs 19, 21) and see also the proportions of the smaller dentary crown of NHMUK R33 (Fig. 32). The transition in size and shape of teeth along dental magazines is, in all instances so far known, a gradual one, rather than extremely abrupt as depicted in the Owen lithograph. It is considered most probable that the small crown was found loose in the sediment nearby and placed in this position on the jaw during the hasty restoration/conservation of the jaw that took place at the time of its excavation. When first examined by the author in the mid-1970s, this lower jaw preserved no trace of this enigmatic small tooth.

A note on taxonomic names associated with NHMUK R1831. The right dentary (Fig. 36) as well as some associated forelimb elements belonging to the same individual were reinterpreted by (Paul, 2008). Using Owen's (1874: pl. I, fig. 1) illustration of this dentary, it was noted that in "the dentary of BMNH R1831 … the ventral diastema is so long, and the tooth row so short, that it is reminiscent of the long-snouted hadrosaurid *Edmontosaurus (Anatotitan) annectens*." (Paul, 2008: 208). A little earlier in the same article it was stated that the "dentary BMNH R1831 is very elongate, matching or exceeding that of the *D[ollodon] bampingi* holotype. Anterior elongation of the dentary combined with a tooth row that is, in contrast to the great length of the mandible, much shorter than that of any other iguanodont (a consequence of both the tooth position count and the reduced size of the anterior teeth), produce a diastema that is much longer than any other iguanodont" (Paul, 2008: 205). As a consequence he concluded that a "set of remains [NHMUK R1831] of similar age to *I. fittoni* and *I. hollingtoniensis* appear to combine a specialized, elongate dentary with massive arms: it either belongs to one of the contemporary taxa, or is a new, unnamed taxon" (Paul, 2008: 192).

In 2012 Paul created *Darwinsaurus evolutionis* for this specimen and some associated (as well as some unassociated) skeletal elements that were designated as the holotype of his new taxon: "NHMUK R8131[sic]/1833/1835/1836" (Paul, 2012: 124). Careful examination of NHMUK R1831 refutes all of the anatomical claims and interpretations of Paul (2008, 2012).

In summary it can be stated categorically that the taxon *Darwinsaurus evolutionis*, as constituted and diagnosed by Paul, is a nomen dubium and that the taxonomic name should be suppressed (Norman, 2013). The material designated as the holotype of this taxon is a composite of skeletal remains collected from two localities of different geological ages: the coast at St Leonards (Valanginian) and the Isle of Wight (Barremian). The specimens that form the alleged 'holotype' can be referred respectively to *H. fittoni* (NHMUK R1831, R1833, R1835) and *Mantellisaurus atherfieldensis* (NHMUK R1836).

The forelimb of NHMUK R1831. Owen (1872: pls I-III) illustrated and reconstructed a substantial part of the forelimb of the skeleton collected near St Leonards (Figs 38-40).

The *radius* (Fig. 38, RA) is slightly flared proximally, creating a planoconcave articular face with everted margins for the lateral epicondyle of the humerus. There is a cleft region ventrolaterally, associated with the facet for articulation with the ulna (as seen also in *B. dawsoni*, Norman, 2011: 184). The shaft is stout and straight and there is an unusual abscess-like depression (abs) on its lateral surface. Distally, the shaft expands dorsoventrally and develops a keel and facet for a ligament-bound articulation with the dorsal edge of the ulna (uf). The distal end of the radius expands dorsoventrally, and forms a convex articular surface that fits into a recess in the carpometacarpal block (MCB) and most likely expands proximodorsally where metacarpal I is expected to overlap the distal end of the radius. Precise anatomical details are however obscured by the fusion of the distal end of the radius to a mass of (hyperostosed?) bone that forms a 'pollexocarpometacarpal' block.

The *ulna* (Fig. 38, UL) has a prominent olecranon (ol), which is partly damaged, and the proximal part of the shaft is expanded to form a vertical medial flange (mf) adjacent to which there is a lateral shelf (ls). The latter extends distally along the shaft as a thick ridge supporting the articulation with the radius (rf) proximally, and strengthening the ulnar shaft distally. Beyond the articular region the shaft of the ulna contracts before re-expanding to form a sutural facet dorsally for the radius (rf) and a more generally globular articular surface for the carpometacarpal block. Unlike the radius, the ulna does not appear fused to the carpal block so that, even in this individual, evidently suffering from some form of pervasive and generally non-arthritic hyperostotic condition, some limited mobility may have existed between the distal ends of the radius and ulna (and perhaps the ulna, carpus and more lateral digits).

<< INSERT FIGURE 38 NEAR HERE>>

The *carpometacarpal block* (Figs 38, 39, MCB) forms an irregular (and incomplete) mass of bone plastered around the distal ends of the radius and articulating more loosely against the ulna. The distal surfaces show some structure in that there is a deep recess for the articulation of the proximal end of metacarpal II and shallower, broader facets for metacarpals III and IV. The lower portion of the carpal block that would have supported metacarpal V is not preserved (or has not yet been recognised among the broken and scattered fragments still associated with this specimen).

The *manus*. The pollex ungual (Fig. 38, PO) is very large, conical and transversely compressed. It bears an elongate claw groove (c.gr) running down its posterior edge. Its proximal surface is abruptly truncated and seems to have broken away from the fused mass of the carpometacarpal block, to which it was also undoubtedly fused. There is no way of knowing whether a flattened proximal phalanx intervened between the pollex ungual and metacarpal 1, but such was probably the case (Norman, 1980). The left pollex, though less complete, is preserved very rigidly co-ossified to the carpometacarpal block (Owen, 1972: pl. II).

The metacarpals and phalanges of the other digits were collected, probably hurriedly, and may have been associated or at least partly articulated. Representative elements from all four digits (some left, some right) are preserved and an attempt has been made to re-assemble them (Fig. 39). Metacarpals II, III, IV and V of the right manus are present and, apart from mc III (which shows some lateral compression), well preserved (Fig. 39A,G).

<< INSERT FIGURE 39 NEAR HERE>>

Digit II (Fig. 39A,D) is represented by left and right metacarpals. The right metacarpal is short and comparatively slender; its proximal end is convex and the shaft laterally compressed, with its lateral surface notably flattened and scarred by ligaments that bound it to the shaft of metacarpal III. The distal end forms a dorsoventrally convex, but transversely rather flat, articular condyle surrounded by well-marked collateral ligament ridges. Phalanx 1 is block-shaped (Fig. 39D), but somewhat twisted (resembling the equivalent element in the manus of *I. bernissartensis* – Norman, 1980: figs 60, 61); its proximal surface is shallowly concave and is larger than the adjacent articular surface of its metacarpal. The short shaft is twisted medially and the distal articular facet is also offset medially, implying that the digit would have been twisted medially and therefore away from the main axis of the three central metacarpals. Phalanx 2 is proximodistally short and irregular, its proximal articular face fits closely against that of phalanx 1 and its distal articular surface is pulley-like. The ungual phalanx is considerably larger, but also very irregular, with much excess bone growth, although it does retain a proximal articular facet and a generally flattened ventral surface.

Digit III (Fig. 39A,C,E) is represented by the left and right metacarpals, neither of which is complete. The most complete is transversely crushed, as revealed by a ventral crease and comparison with the better-preserved uncrushed metacarpal III of NHMUK R33 (Fig. 39B). There is a substantially larger facet for the articulation of mc III on the carpometacarpal block (Fig. 38, III). Metacarpal III is stout and the longest of the metacarpal series; it has a broad, slightly convex, proximal articular condyle that contracts distally into a slightly tapered shaft. The sides of the shaft show rugosities associated with the presence of inter-osseous ligaments. It is clear that metacarpal IV was particularly strongly bound along much of the shaft. Distally, the condylar surface is transversely expanded and relatively flat, while dorsoventrally the articular surface is more obviously convex. The articular surface extends on to the dorsal part of the shaft confirming that the proximal phalanx could be hyperextended. Phalanx 1 is block-like but more symmetrical than that seen in the equivalent phalanx of digit II, there is also more correspondence in size between the metacarpophalangeal articular surfaces. This suggests that there was a more simple form of flexion-extension occurring at this joint, rather than the axial torsion that was evidently taking place along the axis of digit II. Phalanx 2 was probably considerably more abbreviated (as in digit II) but cannot be identified in this collection. However, the ungual phalanx is, as in the preceding example, distorted by excessive bone growth. A comparatively typical ungual phalanx of digit III of the manus (NHMUK R33) is illustrated in Figure 38H, H1.

Digit IV (Fig. 39A, F) includes a well-preserved right metacarpal that is slightly shorter than mcIII. Its proximal end is very broad and flattened and extends distally into a thickened and curved shaft that bears a very notable rugose strip of bone, manifesting hyperostosis of the intermetacarpal ligaments. This suggests that mcIII and IV were tightly bound together in life. The distal articular surface is little expanded and quite closely resembles that of mc II. Phalanx 1 is block-like though slightly smaller and more slender that the equivalent bone in digit III. Phalanges 2 and 3 become progressively smaller and the latter ends in a small, blunt terminus; this digit may not have borne a hoof. The joint surfaces of these phalanges correspond particularly well and when articulated in ‘neutral’ positions adopt a hyperextended position.

Digit V (Fig. 39G) is reconstructed from the elements that remain, and by reference to the morphology of the manuses of *Iguanodon bernissartensis* (Norman, 1980) and *Mantellisaurus atherfieldensis*

(Norman, 1986). Metacarpal V (of which both are well-preserved) differs considerably from the three previous examples in that it is short and spool-shaped. Its proximal articular surface is concave implying that its range of movement was not particularly constrained by the carpus. It was clearly not bound tightly to the adjacent metacarpal and, as in the above named taxa, diverged from metacarpal IV. The distal articular surface is a simple convex ball, which would also have permitted considerable freedom for movement of the first phalanx. What are presumed to have been phalanges 1 and 2 are more dorsoventrally flattened, but retain very simple (unconstrained) convexo-concave articular surfaces. At least one phalanx is missing from this series and a terminal phalanx 4 has a simple proximal articular facet and terminates is a flattened rugose margin that was unlikely to have supported a hoof or claw of any great importance.

<< INSERT FIGURE 40 NEAR HERE>>

The reconstructed antebrachium and manus (Fig. 40), is robust and presents a morphology typical of that seen in many large-bodied ornithopods (Taquet, 1976; Norman, 1980, 1986; Taquet & Russell, 1999; Wang, et al., 2010; Wu & Godefroit, 2012). Digit I is abbreviated by the incorporation of the metacarpal into the carpal block, the reduction of the first phalanx to a thin plate that may have been fused to the base of the ungual and the ungual phalanx is converted into a transversely flattened, tapered spine (PO). Digits II-IV are supported by moderately elongated metacarpals that were firmly bound together by inter-osseous ligaments and support digits that could be hyperextended, and simultaneously splayed, to create a weight-supporting/locomotor ‘foot’, rather than a hand-like grasping structure (Norman, 1980). The asymmetry in development of the ungual phalanges on digits II and III is typical of these forms (although this feature is somewhat obscured in this pathologically deformed individual). Digit V is shown diverging from adjacent digits because of its likely oblique articulation against the carpus; it is more slender and elongate and, judged by the simplicity of the articular surfaces between it metacarpal and phalanges, had some potential to be prehensile.

<< INSERT FIGURE 41 NEAR HERE>>

Note on manus and pes osteology. The unusual and somewhat distorted (pathological) bony growths associated with the articular regions that were noted in the forelimb are also exhibited in the pes but more particularly localized. The tarsals, metatarsals and phalanges of the pes are well-preserved and exhibit ‘normal’ anatomy. However the pedal unguals (Fig. 41) are notable for being almost unrecognisable (they are not classically ‘arrowhead’ hoof-shaped) and show no trace of the claw grooves that are normally so distinctive in these types of dinosaur (Norman, 1980, 1986). The proximal articular surfaces (art) for their penultimate phalanges are visible but these are surrounded by irregular bony growth and the distal portions of each are irregularly formed and flattened ventrally.

Pubis and ischium. The proximal end of the right ischium and a major portion of the right pubis are still embedded in plaster-of-Paris, but their shattered appearance suggests that more damage was caused by trying to remove the plaster. The pubis (Fig. 42), which is better preserved in terms of completeness and shape, includes the iliac peduncle (il.p) the acetabular rim which is well-developed, the base of the pubic shaft (p.pu) and the apparently complete prepubic process (ap). The latter is deep, transversely compressed and slightly dilated distally through the expansion of the dorsal and ventral edges. In its shape and proportions the pubis is similar to that of NHMUK R811 (Fig. 31) and shows the likely profile of the prepubic process. The prepubic process resembles somewhat that of the referred specimen of *B. dawsoni* (Norman, 2011a: text-fig. 12A) but the angulation between the prepubic process and the pubic shaft is more obtuse and the pubic shaft is not dorsoventrally compressed and strap-like as in *B. dawsoni*. The morphology of the pubis is distinct from that seen in either *M. atherfieldensis* (Norman, 1986) or *I. bernissartensis* (Norman, 1980). The ischium (though recognizable as such) is represented by a portion of the shaft and is very poorly preserved on a bed of plaster.

<< INSERT FIGURE 42 NEAR HERE>>

R1831 (R1835). The co-ossified sternal plates and median ‘intersternal ossification’ (*sensu* Norman, 1980) was first figured by Hulke (1885). Hulke, proposed an unconventional (inverted) placement for this part of the pectoral girdle, which was subsequently proved to be incorrect, on the basis of articulated skeletal remains, by Dollo (1885).

This fused mass of bone is unusual and notable (Fig. 43) but can be interpreted by reference to the osteology of the sternal region seen in some skeletons of *Iguanodon bernissartensis* (Norman, 1980: figs 55, 56). The general shape of the individual sternal bones can be discerned and exhibit the classic styracosternan condition: there are stout, short, posterolaterally directly handles (‘h’) that terminate in expanded condylar structures (con) that represent the points for attachment of the principal rib cartilages for the largest dorsal ribs; each handle merges with a central blade and becomes considerably thinner and plate-like. The posterior margin of the blade is hooked posteriorly and forms a thin apron (apr) as it approaches the midline before swinging anteriorly with its edge a short distance from the adjacent sternal blade. However, the intervening gap, normally spanned by cartilage in these ornithopods, is filled by calcified tissue. As articulated in this specimen, these two plates form a slight midline keel. Farther anteriorly, the blades diverge and thicken before swinging outward to form a robust outer edge that follows a concave margin as it curves posterolaterally to form the anterior edge of the handle. The external surface of the conjoined plates is generally convex. The thickened anterior region of the sternal plates is capped by a very thick and rugose mass of bone (iso) that also forms a more distinct midline keel (Fig. 43A,k); the lateral margins of this block, posterior to the slots (co.s) for the attachment of the medial edges of the coracoids produce a slender posterior extension (Fig. 43B,lf) that overlaps the lateral margin of the sternal plates. The anterior edge of the intersternal ossification is irregularly finished and its lateral margins are thickened and also bear elongate grooves with broken edges. These imply that the grooves would have been capable of securing the adjacent medial edges of the coracoids so that the entire chest region would have become a nearly-rigid sternal plate. Despite the extensive co-ossification it appears that slight flexibility was retained across the coracosternal articulations.

<< INSERT FIGURE 43 NEAR HERE>>

Sternal plate structure is not uniform across ankylopollexians and may prove to be of some value diagnostically. Basal forms such as *Hypselospinus* have comparatively short, flattened, robust and forwardly located sternal 'handles' and a blade with a prominent posterior apron that extends as far posteriorly as the distal ends of the handles. In *I. bernissartensis* and *M. atherfieldensis* the handles are considerably more posteriorly positioned, longer, cylindrical and more slender (and bowed in the opposite sense in *I.bernissartensis*), and the apron is more abbreviated (Norman, 1986). The precise form of the complete sternal bone in *Barilium dawsoni* is unknown, although the handle (NHMUK R2357, Norman, 2011) was clearly short, larger and even more robust than that seen in *Hypselospinus fittoni*.

7. ***NHMUK R1834***

The material with this registered number represents a partial, smaller (probably immature) ornithopod skeleton collected at Silver Hill (according to older specimen cards). Beckles collected the material during 1871 while foundations were being prepared for 'Silverlands House' at Silverhill-Tivoli (Fig. 1 – Silverlands Road still exists in this area of Hastings). The skeleton comprises: a partial left dentary (no teeth preserved); vertebrae 50+: 2 cervicals, 11 dorsals with several additional fragments, 39 caudal centra with a few additional fragments; scapula; radius: proximal and distal portions; ulna: two distal fragments; ilium nearly complete; pubis (only the proximal end of the pubic shaft); ischium (proximal end and some distal fragments); fibula (proximal end); astragalus (portions of both); metatarsals (left II and IV, right distal III and IV); 3 pedal phalanges.

Lydekker (1890a) noted the existence of this specimen and commented on the similarity that its ilium bore to that of the holotype of *Iguanodon fittoni* (NHMUK R1635 – Figs 3, 9): "This ilium shows the peculiar outward curvature of the preacetabular process, which is obscured through fracture in the type; it has the same inflection of the inferior surface of the postacetabular as in the latter; and also the rounded surface of the bone in the preacetabular notch." (Lydekker, 1890a: 43); he also mentioned a femur [not identified in this collection] and pubis of this specimen and remarked that the femur "shows that the inner trochanter [4th] was of the "crested" type of *I. Mantelli*, and quite different from the "pendant" type of that of *I. hollingtoniensis* (fig. 2) so that we have now decisive evidence of the distinctness of the latter from *I. Fittoni*." (Lydekker, 1890a: 43-44). It is regrettable that a femur does not appear to be preserved in this collection today – although the possibility that Lydekker was describing the shattered femur of NHMUK R1831 cannot be entirely excluded because both specimens would have been donated to the museum at the same time, following Beckles's death that year. Lydekker noted that some vertebrae in this specimen were fused together, while others were procoelous and he suggested that these features might have been caused by injury sustained during the lifetime of the individual. There are two examples of mid-caudal vertebrae that exhibit fusion.

Sauropod dinosaur. The procoelous caudal vertebra is anomalous and its anatomy is more typical of that seen in sauropod caudals (this identification was later confirmed by P. Mannion, pers. comm. 25 May 2011).

<< INSERT FIGURE 44 NEAR HERE>>

Dentary (Fig. 44A-C). The specimen was illustrated in lateral view by McDonald, et al. (2010: fig. 1A) and referred to *Barilium dawsoni*. The ventral portion of the dentary is well preserved and undistorted, and demonstrates that the ramus was gently arched along its length. A small section of the slot-and-lip (sl) posterior portion of the dentary symphysis (ds) is exposed. A shallow trough extends posteriorly along its ventromedial edge, marking the anterior portion of Meckel's groove (mgr); above this, the body of the dentary, which is laterally compressed and spout-shaped anteriorly (Fig. 44C), thickens transversely farther posteriorly in order to accommodate the alveoli for the dental magazine (alv) but much of the posterior portion of the dentary ramus is broken away. The line of a vascular channel (vc) marks the ventral edge of the alveolar region, but the alveolar parapet above is sheared away and the dentition is entirely missing. A remnant of the lateral alveolar wall can be see in places (am), as can the scalloping that marks the upper edge of the dentary. At its anterior end the vascular channel converges on the alveolar margin, beyond this imaginary point the dorsal edge of the dentary forms a comparatively short edentulous ridge, which would have formed the equivalent of a 'diastema' (Fig. 44, dias) of quite modest proportions given the inevitable proximity of the posterolateral arm of the predentary. Posteriorly the dentary is represented by a tongue of bone that would have been sutured to the lateral surface of the surangular (sa.s: as seen in *Mantellisaurus* Norman, in prep).

<< INSERT FIGURE 45 NEAR HERE>>

Vertebrae (Fig. 45). Several examples from the dorsal series (Fig. 45A-C) comprise isolated centra whose neural arches have detached along their neurocentral sutures. This observation supports the view that this was an immature individual. In form these elements are indistinguishable from those in the referred skeletons (NHMUK R1148, R33 and R604). Some centra are upright, slightly laterally compressed with a ventral keel, while others have a more posteriorly reclined centrum with thickened articular margins typical of those described in NHMUK R604. The caudal series includes some examples from the anterior-middle series that are indistinguishable from that of the holotype (cf. NHMUK R1635: Fig. 8 and Fig. 45D,E).

Ilium (Fig. 46A-D). This is one of the better-preserved bones in this collection, and has been used to determine the affinities of this skeleton in strikingly contrasting ways. Lydekker (1890a) assigned this ilium to *I. [=Hypselospinus] fittoni* whereas McDonald, *et al.* (2010) referred it to *Barilium dawsoni.* The ilium, which has never been illustrated, though broken in several places, has been repaired; however, it is only missing part of the pubic peduncle (pp) and the medial portion of the postacetabular process (Fig. 46B). It should be noted that the preacetabular process (prp) has an anomalously (pathologically?) thickened and truncated distal tip (bl).

<< INSERT FIGURE 46 NEAR HERE>>

The upper border of the ilium appears to be gently convex in lateral view (Fig. 46A, D), but this is partly manufactured by the break, which runs across the central part of the ilium, and its subsequent repair. The dorsal blade of the ilium is transversely compressed (Fig. 46C) and its dorsal edge is narrow, flat-topped (fdm) and shows a characteristically narrow strip of blister-like rugosities (m.sc) that run parallel to the dorsolateral edge of the iliac blade. In a restricted area of the dorsal edge above and immediately posterior to the expansion ischiadic peduncle this blistered edge is slightly deeper (in just the area that is sheared away in the holotype ilium NHMUK R1635: Figs 3A,B, 9). The preacetabular process is laterally compressed, shallowly concave vertically and shows neither the pronounced twist nor the transverse thickening seen in *B. dawsoni*. The medial surface of the preacetabular process is exhibits a small sacral rib facet and a poorly defined medial ridge (mr). The preacetabular embayment has an acute edge at the transition from lateral to medial surface, as is also the case in NHMUK R1635 (contradicting earlier comments by Lydekker). The pubic peduncle (pp) would have been longer in the complete ilium. The ischiadic peduncle (ip) is laterally expanded and has the ‘stepped’ structure on its laterally expanded surface that is seen in many ornithopods. The postacetabular process tapers to a blunt point and its ventrolateral margin is marked by a lateral ridge (lr) and well-developed brevis fossa (brf). The full development of the fossa (as seen in the holotype ilium) is not seen in this specimen because the medial portion of this process has been sheared off (Fig. 46B), but the well developed lateral ridge and brevis fossa distinguish this ilium immediately from that of the sympatric contemporary *Barilium dawsoni* (Norman, 2011a). In nearly every respect these features resemble those seen in the holotype ilium or other less complete specimens that have been referred to *Hypselospinus,* and differ from those seen in *Barilium dawsoni*.

McDonald, et al. (2010) referred NHMUK R1834 to *Barilium dawsoni*: "NHMUK R1834 is a partial associated skeleton that … is herein considered referable to *Barilium* due to the similar morphologies (e.g., smoothly convex dorsal margin) shared by its ilium and NHMUK R802, the holotype ilium of *Barilium* (*contra* Norman, 2010, who referred NHMUK R1834 to *Hypselospinus*). The ventrally inflected rostral ramus of the dentary of NHMUK R1834 differs from the straight rostral ramus of NHMUK 28660 … suggesting that they do not represent the same taxon." (McDonald, et al., 2010: 2). The ilium (NHMUK R1834) and the ilium of the holotype of *B. dawsoni* (NHMUK R802) do *not* have similar morphologies and cannot be considered to belong to the same taxon.

In summary:

i. The preacetabular process of NHMUK R1834 (cf*. H. fittoni*) is slender, laterally compressed and exhibits no evidence of torsion along its length; in NHMUK R802 (*B. dawsoni*) the equivalent process is very robust, transversely thickened and axially twisted distally.
ii. The medial surface of the base of the preacetabular process in NHMUK R1834 (cf. *H. fittoni*) bears rugosities reflecting the presence of a small rib facet and the associated medial ridge is weakly developed. The equivalent area on the medial side of the base of the preacetabular process of NHMUK R802 (*B. dawsoni*) has an expanded rib facet (visible in lateral aspect) and a prominent medial ridge.
iii. The dorsal margin of the ilium of NHMUK R1834 (cf. *H. fittoni*) is laterally compressed and narrow; the equivalent portion of the iliac blade of NHMUK R802 (*B. dawsoni*) is transversely expanded.

iv. The postacetabular process of NHMUK R1834 (cf. *H. fittoni*) bears a well-marked brevis fossa ventolaterally that is demarcated from the lateral wall of the iliac blade by a prominent ridge; the equivalent area of the lateral iliac wall and postacetabular ramus in NHMUK R802 (*B. dawsoni*) curves smoothly medially and a well-developed brevis fossa is absent.

v. The "smoothly convex dorsal margin" described in NHMUK R1834 – the only shared feature claimed by McDonald, et al. (2010) is manufactured by breakage and repair, and must be balanced against the overwhelming range of differences between these two bones.

In all significant respects, the anatomy of the ilium of NHMUK R1834 resembles the holotype of *H. fittoni* (NHMUK R1635) and other referred specimens (e.g. NHMUK R811b, R1148, R33, R1636) that can be attributed to *H. fittoni*. Contrary to the views of McDonald, et al. (2010) the ilium (NHMUK R1834) differs strikingly in its detailed anatomy from that seen in the holotype of *B. dawsoni*.

NOTE CONCERNING MATERIAL NOT REFERABLE TO *H. FITTONI*

NHMUK R1836 is a partial skeleton consisting of fore and hindlimb elements that is also part of the Beckles Collection. This associated material has been labelled (unhelpfully) as also having been collected at 'Hastings'. However, this material is certainly referable to *Mantellisaurus atherfieldensis* and, judged by its preservational condition, was probably collected from a locality within the stratigraphically younger Wessex Formation (Barremian) of the Isle of Wight, rather than from the rather vague attribution of "Hastings" as claimed on associated labels. Samuel Beckles is known to have collected several large-bodied ornithopod skeletons from Isle of Wight localities during his career, a notable example being the partial skeleton (NHMUK R1829) that includes an articulated hindlimb, the pes of which was described by Owen (1858). A few specimens, that are very clearly part of the skeleton registered as NHMUK R1831 (and found on adjacent shelving in the collection), have been numbered mistakenly as 'R1836'; these mistakes have been noted on the specimen labels.

NHMUK R1840 is an isolated large posterior dorsal centrum reportedly collected from Hastings; this specimen is considered to be referable to *Barilium dawsoni*.

NHMUK R1842 includes several large, matrix-smeared, dorsal and caudal vertebrae collected from Hastings and also labelled as part of the Beckles collection appear, from their size and shape, to be referable to *Barilium dawsoni*.

NHMUK R1939 is a large, nearly complete, anterior-middle cervical vertebra collected from a nodule found on the beach near Hastings by Mr P. Rufford. This specimen seems most probably referable to *Barilium dawsoni* (by default of its probable geological age and very large size). It was illustrated in posterior view, and referred to *I. dawsoni* by Lydekker (1890a: 44, fig. 3).

RECONSTRUCTION OF *HYPSELOSPINUS FITTONI*

Figure 47 is a first attempt to develop a composite reconstruction of the skeleton of *Hypselospinus fittoni*, based upon what is known of the type and referred material described above. Cranial material is unknown. The dentary is based upon NHMUK R1831 and R1834, the axial skeleton is based primarily upon NHMUK R33, R604, R1148 and R1834, the pectoral girdle and forelimb are based upon NHMUK R1831, R1834 and R604, and the pelvic girdle and hindlimb are based upon NHMUK R1635, R604, R811, R1834 and R1148.

Hypselospinus is a large-bodied ornithopod with a body length that probably ranged up to 7 or even 8 metres (judged from the largest fragmentary referred skeleton so far recovered: NHMUK R1627). Its general build would best be described as 'mesomorph': for example, this taxon was not as robustly constructed as the sympatric contemporary

Barilium dawsoni. The forelimb and manus are constructed for weight support and locomotion, so the quadrupedal pose was probably normal, if not obligatory (the precise proportions of forelimb:hindlimb are not known). This pose is also echoed in the evidence of a massive, and reinforced, pectoral girdle. The term 'reinforced', is perhaps exaggerated in this instance because of the hyperostosis (in appearance similar to the medical condition 'DISH' – diffuse idiopathic skeletal hyperostosis) visible in NHMUK R1831; this latter associated skeleton exhibits excessive bone growth adjacent to articular surfaces e.g. across the sternocoracoid plate, antebrachium, carpus, manus and unguals of the pes.

The general pose and gait of this animal as reconstructed here is particularly influenced by the orientation of the pelvic girdle. This is shown tilted posteriorly (and this orientation also applies to the reconstruction of closely related taxa such as *B. dawsoni* (Norman, 2011a: text-fig. 25), *M. atherfieldensis* (Norman, 1980: fig. 83) and *I. bernissartensis* (Norman, 1980: fig. 84). In each of these examples the ilium is notable for having a dorsal acetabular margin that is shallow and smoothly rounded (when the dorsal edge of the iliac blade is positioned horizontally – as it is in most illustrations). The pubic peduncle of the ilium is by contrast stout, triangular in cross-section and bears a prominently lipped supra-acetabular crest. In addition, the pubic peduncle is sutured mediodorsally to the massive, ventrolaterally directed first sacral rib. It is clear from this structural arrangement that the primary weight-bearing capacity of the entire pelvis is located on the pubic peduncle and the adjacent 'keystones' represented by the 1st sacral ribs and sacral centrum, rather than the central section of the iliac acetabulum. In order to reflect these implied articular mechanics at the hip joint the ilium has to be rotated posterodorsally from the horizontal so that the pubic peduncle itself lies horizontally (in lateral view) and its supra-acetabular crest is positioned so that it forms the dorsal margin of the acetabulum. Pelvic rotation affects the overall pose of the animal because of the way in which it alters the pattern of curvature along the vertebral column, especially insofar as it lowers the anterior caudal series.

There has, in recent decades, been a near universal tendency to adopt by default 'high-tailed' and dynamic silhouette-style reconstructions for ornithopod dinosaurs (starting with Peter Galton's (1970) "*Anatosaurus* in a hurry"). These artistic renderings are attractive to the eye and chime with the dynamic interpretation of dinosaurs promoted most notably by Robert T. Bakker during the 1970s. While some of these reconstructions (notably those for theropod dinosaurs), seem biologically plausible, it has been realized that the anatomy portrayed in some dinosaur images has been compromised. The 'cocked' wrists and 'rotating' shoulder blades depicted in Gregory Paul's earlier reconstructions of large-bodied ornithopods such as *Iguanodon* (Brett-Surman, 1997: fig. 24.6A) suggest the influence of Eadweard Muybridge's stop-frame photographs of mammalian (horse) locomotion. The re-orientation of the pelvis in *Hypselospinus* (and related ornithopods) has the visual effect of 'cramping' the pose and implied gait in these reconstructions because it removes some of the intrinsic dynamism of the pose of these dinosaurs.

COMPARATIVE ANATOMICAL AND TAXONOMICAL OBSERVATIONS

The foregoing account establishes a hypodigm for the taxon *Hypselospinus fittoni* based upon the holotype and a selection of referred material. The detailed description of the individual elements, their historical context, and the occasionally complex justification for inclusion within the hypodigm, has obviated all but the most immediate comparative comments – most of which are focused upon its sympatric contemporary (*Barilium dawsoni* see Norman, 2011a), whose remains would be confused most readily with those of the hypodigm. The following section addresses the need for comparative anatomical observations and will deal with iguanodontian taxa that are morphologically similar. Although the primary focus is upon morphologically similar taxa, comparisons have been broadened to include a range of distinct, and generally more basal, ornithopods (*sensu lato*) e.g. Rhabdodontidae (Weishampel, et al., 2003; Osi, et al., 2012), tenontosaurs (Butler, et al., 2008), Dryosauridae (Barrett, et al., 2011) and *Camptosaurus*-grade taxa (McDonald, 2011, 2012a). Anatomically more derived ornithopods, referred to as hadrosauromorphans (Norman, 2014) are also considered as part of the analysis because they represent an evolutionary continuation of the iguanodontian lineage. Finally, taxonomic names that have been created recently and applied to Wealden-aged iguanodont material are assessed so that they can be excluded from further consideration (Norman, 2013).

Barilium dawsoni (Lydekker, 1888a) – Norman, 2011a

Although a sympatric contemporary of *Hypselospinus* this taxon can be readily distinguished anatomically (Norman, 2010, 2011a).

Teeth and jaws. The dentary teeth of *Barilium* have a simpler ridge pattern on the enamelled lingual surface of the crown (Norman, 2011a: text-fig. 20): the primary and secondary ridges are clearly demarcated and sub-equal in size and there are very few strand-like accessory ridges The referred dentary of *B. dawsoni* (NHMUK OR28660 – see *Kukufeldia tilgatensis* below) is very large, robust and straight and similar in shape to that seen in *Iguanodon bernissartensis* (see also discussion below) – as noted by Lydekker (1888b), rather than being arched anteriorly as in the case of *Hypselospinus*.

Axial skeleton. The dorsal vertebrae of *Barilium* are large and cylindrical, and have wide and comparatively tall neural spines (when viewed laterally), compared to those of *Hypselospinus*; the latter are more slender and taller. The anterior caudal vertebrae of *Barilium* are low and angular sided, whereas those of *Hypselospinus* are more cylindrical, axially compressed and bear very elongate, narrow, neural spines; the more posterior caudals of *Barilium* tend to have strongly amphicoelous articular faces to the centrum.

Appendicular skeleton. The shoulder girdle and forelimb in these two taxa are very similar. However, the pollex spine of *Barilium* is short, blunt and transversely compressed while that of *Hypselospinus* is tall, inclined and pointed. The pelves have distinctive ilia: unlike *Hypselospinus*, *Barilium* has a thick, axially twisted preacetabular process, the dorsal edge of the ilium is transversely thick and rounded. The postacetabular portion of the iliac blade has a deep, medially curving surface with a posterior margin that is rounded in lateral view; it also lacks the well-developed brevis fossa demarcated by a prominent lateral ridge that is present in ilia of *H. fittoni* (Norman, 2010, 2011a). The hindlimb bones appear to be generally similar in these two taxa (although these elements are poorly represented in *Barilium*).

Kukufeldia tilgatensis McDonald, Barrett and Chapman, 2010

This taxon is a potential sympatric contemporary of *H. fittoni* (Fig. 2) and was established upon an isolated, large and robust dentary with two dentary teeth in place (NHMUK OR28660) that was collected from one of the historically important Whiteman's Green Quarries near Cuckfield, West Sussex, England (Fig. 1). The quarry area is generally understood to expose lower Wealden strata (Hastings Group [Grinstead Clay Formation] Fig. 2, GC Fm) of middle-late Valanginian age.

Teeth and jaws. The dentary teeth are broad, shield-shaped and the primary ridge is distally offset on the lingual surface of the crown; and a slightly less prominent secondary ridge subdivides the mesial portion of the crown face into more or less equal sectors. Accessory (tertiary) ridges are either very few or entirely absent (poor preservation). These principal features differ markedly from those described in the dentary crowns of *H. fittoni*. The robust, straight dentary ramus of NHMUK OR28660 differs from the comparatively slender and anteriorly down-turned dentary of *H. fittoni* (NHMUK R1831, R1834).

Postcranial skeleton. Unknown.

Taxonomic note. This taxon is currently diagnosed on the basis of a single autapomorphy: an allegedly unique pattern of vascular openings seen on the external surface of the anterior end of the dentary. It should be noted that the pattern of vascular openings on the surface of any dinosaurian dentary can vary between individuals referred to the same taxon, and that such variation can also occur between left and right dentaries of the same individual. A single autapomorphy of this quality undermines the status of *Kukufeldia tilgatensis*. Additional anatomical evidence used as supplementary support for this new taxon (McDonald, Barrett & Chapman, 2010) relied upon the mistaken reference of additional jaw material (NHMUK R1834) to *B. dawsoni* (Norman, 2011a); this latter material is unambiguously referable to the Valanginian taxon *Hypselospinus fittoni* (Norman, 2010, 2011b and herein).

In reply to critical comments concerning the status of *Kukufeldia* McDonald (2012) accepted that the teeth referred to *B. dawsoni* (Norman, 2011a,b) resembled those seen in the dentary of *Kukufeldia*. However, he observed that similar dental morphologies are to be seen in the sympatric taxa *Mantellisaurus* and *Iguanodon* and that attribution of the teeth in the jaw of NHMUK OR28860 to *B. dawsoni* was therefore unsafe. While the dental resemblances noted by McDonald are true, the two latter species are not Valanginian contemporaries of *B. dawsoni* (both are substantially younger, having a upper Barremian–Lower Aptian stratigraphic range – Fig. 2). There are at present two alternative explanations available for this unsatisfactory situation. Firstly, the jaw collected at Cuckfield might actually pertain either to the Hauterivian or the Weald Clay Formation (Barremian). Inliers of younger beds are known to occur as slivers in the western part of the Hastings Group outcrop area – Topley, 1875; Batten & Austen, 2011). It is at least possible that the Weald Clay was exposed at Cuckfield at the time the original specimen was collected and that the dentary in question can be referred to *Iguanodon bernissartensis*. In this regard, it is interesting to note that within the Mantell Collection (NHMUK) there are several specimens, notably a sternal bone, pubis and ischium all labelled as having been collected from "Tilgate Forest" that resemble the equivalent bones of the Barremian-Lower Aptian aged *Mantellisaurus* (Fig. 2 – Norman, in prep). Unfortunately, there is no more specific locality information associated with these specimens. If a range extension into the Hauterivian/Barremian is considered inadmissible, the balance of probability appears to favour the assertion that the dentary assigned to *Kukufeldia tilgatensis* is from the Grinstead Clay Formation (Valanginian). The only specimen attributed to this latter taxon can be referred to *Barilium dawsoni*; this view is now supported by Andrew McDonald (pers. comm. 5 October 2013).

Fukuisaurus tetoriensis Kobayashi and Azuma, 2003

This taxon is based upon a disarticulated partial skull and an isolated sternal plate of a comparatively small (~4 metres long) ornithopod collected from Kitadani Quarry, Fukui Prefecture, Japan. The geological age of the material is late Hauterivian-Barremian.

Teeth and jaws. The dentary crowns (Kobayashi & Azuma, 2003: fig. 5C,D) are similar in general shape to those described in *H. fittoni*. The published description (Kobayashi & Azuma, 2003: 170-171) is at variance with the actual the appearance of the teeth: a well-defined primary ridge is clearly distally offset on the lingual surface of the crown and there is a mesially positioned secondary ridge and minor accessory ridges are present extending thecally from the marginal denticles on the mesial edge of the crown. Details of the secondary ridge and accessory ridges differ from those seen in *H. fittoni* dentary crowns. The dentary (Kobayashi & Azuma, 2003: fig. 4C, D) is robust and comparatively short, has an anterior end that is straight and somewhat tapered (rather than being arched) and there is a tall, perpendicular coronoid process; all these features are distinct from those seen in material referred to *H. fittoni*.

Appendicular skeleton. A hatchet-shaped sternal, very similar in outline to that seen in *M. atherfieldensis* (Norman, 1986: figs 45-46) and distinct from the robust, posteromedially 'aproned' form seen in *H. fittoni* is the only element so far reported in this taxon.

Delapparentia turolensis Ruiz-Omenaca, 2011

Based upon a partial associated skeleton collected at Galve in the Province of Teruel in the Autonomous region of Aragon (Camarillas Formation: lower Barremian).

Axial and appendicular skeletons. The skeletal elements include an articulated series of anterior caudal vertebrae a variety of cervical and dorsal ribs fragments and portions of all three pelvic bones. Suggested autapomorphies of this taxon include the 'stepped' form of the capitulum and tuberculum in posterior dorsal ribs, ossified sternal ribs, pneumatic foramina in dorsal ribs, a transversely expanded preacetabular process of the ilium, and a very large ischium. The posterior rib-head characters cannot be used to distinguish this taxon from *H. fittoni*, which has similarly 'stepped' posterior dorsal ribs (this is a feature common to all ornithopod dinosaurs); the presence of ossified sternal ribs and pneumatic dorsal ribs are unique and unexpected in ornithischian dinosaurs. The preacetabular process of the ilium differs significantly in shape from that seen in *H. fittoni*; and, although the structure of the proximal end of the ischium is similar to that seen in ornithopods generally, its large size relative to the ilium is highly unusual.

Taxonomic note. The stepped rib-head character is not a valid autapomorphy because it is widely seen in tetrapod vertebrates. The reported presence of ossified sternal ribs and pneumatic openings in some dorsal ribs would be unique. However, there is a pressing need to exclude the likelihood that these fragmentary elements belong to the large theropod whose remains were collected at the same locality (Ruiz-Omenaca, 2011: 85). The preacetabular process of the ilium closely resembles that described in *Iguanodon bernissartensis* (Norman, 1980) and the ischium [and pubis], judged by their comparative size, cannot belong to the same individual as the ilium; this suggests that there has been some mixing of skeletal elements from different individuals. Subject to further study this taxon is considered provisionally to be a *nomen dubium*.

Iguanacolossus fortis McDonald, Kirkland, DeBlieux, Madsen, Cavin, Milner and Panzarin, 2010b

This taxon is based upon a partial, disarticulated individual skeleton collected from a single location in Grand County, Utah, USA. The material was recovered from the lower Yellow Cat Member of the Cedar Mountain Formation (lower Barremian – Hunt, et al., 2011).

Teeth and jaws. The dentary teeth are broad and shield-like and the lingual surface of the crown is subdivided vertically by a prominent primary ridge that is distally offset and a lower and more mound-like secondary ridge that partially subdivides the mesial portion of the crown surface. In addition, there are a number of accessory (tertiary) ridges distributed across the areas medial and distal to the primary ridge; these latter are not as strand-like and irregular as in the case of *H. fittoni*. The dentary is not preserved.

Axial skeleton. Posterior dorsal vertebrae possess robust and comparatively short neural spines unlike those seen in *H. fittoni*.

Appendicular skeleton. The ilium has a similar transversely flattened preacetabular process, but the dorsal edge of the ilium is more strongly laterally everted above the ischiadic peduncle (McDonald, *et al*. 2010b, fig. 14A,B). The prepubic process appears to be deep, transversely compressed and strongly expanded distally (McDonald, *et al*. 2010b, fig. 14C,D) and therefore differs in morphology from material that has been referred to *H. fittoni*.

Hippodraco scutodens McDonald, Kirkland, DeBlieux, Madsen, Cavin, Milner and Panzarin, 2010b

This taxon is based upon a nearly complete skull and fragmentary skeleton of a single individual collected from a different locality and stratigraphic horizon to *Iguanacolossus* in Grand County, Utah, USA (McDonald, et al., 2010b: 14). The material was recovered from the upper Yellow Cat Member of the Cedar Mountain Formation and is regarded as Barremian in age (Hunt, et al., 2011).

Teeth and jaws. The dentary teeth are described as being too badly damaged or matrix obscured for adequate description; they are evidently shield-shaped and bear a distally offset primary ridge, but no further details are available (McDonald, et al., 2010b). The lower jaw appears to have a straight (not arched) dentary and a short diastema, the form of the coronoid process cannot be described because of overlying bones.

Axial skeleton. Dorsal vertebrae have comparatively short, ‘plank-like’ neural spines (McDonald, et al., 2010b: fig. 27), quite distinct from the form of those seen in equivalent vertebrae of *H. fittoni*.

Appendicular skeleton. The scapula of *H. scutodens* (McDonald et al., 2010b: fig. 30C,D) is typically ornithopod, and very similar in shape to that seen in *H. fittoni*. The sternal bone (McDonald, et al., 2010b: fig. 30A,B) is similar in morphology to that of *H. fittoni* with a broad, flattened ‘handle’ and a well-developed ‘blade’; however there is no evidence of medial fusion into a conjoined sternal plate as seen in one specimen of *H. fittoni*. The remainder of the skeleton is poorly preserved and comparisons between these two taxa are uninformative.

Iguanodon (?Dakotadon) lakotaensis Weishampel and Bjork, 1989

This taxon was recovered from the Lakota Formation (Barremian) of Lawrence County, South Dakota and comprises a major portion of an articulated skull of a large (~8 metres long) ornithopod.

Teeth and jaws. Individual dentary crowns exhibit a distally off-set primary ridge that is paralleled by a lower, mesially off-set secondary ridge, there is little evidence of tertiary (accessory) ridges as seen in *Hypselospinus*. Dentary teeth are very similar in appearance to those seen in both *Barilium dawsoni* and *Iguanodon bernissartensis*. Maxillary teeth are narrower than those of the dentary and display a very prominent primary ridge that is slightly distally off-set and few, if any tertiary (accessory) ridges. The anterior half of the lower jaw exhibits a stout ramus with a buccal emargination posteriorly. The predentary has a denticulate oral margin and a bilobed ventral process. The dentary shares only generalised features with what is known of the dentary of *Hypselospinus*.

Taxonomic note. The preserved skull of *Iguanodon lakotaensis* is similar in its proportions to that of *Iguanodon bernissartensis* (see below). Originally named *Iguanodon lakotaensis* in the description published by Weishampel & Bjork (1989), Paul (2008) proposed the new generic name *Dakotadon* on the basis of an emended diagnosis (Paul, 2008: 199). The new diagnosis appears to contain a mixture of anatomy that is at variance with the original description and observations that are, at best, subjective in nature. As originally pointed out by Weishampel & Bjork (1989), the anatomy of the skull and dentition closely resembles that seen in *Iguanodon bernissartensis*. Anatomical differences: the pattern of sutures between the lacrimal, jugal and maxilla on the posterior border of the antorbital fenestra, the single (rather than double) opening for cranial nerve VII on the lateral wall of the proötic, the structure of the supraoccipital (the absence of a median ridge). And, though not alluded to be Weishampel & Bjork (1989), the comparatively low maxillary tooth position count (19). The structure of the supraoccipital was suspected to be a preservational artefact and the incomplete nature of the neurocranial suturing further suggested to the authors that this was a sub-adult individual; this latter factor may also explain the slightly reduced number of tooth positions.

Paul (2008) does not offer a valid reason for the new generic assignment of the holotype of *I. lakotaensis* and, on the basis of what is currently known this specimen, it would seem preferable to refer to this as cf. *Iguanodon lakotaensis*.

Iguanodon bernissartensis Boulenger, 1881 (*in* Beneden, 1881) – (Norman, 1980)

This upper Barremian–Lower Aptian (Fig. 2) sympatric taxon is large (10+ metres long) with a robustly constructed skeleton that is reminiscent of that of the Valanginian *Barilium dawsoni*.

Teeth and jaws. Individual dentary crowns (Norman, 1980: fig. 19) lack the complex pattern of primary, secondary and accessory ridges seen in *Hypselospinus* and are indistinguishable from those currently referred to *Barilium*. The lower jaw is deep, robust and essentially straight (although some relatively uncrushed specimens (RBINS R56 [IRSNB 1680]) exhibit modest arching of the dentary ramus anteriorly); this morphology contrasts with the more slender and arched dentary ramus morphology of the referred dentary of *Hypselospinus* (NHMUK R1834: Fig. 44). The coronoid process is also distinct in being tall and perpendicular to the long axis of the jaw in *I. bernissartensis* (Norman, 1980: pls I-IV) by comparison with the shorter and more obtuse-angled coronoid process in the referred specimen NHMUK R1831 (Fig. 36). It should be noted that breakage and remedial reconstruction of NHMUK R1831 might account for some of the differences noted here.

Axial skeleton. Cervical and dorsal vertebral centra are generally similar in shape and proportions, but are substantially larger and do not exhibit the extreme eversion of their articular rims seen in *Hypselospinus*. The dorsal neural spines of *I. bernissartensis* are typically thick and tall (‘plank-like’: Norman, 1980: figs 34-40) compared to the very slender and elongate neural spines seen in some of the better-preserved dorsals of *Hypselospinus*. Caudals of *I. bernissartensis* also lack the tall, narrow neural spines that are characteristic of *H. fittoni*.

Appendicular skeleton. The robust shoulder girdle and forelimb of *I. bernissartensis* resembles that seen in *Hypselospinus*, except that in the former the proportions of the limb are overall more elongate. The former taxon has a deeply notched coracoid foramen (rather than a fully enclosed foramen) and a more elongate, curved and conical (rather than laterally compressed) pollex ungual. The manus of *I. bernissartensis* is proportionally larger and it has more elongate metacarpals (Norman, 1980: figs 52-62). Both taxa share a tendency to ossify the connective tissue of the median sternal area between the coracoids and sternals in a manner reminiscent of secondary cartilage ossification (this was referred to as an intersternal ossification – Norman, 1980: 47). One example of *Hypselospinus* (NHMUK R1831 – Fig. 43) exhibits co-ossification of the sternals and this pathology may have involved the coracoids (fusion between the sternal bones has not been observed in any specimens referred to *I. bernissartensis,* although coracoid articulation against the intersternal ossification appears probable). The pelvis is structurally distinct: the ilium of *I. bernissartensis* is notable for its thick, robust preacetabular process; the thickened and rolled posterodorsal edge of the iliac blade, and the extremely elongate, tapering postacetabular ramus with its pronounced lateral ridge and very broad brevis fossa (Norman, 1980: fig. 64). The pubis has a thick, but comparatively narrow, proximal prepubic process that expands abruptly distally; this is quite distinct in outline from what is known of the shape of the prepubic process of *Hypselospinus*. The hindlimb is similar in overall morphology in both taxa, although the femoral shaft appears to be less markedly angular-sided and less bowed along its length in *Iguanodon bernissartensis*.

Mantellisaurus atherfieldensis (Hooley, 1925) – (Norman, 1986)

This is an upper Barremian-Lower Aptian sympatric Wealden taxon (Fig. 2). It has a more gracile morphology than *H. fittoni*. Osteologically mature skeletons of *M. atherfieldensis* appear to range between 6-7 metres in body length.

Teeth and jaws. Individual dentary crowns are smaller and lack the complexity of ridge patterning when compared to that of *Hypselospinus* (Norman, 1986: figs 19, 21). The dentary ramus is slender and arched anteriorly and the coronoid process rises perpendicular to the long axis of the jaw, rather than at an obtuse angle, as appears to be the case in NHMUK R1831 (Fig. 36).

Axial skeleton. The dorsal column of *M. atherfieldensis* reveals centra that are smaller and more gently waisted; the do not show the pronounced thickening noted on the articular rims of the centra, the oblique inclination of the centra, or extreme slenderness and elongation of dorsal and caudal neural spines (Norman, 1986: figs 29-32).

Appendicular skeleton. The pectoral girdle is more lightly built in *M. atherfieldensis*. In this latter taxon, the scapula has a narrow proximal portion and a flared distal blade. The coracoid has a completely enclosed coracoid foramen (Norman, 1986, 2011b: text-fig. 27.43). The proportions of the sternals also differ: there is a broader and more elongate posteromedial extension to the sternal 'blade' in *H. fittoni* compared to that in *M. atherfieldensis* (Norman, 1986: fig. 45) as well as a shorter, somewhat flattened and more robust 'handle'. The forelimb is slender and lightly built in *M. atherfieldensis*, reflected in the shorter, sinuously-shafted humerus and the slender, bowed radius, the partial co-ossification of the carpals and the comparatively short, conical pollex ungual. The metacarpals are also comparatively slender and elongate (Norman, 1986: figs 50, 51; 2011b: text-fig. 27.44). The pelves are distinct (Norman, 2011b: text-fig. 27.10): the pubis of *M. atherfieldensis* has a very thin and dorsoventrally expanded prepubic process; the shaft of the ischium is essentially straight, angular-sided (with a slight curvature apparently present in some specimens) and narrow with a small, distal anteriorly expanded 'boot'. The ilium resembles (in simple outline shape) that of *H. fittoni*. However, in detail (Norman, 1986: fig. 54) the blade is lower and the preacetabular process is narrower proximally and develops an expanded medial ridge, which is very different when compared to that seen in *H. fittoni*. The postacetabular process develops a much less extensive and more posteriorly positioned brevis fossa. The hindlimb of *M. atherfieldensis* is less robust than that of *H. fittoni*; the femur (Norman, 2011a: text-figs 27.11, 27.46) has a less angular-sided shaft, the anterior trochanter is positioned more laterally and is narrow and blade like, the fourth trochanter is more proximally positioned and proportionally smaller than that seen in *H. fittoni*. The more distal portions of the limb and pes differ only in their comparative gracility.

Jinzhousaurus yangi Wang and Xu, 2001

This taxon is based upon the nearly complete skull and postcranial skeleton of an ornithopod, of about 5 metres body length, collected from the Yixian Formation of Liaoning Province, China and dated as early Aptian (Swisher, et al., 1999). Following the initial brief description and naming of this specimen two detailed papers describing the skull (Barrett, et al., 2009) and postcranial skeleton (Wang, et al., 2010) make this the best-illustrated and described Chinese derived ornithopod to date.

Teeth and jaws. Lateral crushing of the skull means that it is impossible to describe the structure of the lingual surface of individual dentary crowns. The lower jaw is robust and parallel-sided (Barrett, et al., 2009: fig. 1) and shows no indication of the arching of its ventral margin as seen in *H. fittoni*.

Axial skeleton. The cervical and dorsal series are typical in general conform to those of typical derived (non-camptosaur-grade) ornithopods. In particular there is no evidence of pronounced thickening of the articular margins of the centra as noted in *H. fittoni* and the neural spines (Wang, et al., 2010: figs 2-3) are comparatively short and broad (and very distinct from the tall and slender form of spines described in *H. fittoni*).

Appendicular skeleton. The pectoral girdle and forelimb (Wang, et al., 2010: figs 6-8) are similar in shape and proportions to those described for *H. fittoni.* The scapular blade appears to be more flared distally, but the sternals are very similar in shape and in both taxa there is a well-developed posteromedial apron on the blade; however there is no indication of fusion or co-ossification of sternals in the skeleton of *Jinzhousaurus* (Wang, et al., 2010: fig. 6). The radius and ulna are robust in *J. yangi* and more closely resemble those of *H. fittoni*. The carpus is partially fused, block-like and incorporates metacarpal I, which thus sets digit I off at an acute angle from the palmar metacarpals (II-IV). The principal manus elements resemble those seen in *H. fittoni*: the pollex ungual is spine-like, curved along its length and laterally compressed; it also appears to retain remnants of the claw grooves (Wang, et al., 2010: fig. 8). Metacarpals II-IV are subequal in length and appear closely appressed when articulated naturally. Digits II and III end in well developed, flattened unguals (which are not present on digits IV and V). The pelvis and hindlimb are less well preserved and more difficult to interpret. The postacetabular process of the ilium bears a lateral ridge and brevis fossa that resembles that seen in *H. fittoni*. The ischium is robust and has a slightly curved shaft and modestly expanded ischiadic ‘boot’ at its distal end. The femur is also robustly constructed and, although crushed, the structure of the anterior and fourth trochanters and the form of the shaft are reminiscent of the structures seen in *H. fittoni*. Attention is drawn to the similarities between this taxon and *Bolong* (below).

Bolong yixianensis Wu, Godefroit and Hu, 2010

A partial skull and articulated skeleton of a medium-sized (3-4 metres long) ornithopod that was collected at Bataigou, Toutai, Yixian County, western Liaoning Province, China (middle Yixian Formation: late Barremian-early Aptian). This specimen was first reported on the basis of its cranial remains (Wu, et al., 2010), but a more complete description has now been published (Wu & Godefroit, 2012).

Teeth and jaws. The dentary teeth display a distally off-set primary ridge and less prominent secondary ridge that divides the mesial sector of the crown; there are no multiple accessory ridges seen on these crown surfaces as are present in crowns of *H. fittoni*.

Axial and Appendicular skeletons. The dorsal and caudal vertebrae display rectangular slightly posteriorly inclined neural spines, but these are not narrow and elongate as in *H. fittoni*. The comparatively short and robust antebrachium resembles that seen in *H. fittoni*, but is capped distally by a group of six separate carpals, rather than a fused carpometacarpus. In the manus a flattened proximal phalanx is preserved at the base of the mobile, triangular and laterally compressed pollex ungual. The metacarpals of digits II-IV are comparatively short, robust and mcII is typically shorter than the other two. The second and third digits have flattened hoof-life unguals, the fourth digit has two small phalanges only and the fifth digit seems to have been divergent. The pelvis is poorly preserved, but the postacetabular process of the ilium appears to form a narrow rectangular plate, unlike that seen in *H. fittoni*. In other respects what can be seen of the pelvic and hindlimb elements seems to resemble the morphology of *H. fittoni*.

Taxonomic note. Wu & Godefroit (2012) reported that the caudal ribs of this specimen are unfused to their centra, which led them to suspect that this specimen had not attained adult size. The lack of co-ossification of the carpal elements may therefore also be a reflection of ontogenetic immaturity. Nevertheless the dental morphology, structure of the dorsal and caudal vertebrae as well as the structure of the postacetabular process of the ilium serve to distinguish *Bolong* from *Hypselospinus*. It is noted that these taxa share a number of anatomical similarities, despite their apparent incongruent stratigraphic (Valanginian vs late Barremian) and geographic (Europe vs Asia) distributions. It should also be noted, in passing, that *Jinzhousaurus* and *Bolong*, though they differ in size are sympatric, very similar anatomically and approximately coeval.

Siamodon nimngami Buffetaut and Suteethorn, 2011

Siamodon is based upon a well-preserved isolate maxilla with some teeth still in place. In addition, an isolated tooth and partial neurocranium have also been referred to this taxon. Collected at Ban Saphan Hin, Nakhon Ratchasima Province, NE Thailand, from the Khok Kruat Formation (Aptian – Buffetaut & Suteethorn, 2011: 52). These specimens are based upon material cannot be compared directly with the hypodigm of *H. fittoni*.

Taxonomic note. The diagnosis of this taxon does not include any autapomorphic states, which suggests that until more material is collected and described, this taxonomic name should be considered a *nomen dubium*. It is possible that this material is referable to *Ratchasimasaurus,* which was described (almost simultaneously) by another group of researchers (Shibata et al., 2011). However, the latter authors suggest, (based upon undescribed maxillae) that there may have been two distinct taxa in the Khok Kruat Formation.

Ratchasimasaurus suranareae Shibata, Jintaskul and Azuma, 2011. Comprises an isolated, toothless, left dentary collected from Khok Kruat Subdistrict, Muang Hakhon Ratchasima, Nakhon Ratchasima Province, NE Thailand (Khok Kruat Formation: Aptian). Diagnosed on the basis of its elongate and dorsoventrally shallow dentary ramus, this specimen displays the crown-shaped impressions in the replacement channels exposed in the medial view of the lateral alveolar wall (Norman, 2002); it also displays a low and oblique, but notably anteroposteriorly expanded coronoid process. The lower and more elongate form of the dentary ramus, the lower and transversely expanded symphyseal region and unusually thickened coronoid process, distinguish this material from the dentary elements referred to *H. fittoni*.

Taxonomic note. See *Siamodon* (above).

Ouranosaurus nigeriensis Taquet, 1975
Ouranosaurus is a well-described ornithopod from the Aptian (Taquet, 1976) or Aptian-Albian (Sereno, et al., 1999) of Niger. Comparatively slender in build, this animal attained a length of 6-7 metres when mature and is notable for the extremely elongate and expanded neural spines across its dorsal, sacral and caudal series (Taquet, 1975, 1976).

Teeth and jaws. The dentary teeth (Taquet, 1976: pl. XX) though similar in general shape to those of *H. fittoni,* do not show the complexity of morphology of secondary and accessory ridges seen in the latter taxon. The dentary of *O. nigeriensis* (Taquet, 1976: fig. 29) is extremely elongate, has a long edentulous region and its ramus deepens anteriorly, and therefore differs in structure from that seen in material referred to *H. fittoni*, although the comparative size and oblique orientation of the coronoid process of the dentary is similar in both taxa.

Axial skeleton. Both of these taxa can be distinguished by the remarkable elongation of their dorsal, sacral and caudal neural spines; however, those of *O. nigeriensis* are not only extremely elongate, but widen apically to create a completely different profile (Taquet, 1976: fig. 40) and have none of the complexity seen on the preaxial and postaxial edges seen in *H. fittoni*.

Appendicular skeleton. The postcranial skeletons of both taxa are generally similar although that of *O. nigeriensis* is more lightly constructed. The forelimb is more slender, notably the radius and ulna, but the carpometacarpal block is well developed and the pollex ungual is tall, sub-conical, bluntly pointed and exhibits little curvature (Taquet, 1976: fig. 57c). The pelvis differs from that of *H. fittoni* (Taquet, 1976: figs 58, 59). The femur is straighter than that of *H. fittoni* (Taquet, 1976: fig. 62) has a less angular shaft and has a laterally flattened anterior trochanter, the extensor intercondylar groove may have been more open when compared to that of *H. fittoni*. The remainder of the hindlimb has no obviously distinguishing anatomy although the pedal unguals may be shorter, more blunt and may lack claw grooves (Taquet, 1976: fig. 71d).

Lurdusaurus arenatus Taquet and Russell, 1999

Lurdusaurus is known from a partial articulated skeleton that has yet to be published in detail (Taquet & Russell, 1999; see Chabli, 1988). The specimen was collected at Gadouafaoua, Niger, N. Africa from deposits that are dated as Aptian (Taquet, 1976; Taquet & Russell, 1999) or Aptian-Albian (Sereno, et al., 1999). The specimen represents an extremely large, robustly constructed ornithopod that was a sympatric contemporary of *Ouranosaurus*.

Axial skeleton. The cervical and dorsal series are constructed similarly to those seen in other large-bodied ornithopods. The dorsal and caudal vertebrae appear to bear relatively short, and have thick neural spines, completely unlike those seen in either the sympatric contemporary *O. nigeriensis* or *H. fittoni*.

Appendicular skeleton. The pectoral girdle and forelimb are extremely robustly constructed. There is evidence for the presence of an intersternal ossification (Chabli, 1988) similar in morphology to that reported in *I. bernissartensis* (Norman, 1980) but this has not led to fusion between the sternal plates as seen in *H. fittoni*. The humerus is considerably longer than the very short, stout radius and ulna. The carpometacarpus is heavily co-ossified and the pollex is conical, curved and very large (similar to that seen in *I. bernissartensis*). The metacarpals are comparatively short and more closely resemble those typical of camptosaurians, which implies that the digits of the hand could be widely spread (Gilmore, 1909; pers. obs, USNM October 2011). What is known of the pelvis and hindlimb also differs significantly from the equivalent elements in *H. fittoni* (Chabli, 1988).

Jintasaurus meniscus You and Li, 2009

Jintasaurus comprises an incomplete posterior skull roof and braincase. It was found in the Yujingzu Basin, Jinta County, Ganzu Province, China and derives from the Xinminpu Group (Aptian-Albian).

Cranium. The skull roof is broad and flat, and the frontal contributes to the dorsal margin of the orbit. The skull profile (in occipital view) is low and broad and resembles that seen in *Ouranosaurus* (Taquet, 1976); the paroccipitals are elongate, curved and taper to a blunt point.

Taxonomic note. It is impossible to draw comparisons between the cranial elements of *Jintasaurus* (well described and illustrated) and the remains of its sympatric contemporary *Xuwulong* (below). Doubts must be expressed over the validity of *Jintasaurus* and *Xuwulong* as separate taxa.

Xuwulong yueluni You, Li and Liu, 2011

Xuwulong is represented by a complete skull, most of the vertebral column, the ribcage and the left pelvic girdle. The skeleton was collected from the Yujingzi Basin in Jinta County, northwestern Gansu Province, China and from the Xinminpu Group (Aptian-Albian), as does *Jintasaurus* (see above). The specimen has been described briefly, with some accompanying photographs and a simple interpretative outline of the skull.

Cranium. The skull, though slightly crushed, exhibits a flat skull roof and the frontal contributes to the dorsal margin of the orbit. A long, tapering palpebral crosses the orbit; the nasals from elongate rostral spines that are lodged against the mediodorsal premaxillary process; the external nares are enlarged and the premaxilla appears to be ventrolaterally flared. The quadrate is pillar-like and its jugal wing is deeply notched to receive the quadratojugal (a paraquadrate foramen may be present).

Teeth and jaws. A single functional tooth and one replacement crown are present in each alveolus. The maxillary crowns are described as possessing a single prominent primary ridge that is slightly offset distally on the crown face; occasional smaller secondary ridges may also be present. Dentary crowns are described as bearing two low ridges, with some additional weak ridges. The margins of the maxillary and dentary crowns are denticulate. The dentary is robust and bears a prominent, laterally offset and prominent coronoid process; the dentary ramus is robust and comparatively short, terminating in an obliquely positioned predentary, which bears a denticulate margin and a bifurcated ventral process.

Axial skeleton. A complete series of 11 cervicals are preserved, and it has been suggested that there are 16 dorsals; the sacral region is obscured by the pelvic bones, but it has been estimated that at least six sacrals are present. Nineteen caudals from the anterior and middle portion of the tail are preserved, along with their haemal spines. The dorsal vertebrae appear to support oblique, rectangular spines that are considerably shorter than those seen in *Hypselospinus.* Caudal vertebrae support narrower and taller neural spines.

Appendicular skeleton. The ilium is well preserved and resembles in the details of its form and proportions that of *Hypselospinus*. The pubis has an extremely elongate, expanded and down-turned prepubic blade and an elongate rod-shaped posterior pubic ramus. The ischium has an elongate, somewhat angular-sided, shaft that is arched dorsally and terminates in an anteriorly expanded boot; this bone appears to resemble the ischium of *Hypselospinus* in its general shape and proportions.

Taxonomic note. See *Jintasaurus* (above).

Proa valdearinnoensis McDonald, Espílez, Mampel, Kirkland and Alcalá, 2012b

Proa comprises cranial and postcranial remains of several individuals of a medium sized ornithopod (5-6 metres long) collected from the Escucha Formation (lower Albian) of Teruel, Spain. This taxon is only known from a preliminary description of some of the principal cranial bones, the pelvis and femur (McDonald, et al., 2012b).

Teeth and jaws. Maxillary crowns are morphologically similar to those of *H. fittoni* in that they are typically lozenge-shaped with a distally offset high primary ridge flanked by a variable number of strand-like accessory ridges (McDonald, et al., 2012b: fig. 7). Dentary crowns are broader and more shield-shaped but appear to lack the shoulder-like coronal margin seen in the crowns of *H. fittoni*, and have a rather more symmetrical (almost triangular) profile in lingual aspect. The primary ridge is distally offset and the secondary ridge (mesially positioned) is described as being of equal prominence, and faint multiple accessory ridges are also present. One functional tooth and one replacement crown is present in each alveolus. The dentary is well preserved and has a prominent, perpendicular coronoid process that has an expanded apex. The dentary ramus is arched along its length and is comparatively stout; its external surface of its distal end is modified to form a horizontal ridge and adjacent channel to accommodate the lateral arm of the large predentary bone. The alveolar recess is marked by replacement grooves for the teeth that do not form parallel grooves, but are shaped to accommodate the expanded crowns. The posterior alveoli extend posteriorly as far as the posterior margin of the base of the coronoid process.

Appendicular skeleton. The ilium has a prominent thick preacetabular process that is twisted axially, terminating in a horizontally orientated flange. The dorsal margin of the ilium is convex and posterodorsal to the ischiadic peduncle there is a prominent bulbous facet. The dorsal edge of the postacetabular process is elongate and curves smoothly ventrally, with no obvious abrupt break in slope; the ventral edge of this process was not described. In the structure of the preacetabular process, the dorsal margin of the iliac blade and the bulbous facet this ilium is distinct from that of *H. fittoni*. The pubic peduncle appears to show a well-developed supra-acetabular crest that does not form a lip along the dorsal margin of the acetabulum. The pubis has a notably elongate prepubic process, which forms a parallel-sided, comparatively narrow plate that is not expanded toward its distal end;

this morphology is unlike that seen in *H. fittoni*. The femur, though somewhat crushed and distorted, appears to have a straight shaft, and does not seem to display the angularity of the shaft see in *H. fittoni*. The femoral head is globular and offset medially, but it is unclear whether the posterior side of the head was notched; the anterior trochanter appears to be robust and similar in form to that of *H. fittoni*, and the 4th trochanter is large and of the crested form. The extensor intercondylar groove is completely enclosed by expansion of the adjacent condyles, and unlike the morphology seen in *H. fittoni*.

Altirhinus kurzanovi Norman, 1998

Altirhinus includes the skull and partial skeleton of a medium-large sized ornithopod (~8 metres long) collected from the lower Albian of Khuren Dhuk, Mongolia (Norman, 1998; Hicks, et al. 1999).

Teeth and jaws. The dentary teeth (Norman, 1998: figs 21, 22) have broad, shield-like lingual surfaces divided by ridges. There is a distally offset primary ridge and a mesial secondary ridge, but there is a consistent additional pattern: distally positioned accessory (tertiary) ridges give the crown a more symmetrical appearance. None of the mesially placed strand-like accessory ridges, seen in the dentary crowns of *H. fittoni,* are present on the crowns of *A. kurzanovi*. At least three teeth (two replacement and one functional) appear to be present in each alveolus of the dentary. In some instances two crowns within the same alveolus contribute to the occlusal surface of the dentary (Norman, 1998: fig. 22). The dentary has a generally similar form (Norman, 1998: fig. 16) to that seen in *H. fittoni*. However, the anterior portion of the dentary of *A. kurzanovi* is longer and more strongly arched near the symphysis and the coronoid process is both taller and more obviously perpendicular to the long axis of the jaw.

Axial skeleton. This part of the skeleton is poorly represented in the original material. Short and broad neural spines are found on the anterior caudals (Norman, 1998: fig. 24) and distinguish these from those seen in *H. fittoni*.

Appendicular skeleton. The forelimb resembles that which is seen in large-bodied ornithopods, except that the radius and ulna are more slender and elongate (Norman, 1998: fig. 28). The carpals are not co-ossified (Norman, 1998: fig. 29) and the manus is notable for the elongation and close opposition of metacarpals II-IV. The pollex ungual (Norman 1998: fig. 31A,B) is large, pointed, laterally compressed and retains paired claw grooves; it has a narrower base than that seen in *H. fittoni*. The pelvis is distinct from the latter species in having an ilium with a well-developed medial ridge on the preacetabular process, a pronounced eversion along the dorsal margin in the region just posterior to the ischiadic peduncle and no obvious development of a lateral ridge-brevis fossa complex along the ventrolateral edge of the postacetabular process. The prepubic process is blade-like, laterally compressed, expands distally and is arched ventrally along its length and quite distinct from that seen in *H. fittoni*. The ischium has a narrow straight shaft, quite distinct from that seen in *H. fittoni*, but the form of its distal end is unknown (Norman, 1998: figs 32-34). The remainder of the hindlimb is poorly preserved (Norman, 1998), but the femur is reported to have had a curved (rather than straight) shaft, and what is known of the remainder of the hindlimb differs in no obvious way from what is known in medium to large-sized iguanodontians.

Penelopognathus weishampeli Godefroit, Li and Shang, 2005

This taxon is based upon an isolated dentary, with some embedded tooth crowns, belonging to a medium-sized (~3.5 metres long) ornithopod. It was collected at Qiriga, Inner Mongolia, China, and was recovered from the Bayan Gobi Formation, which is dated as Albian (Godefroit, Li & Shang, 2005).

Teeth and jaws. The dentary crowns appear to be remarkably similar to those seen in taxa such as *M. atherfieldensis* (compare Godefroit, Li & Shang 2005: fig. 3, with Norman 1986: fig. 21), and are thus distinct from those referred to *H. fittoni*. The dentary ramus is straight, rather than arched anteriorly; the coronoid process is tall and perpendicular to the long-axis of the dentary, rather than short and oblique as appears to be the case in *H. fittoni*.

Taxonomic note. The diagnosis of this specimen lacks any characters that might be considered unique among iguanodontian ornithopods, and this taxon is therefore considered a *nomen dubium*. Despite the claim that this is an Albian-aged taxon, the morphology of the dentary and its teeth to resembled those seen in the Barremian-Lower Aptian taxon *M. atherfieldensis* (e.g. NHMUK R5764 – Norman, in preparation).

Lanzhousaurus magnidens You, Ji and Li, 2005

Lanzhousaurus is known from some skull bones and teeth, parts of the vertebral column and some individual appendicular elements. Collected from Zhongpu, Gansu Province, China, and reported as coming from the Hekou Group ("Early Cretaceous" – You, Ji & Li, 2005: 786).

Teeth and jaws. The dentary teeth resemble those described in *H. fittoni* quite closely in outline and in the details of the ridge pattern on the lingual enamelled surface of the crown. The teeth of *Lanzhousaurus* are substantially larger than those of *H. fittoni* (some being reportedly 75mm wide across the enamelled face – You, Ji & Li, 2005: fig. 2E) and there are far fewer tooth positions (14) in the dentary of *L. magnidens*. The dentary is arched anteriorly and there is a large, obliquely inclined coronoid process (You, Ji & Li, 2005: fig. 1A,D).

Axial skeleton. The centra of cervical vertebrae are opisthocoelous and the anterior dorsal series exhibits tall, but comparatively thick neural spines (You, Ji & Li, 2005: fig. 3A) that are more closely comparable to those of *B. dawsoni* or *I. bernissartensis* than the slender and elongate morphology seen in *H. fittoni*.

Appendicular skeleton. A sternal plate (You, Ji & Li, 2005: fig. 3B) is preserved and is similar in outline to that see in *H. fittoni* in having a large 'blade' and a comparatively short, flattened 'handle'. The pubis (You, Ji & Li, 2005: fig. 3C) shows a deep, laterally compressed prepubic process that is strongly expanded distally; this is unlike the general form inferred in material assigned to *H. fittoni*.

Equijubus normani You, Luo, Shubin, Witmer, Tang and Tang, 2003 – (McDonald, et al., 2014)

Equijubus was collected from the “Middle Grey Unit”, Xinminpu Group (Albian: Tang, et al., 2001), Gongpoquan Basin, Gansu Province, China (You, et al., 2003). The specimen comprises a nearly complete skull and a very incomplete postcranial skeleton comprising a series of articulated cervical and dorsal vertebrae, as well as some pectoral, pelvic and hindlimb fragments (McDonald, et al., 2014).

Teeth and jaws. The dentary teeth are broad and shield-shaped and similar in general outline to those of *H. fittoni* in having a distally offset primary ridge (but this is generally rather less prominent and poorly developed compared to *H. fittoni*), an indistinct secondary ridge and multiple strand-like accessory ridges. The dentary crowns have a narrower coronal margin and a less pronounced mesial ‘shoulder’ than seen in *H. fittoni*. The marginal denticles form simple conical structures, but those found on the mesial and distal edges of the crown form curved ledges that wrap around these edges and are mammillate. Though two replacement crowns were reported to be present beneath each functional tooth (You, et al., 2003), this seems to be contradicted by McDonald, et al., (2014) and a single replacement crown seems to have been present, as in *H. fittoni* (NHMUK R1831).

Axial skeleton. The cervicals and dorsals show no particularly distinguishing characters. The bases of some neural spines suggest that the neural spines were thick and robust, and not narrow and elongate, as in *H. fittoni*.

Appendicular skeleton. The sternal resembles that of *Mantellisaurus* in having an elongate, dorsoventrally compressed ‘handle’ and a relatively small ‘blade’ and small posterior process (unlike that of *H. fittoni*). The incomplete ilium is attached to the sacrum. In general outline the preserved central portion resembles, in its proportions, that of *H. fittoni* but the brevis fossa appears to be absent and there is a more strongly everted facet on the dorsal margin of the blade, posterodorsal to the ischiadic peduncle. A fragment of the prepubic process is preserved and this suggests that this bone formed a laterally compressed plate with a pronounced distal expansion. The remnants of the femur indicate that the extensor intercondylar groove was completely enclosed and the distal portion of the femoral shaft was probably straight, rather than bowed.

Nanyangosaurus zhugeii Xu, Zhao, Lü, Huang, Li and Dong, 2000

This taxon is based upon an incomplete postcranial skeleton of a medium sized (~4.5 metres long) ornithopod collected from the Sangping Formation of Neiziang, Henan Province, China (Xu, et al., 2000). This formation was described as "Early Cretaceous" in age but the support for this dating is vague. *Nanyangosaurus* is incompletely described and will benefit from an accurate description, so that its anatomy and relationships can be clarified.

Teeth and jaws. Are unknown in *Nanyangosaurus*.

Axial skeleton. What little is known suggests that this ornithopod had dorsal vertebrae with neural spines (Xu, et al., 2000: fig. 1) that were neither narrow nor very elongate, as they are in *H. fittoni*.

Appendicular skeleton. The forelimb was more lightly constructed than in *H. fittoni*, with the radius and ulna being comparative slender and bowed along their length (Xu, et al., 2000: fig. 2D). There is no evidence for the presence of a pollex spine, and the carpus was not described although it was mentioned in translation as being "reduced" (this structure might be able to provide additional information on the presence/absence of digit I in the manus). The femur (Xu, et al. 2000: fig. 2G,H) differs from that of *H. fittoni* in that it appears to have a straight shaft and the extensor intercondylar groove is deeply recessed. The latter is not, however, completely tunnel-like by being enclosed by bony lips developed from the edges of distal condyles.

Eolambia caroljonesa Kirkland, 1998 - (McDonald, et al., 2012a)

Eolambia is represented by several partial skulls and postcranial material collected from the Mussentuchit Member of the Cedar Mountain Formation (lower Cenomanian) of eastern Utah, USA (Hunt, et al., 2011). Material indicates a medium-large sized ornithopod (~7-8 metres in length).

Teeth and jaws. Dentary teeth are narrower, lanceolate and more nearly symmetrical in lingual view (Kirkland, 1998: fig. 7B) than those described in *H. fittoni*. The primary ridge is dominant and only slightly distally offset on the crown surface and there is no obvious secondary ridge (although there is a slight thickening along the mesial edge that may represent a remnant of the secondary ridge (Norman, pers. obs. 1998). There is little evidence of strand-like accessory ridges. The dentary expands anteriorly and shows comparatively little evidence of a ventral arch (Kirkland, 1998: figs 5H,J - 6A,B); the coronoid process is also very tall and perpendicular to the long-axis of the dentary (compared to the short, oblique coronoid process in the dentary referred to *H. fittoni*).

Axial skeleton. The vertebral column displays cervicals that resemble those of *H. fittoni*, but the dorsal series has comparatively short, plank-like neural spines and the centra do not have the expanded rims seen in *H. fittoni*.

Appendicular skeleton. The pectoral girdle displays a narrow bladed elongate scapula with a J-shaped acromial process. The coracoid has a fully enclosed coracoid foramen and the sternals are hatchet-shaped with an elongate, dorsoventrally flattened ‘handle’ that projects from the posterolateral edge and a comparative short ‘blade’. The humerus is sigmoid and resembles that of Mantellisaurus quite closely. And the radius and ulna are relatively slender and elongate compared to the short and robust morphology of *H. fittoni*. Carpal elements have not been described, nevertheless many isolated manus elements are known (McDonald, et al., 2012a: fig. 29, 30). These include what appears to be a large pollex ungual that is laterally flattened and bluntly truncated (broken?) and bears a remnant of the claw groove (CEUM 5212; Norman, pers. obs. 1998). A smaller conical pollex ungual was found by the author in the Mussentuchit Member of the CMF of Utah in 1998 (CEUM 52962 – McDonald, et al., 2012a: fig. 30A); this suggests that an abbreviated metacarpal 1 and ossified carpus may have been present. Individual manus elements (metacarpals) suggest that the manus was relatively slender and elongate: intermediate between the proportions of *Mantellisaurus* metacarpals (Norman, 1986) and the more elongate metacarpals of *Probactrosaurus* (Norman, 2002).

Unlike *H. fittoni*, the preacetabular process of the ilium is elongate and expands distally to form an enlarged flange; near its base this process has a pronounced medial ridge. The dorsal margin of the ilium (Kirkland, 1998: fig. 10A; McDonald, et al., 2012a: fig. 31A,B) bears an everted bevelled edge in the region posterodorsal to the ischiadic peduncle; this differs from the structure in this area in *H. fittoni*. There is no brevis fossa (McDonald, et al., 2012a: 30), in contrast to *H. fittoni* in which this structure is very well developed. The pubis has a deep, narrow prepubic process that is expanded distally and has a very different profile to that seen in *H. fittoni*. The ischium has a narrow and straight shaft that terminates in an anteriorly expanded 'boot' (McDonald, et al., 2012a: fig. 31E,F). The remainder of the postcranium has not been described in sufficient detail for further comparison. The femur has a shaft that is curved medially, but straight when viewed in lateral aspect, unlike the bowed femoral shaft of *H. fittoni*. The distal elements differ in no significant way from those seen in other large-bodied iguanodontians: there are three well-developed metatarsals, and the ungual phalanges have an arrowhead-like profile and prominent claw grooves when viewed dorsally.

Protohadros byrdi Head, 1998

Protohadro is represented by a partial skull and fragments of the postcranium collected from the Cenomanian of Texas (Head, 1998). This represents a comparatively derived ornithopod whose anatomy differs substantially from that of *H. fittoni*.

Teeth and jaws. Dentary teeth (Head, 1998: fig. 13) appear to be narrower in lingual view than those seen in *H. fittoni* and more symmetrical, exhibiting a prominent sub-median primary ridge. The lower jaw is represented by a well-preserved dentary that is deeply expanded anteriorly, as well as being strongly arched along its length. The dentition was clearly borne in a deep alveolar trough and posteriorly there is a tall perpendicular coronoid process (Head, 1998: fig. 11).

Postcranial skeleton. What little is currently known (Head, 1998) cannot be compared to that of the hypodigm of *H. fittoni*.

Probactrosaurus gobiensis Rozhdestvensky, 1952 - (Norman, 2002)

Remains of this taxon indicate the presence of a medium-sized iguanodontian (attaining ~6 metres in length) collected from the Ulansuhai Formation (Turonian), Maortu, China (Kobayashi & Lu, 2003).

Teeth and jaws. The dentary crowns of this taxon (Norman, 2002: figs 14-16) are narrower and less ornate than those described in *H. fittoni* (Fig. 37). The marginal denticles support mammillations, but these are less numerous than in the case in *H. fittoni* and the denticles do not form a curved shelf as they do in *H. fittoni*. The roots of the teeth are also fluted for the compaction of adjacent functional and replacement crowns that form the dental magazine. There are at least two replacement crowns in each alveolus in the deeper portions of the dentary and the occlusal surface is broad because it comprises at last two dentary crowns, unlike *H. fittoni*. The dentary of *P. gobiensis* is comparatively shorter and deeper than that of *H. fittoni* with a larger and deeper area devoted to the dental magazine as well as a tall, perpendicular coronoid process (Norman, 2002: fig. 12).

Axial skeleton. What is known of the dorsal vertebral series (Norman, 2002: fig. 17) shows neither the thickening of the articular margins of the centra, nor any clear indication of the narrow and very tall neural spines that are displayed in *H. fittoni* (this is confirmed by reference to the shape of the anterior caudals – Norman, 2002: fig. 18).

Appendicular skeleton. Most of the postcranial anatomy of *P. gobiensis* (Norman 2002: figs 20-33) appears to be gracile and generally comparabnle to that seen in *M. atherfieldensis* (Norman, 1986) rather than *H. fittoni*. The forearm and manus are notably slender and lightly built in *P. gobiensis*, and the pollex ungual is small, narrow and conical (Norman, 2002: figs 22-26) in marked contrast to these structures in *H. fittoni*. The ischial shaft is heavy, robust and J-shaped (Norman, 2002: fig. 29) and resembles that seen in *H. fittoni*.

Jayewati rugoculus McDonald, Wolfe and Kirkland, 2010c

This taxon is based upon a partial disarticulated skull and fragmentary postcranium of a single (medium sized ~4 metre long) individual. It was collected in Catron County, New Mexico, USA, from the Moreno Hill Formation, which is regarded as middle Turonian in age.

Teeth and jaws. The dentary teeth in lingual aspect are narrow and lanceolate and have a simple, slightly distally offset, carina (primary ridge) and accessory ridges are few and distributed on mesial and distal fields, on either side of the primary ridge (McDonald, et al., 2010c, fig. 6A). There are at least two replacement crowns beneath the functional row of crowns within the dental magazine. The dentary (McDonald, et al., 2010c: fig. 5C-E) is long and slender with a pronounced diastema; the dentary is arched along its length and the coronoid process is perpendicular and its distal portion is anteriorly expanded. In all respects the teeth and jaws are distinguishable from those referred to *H. fittoni* and strongly resemble the features exhibited by hadrosauromorph ornithopods.

Axial and Appendicular skeletons. No comparison is possible.

Levnesovia transoxiana Sues and Averianov, 2009

Levnesovia comprises a partial skull roof and braincase, supplemented by a range of referred cranial and postcranial elements collected at Dzharakuduk, Uzbekistan from the Bissekty Formation (middle-late Turonian).

Teeth, jaws and cranial skeleton. Dentary teeth in lingual aspect are relatively narrow and diamond-shaped, and strongly resemble those described in *Probactrosaurus* (Norman, 2002) and *Bactrosaurus* (Godefroit, et al., 1998). A prominent primary ridge is positioned slightly distally on the crown and there is an indistinct secondary ridge on the mesial portion of the crown; the coronal region possesses a distinct 'shoulder'. Maxillary crowns are lanceolate and retain a remnant shoulder along the coronal margin and a very prominent primary ridge and no supplementary ridges. The predentary has a crudely denticulate margin and a pair of large vascular foramina on either side of the midline, with broad, oblique vascular channels (the general configuration resembles that described in *Probactrosaurus*). The dentary ramus is comparatively slender and slightly arched anteriorly (as in *H. fittoni*); there is a short diastema and the alveolar wall is marked by inclined, parallel tooth grooves. The alveolar trough extends medial to the coronoid process, from which it is separated by a horizontal shelf and the tooth magazine is reported to terminate approximately level with the apex of the coronoid process. The surangular is reported to lack a foramen.

The ventral half of the quadrate has a laterally expanded condylar region that is stepped so this it forms a rounded lateral condyle separated by a saddle-like region from the flatter medial articular surface. The quadrate embayment appears to be wide and the paraquadrate foramen is completely closed by the quadratojugal. The jugal is tapers anteriorly and has a broad flat facet for its contact with the maxilla – there is no evidence of an ectopterygoid facet. The skull roof is broad and flat and a short section of the frontal exposed in the upper rim of the orbit. In almost every respect, the skull roof and braincase resembles that seen in *Probactrosaurus* and *Bactrosaurus*.

Postcranial skeleton. Vertebrae are poorly preserved, but the dorsals have the low centrum profile that is typical of derived iguanodontians. The prepubic process is laterally compressed, deep and distally expanded unlike that seen in *H. fittoni*. The distal femoral articular condyle has an almost entirely enclosed extensor intercondylar groove and the pedal unguals are notably short and broadly rounded in plan view (Sues & Averianov, 2009: supplementary material 1, fig. t); these features contrast markedly with those seen in *H. fittoni*.

Batyrosaurus rozhdestvenskyi Godefroit, Escuillié, Bolotsky and Lauters, 2012

This taxon comprises a partial skeleton collected at Akkurgan, Kazakhstan from the Bostobinskaya Svita (Santonian-Campanian).

Dentition, jaws and cranium. Dentary crowns are broader than their maxillary counterparts and are broad and shield-like with a distally offset primary ridge, a well-defined secondary ridge and a comparatively short tertiary (accessory) ridge is present near the mesial edge of the crown; there is also a tertiary ridge on the distal portion of the crown. The structure of the crown suggests that a distinct mesial shoulder was present on the coronal margin. The marginal denticles form curved mammillated ledges down the sides of the crown, but are simple and cone-shaped along the upper (coronal) margin). Tooth morphology is very similar to that described in *Altirhinus* (Norman, 1998). The dentary ramus is slightly arched anteriorly and comparatively narrow. The coronoid process is low and oblique and the alveolar trough is marked by tooth grooves that bear the remnant shape of broad tooth crowns (rather than parallel-sided slots). These structures are similar to those seen in *H. fittoni*. The alveolar trough extends medial to the coronoid process and may not have extended beyond the anterior margin of the base of that process (this is obscured by breakage). There was an abbreviated diastema and the predentary which has a denticular oral margin and paired oblique vascular channels adjacent to the midline, also tapers anteriorly (in plan view) and resembles that which was described as a unique feature of *Proa* (McDonald, et al., 2012b). A surangular foramen is present. The cranial roof is broad and flat, and the frontal forms a portion of the dorsal orbital rim. The quadrate has a narrow, semicircular embayment with facets, dorsally and ventrally, for the quadratojugal; this suggests that a paraquadrate foramen was present (this was also argued to be the pattern in *Altirhinus*, *Probactrosaurus*, *Jayewati*, *Bactrosaurus* and *Gilmoreosaurus* – Godefroit, et al., 2012). In most respects the anatomical similarities to those seen in the stratigraphically much earlier *H. fittoni* are close.

Postcranial skeleton. Sternal bones are hatchet-shaped with an elongate 'handle'. The radius appears to be slender (and approximately of equal length to the humerus) although the distal articular end is dorsoventrally expanded. A somewhat eroded and conical (possible?) pollex ungual is described (Godefroit, et al., 2012: fig. 20.11,F).

Tethyshadros insularis Dalla Vecchia, 2009

Tethyshadros comprises a nearly complete articulated skeleton of a hadrosaur-like (hadrosauromorph – see systematics section below) iguanodontian collected near Villaggio del Pescatore, Trieste Province, Italy. The specimen was recovered from the Liburnian Formation (Upper Campanian-lower Maastrichtian).

Teeth and jaws. The dentary teeth, though not exposed, are evidently small and lanceolate and bear a single median carina (primary ridge) flanked on either side by a single accessory ridge (Dalla Vecchia, 2009, fig. 3), and the marginal denticles form simple cones, rather than curved, mammillate ledges. By comparison the dentary teeth of *H. fittoni* are broad and shield-shaped, have a distally offset primary ridge as well as several additional ridges, and the marginal denticles form ledges that are fringed with irregular mammillae. Tooth replacement patterns, the relative sizes of dentary and maxillary crowns, the number of teeth in each alveolus and involved in the occlusal surface are all unknown at present. The lower jaw is elongate and slightly arched anteriorly, as is also the case in *H. fittoni*.

Axial skeleton. Most notably, the dorsal vertebrae of *T. insularis* (Dalla Vecchia, 2009: fig. 1) bear short, reclined, rectangular neural spines in sharp contrast to the tall, narrow spines seen in *H. fittoni*.

Appendicular skeleton. The pectoral girdle has a hadrosaur-like scapula with a straight acromion that follows the dorsal margin of the blade near its proximal end (unlike the J-shaped form seen in *H. fittoni*); the sternal plate is hatchet-shaped and has a narrow, elongate, rod-like ‘handle’. The forelimb is gracile, with a slender, tapering radius and ulna, a reduced carpus and slender, elongate metacarpals (this differs markedly from the robust form of these bones in *H. fittoni*). Digit I of the manus is not present (in striking contrast to *H. fittoni*). The ilium has a strongly everted dorsal margin in the region posterodorsal to the ischiadic peduncle; this area rather than forming a bevelled thickening is developed into a pendant, tab-like structure referred to as a pendule (Norman, 2014). The postacetabular process of the ilium forms a flat rectangular plate with the bevis fossa (if present) restricted to its medial surface. The prepubic process is deep, transversely compressed and expanded distally. The ischial shaft is slender, slightly bowed and tapers distally (there is no terminal boot at the end of the ischial shaft). The femur has a straight shaft. In all these pelvic and hindlimb features this taxon differs markedly from *H. fittoni*.

Telmatosaurus transsylvanicus (Nopcsa, 1900) – (Weishampel et al., 1993)

Telmatosaurus is represented by an associated, but crushed, skull and partial skeleton (~3 metres long) and assorted disarticulated specimens of a hadrosauromorph collected from the Sinpetru-Densus Ciula Formation (Maastrichtian) of the Hateg Basin, Romania.

Teeth and jaws. Dentary crowns are narrow and lenticular with an acutely pointed coronal margin. There appear to be as many as four replacement crowns and two or three worn crowns in the vertical succession. Dentary crowns are curved slightly distally. A median, primary ridge subdivides the enamelled surface but is less prominent than those seen on maxillary crowns. Some crowns have an accessory ridge near the mesial edge of the crown. The crown margins are denticulate, and the denticles found mesially are buttressed by short enamel ridges. The dentary crowns are also not miniaturized (being approximately twice as broad as those in the maxilla). The dentary ramus is straight and the alveolar region occupies a substantial proportion of its vertical depth. The alveoli extend more posteriorly than the posterior of the coronoid process. The coronoid process is very prominent, rises vertically from the dentary and has an anteroposteriorly expanded apex. These features differ markedly from those seen in *H. fittoni*.

Axial skeleton. Although not well preserved the axial skeleton exhibits opisthocoelous cervicals as well as dorsals. The neural spines of dorsals and caudals are comparatively short; there is no evidence of thickened articular rims to the dorsal vertebral centra. These features differ from those see in *H. fittoni*.

Appendicular skeleton. The scapular blade is elongate and flares distally; proximally, the acromion forms a promontory that is in line with the main axis of the scapular blade (rather than being J-shaped as in *H. fittoni*). The humerus is sigmoid with a prominent deltopectoral crest. The ulna is longer than the humerus and tapers distally, indicating the distal elongation of the forelimb and a slender, gracile manus was probably present (this contrasts markedly with comparable bones in *H. fittoni*). The femur is elongate and straight along its entire length. The 4th trochanter is crested, triangular in profile (as in *H. fittoni*) and positioned on the proximal half of the shaft of the femur. The extensor intercondylar groove is entirely enclosed (in contrast to *H. fittoni*). The more distal elements of the hindlimb show no particular features beyond those normally associated with medium-sized iguanodontians.

Bactrosaurus johnsoni Gilmore, 1933 – (Godefroit, et al., 1998)

Bactrosaurus is represented by abundant skeletal remains of a medium-sized (6-7m long) ornithopod collected from the Iren Dabasu Formation, Erenhot, China: Turonian-Coniacian (Sues & Averianov, 2009). However, it should be noted that estimates of the age of these beds have ranged from Albian to Maastrichtian (Prieto-Márquez, 2011a).

Teeth and jaws. The dentary teeth are described as being leaf-shaped and “distinctly … wider” (Godefroit, et al., 1998: 27) than those of the maxillary dentition. Dentary teeth are slightly recurved distally (as in *Telmatosaurus*) and the primary ridge is less prominent than that seen on maxillary crowns. The primary ridge is displaced slightly distally. A secondary ridge is present on the mesial sector of the crown, and some of the posterior teeth in the dentition are described as bearing a third longitudinal ridge. The dentary is robust, straight and had a deep alveolar trough to accommodate the dentition. The coronoid process is tall and perpendicular to the long axis of the dentary and has an expanded apex. The dentition appears to extend posteriorly as far as the posterior edge of the base of the coronoid process.

Axial skeleton. The vertebral column conforms to that seen in medium-large bodied iguanodontians. The cervicals are strongly opisthocoelous and have short, neural spines. Dorsals have spool-shaped centra that retain shallow opisthocoely throughout, and whose articular margins are not very thickened, in contrast to those of *H. fittoni*. The neural spines are elongate, but are thickened axially, and notably transversely toward the apex; they do not exhibit the extreme slenderness and elongation seen in *H. fittoni*.

Appendicular skeleton. The scapular blade flares distally, and proximally the acromial process is developed into a promontory that is in line with the axis of the scapular blade (rather than being J-shaped as in *H. fittoni*). The sternal bones are hatchet-shaped and have an extremely elongate ‘handle’ and a comparatively short ‘blade’ (differing in proportion from those of *H. fittoni*). The humerus is strongly sigmoid and ‘stocky’ with a prominent deltopectoral crest. The ulna is subequal in length to the humerus and is comparatively slender and tapers distally before thickening slightly. The radius is comparatively slender and bowed along its length and again thickens where it articulates with the distal end of the ulna and carpal region. The manus elements (metacarpals) have been described briefly, but remain largely un-illustrated (Godefroit, et al., 1998) and have been described as resembling, in proportions, those of *Mantellisaurus*. Prieto-Márquez (2011a: pl. 4) provided photographs of juvenile metacarpals that confirm Godefroit's description (these are more slender than those of *H. fittoni*).

The ilium has an elongate, untwisted preacetabular process that terminates in a modest flange and there is a prominent medial ridge near its origin on the main blade of the ilium. The ilium illustrated by Godefroit, et al., (1998: fig. 30) is clearly a left ilium (rather than a right as stated) and all the surface-related annotations are incorrect. There is a lateral expansion of the dorsal margin of the iliac blade posterodorsal to the ischiadic peduncle ('supraacetabular process' of Prieto-Marquez, 2011a) and the postacetabular process tapers to a blunt terminus and appears to lack a brevis fossa. The pubis has a thin, dorsoventrally flared, prepubic process (cf. Gilmore, 1933: fig. 37 and Godefroit, et al., 1998: fig. 32, pl. 12) and the ischium has a robust, thick and straight shaft with a distal, anteriorly expanded, 'boot'. The femur has a straight shaft, a triangular, crested 4th trochanter positioned at mid-shaft and the extensor intercondylar groove is tunnel-like. The distal hindlimb elements do not show any unusual characters, being typical of medium-large bodied ornithopods generally, and the pedal unguals are arrow-head shaped in plan view, but have broadly rounded (rather than narrow and bluntly truncated) distal tips and weak development of the lateral claw grooves.

Gilmoreosaurus mongoliensis (Gilmore, 1933) – (Prieto-Márquez & Norell, 2010)

Gilmoreosaurus comprises the partial remains of four individuals of a hadrosauromorph collected from the Iren Dabasu Formation, Erenhot, China: Turonian-Coniacian (Sues & Averianov, 2009). However, it should (again) be noted that estimates of age of these beds have ranged from Albian to Maastrichtian (Prieto-Márquez, 2011a).

Teeth and jaws. Maxillary crowns are narrower than dentary crowns, but have a more prominent median primary ridge. Dentary crowns have a single median (or submedian) lower primary ridge. Neither dentary nor maxillary crowns appear to have accessory ridges. The marginal denticles are also ledge-like and bear mammillae (these were also reported to be present in *Protohadros*, *Lophorhothon* and some lambeosaurines (Prieto-Márquez & Norell, 2010: 18). The dentary ramus is imperfectly known, but differs very little from that described in *Bactrosaurus* its sympatric contemporary. This dental morphology is distinct from that see in *H. fittoni*.

Axial skeleton. The axial skeleton is very similar to that described in *Bactrosaurus*, and displays no distinct characters of significance.

Appendicular skeleton. The pectoral girdle and forelimb are very similar in morphology to that described above for *Bactrosaurus*. The ilium differs in the more posterior positioning of the transverse expansion of the dorsal iliac blade, when compared to that of *Bactrosaurus* and in the development of a bar-like postacetabular process. The pubis has a prepubic process that is less expanded proximally, the distal expansion is less extreme and the process overall appears to be longer than that seen in *Bactrosaurus*. Remaining elements of the pelvis and hindlimb seem indistinguishable in these two taxa; however the unguals of the pes are notable narrower and taper to a bluntly truncated tip, rather than been broad and rounded as in the case of those described for *Bactrosaurus* (cf. Prieto-Márquez & Norell, 2010: fig. 18 and Godefroit, et al., 1998: pl. 14).

Shuangmiaosaurus gilmorei You, Ji, Li & Li, 2003

This taxon is represented by a few cranial elements collected from the Sunjiawan Formation (‘middle’ Cretaceous), Beipiao, Liaoning, China. The specimens: maxilla plus articulated lacrimal and an edentulous dentary, were not associated and show evidence of post-mortem distortion, which may have contributed to the way in which its anatomy has been described and interpreted. In systematic analyses You, et al., (2003) place this taxon as the sister-taxon to the Hadrosauridae (=Euhadrosauria *sensu* Weishampel, et al., 1993; Norman, 2014) and McDonald (2012b) places it at just one further step removed

Teeth and jaws. Only maxillary crowns are known and exhibit a lanceolate shape, have a single median primary ridge and no accessory ridges and the mesial and distal margins of the crowns bear denticles. The dentary is very elongate and slightly arched along its length; it also appears to have had a relatively short diastema. The medial surface of the dentary ramus shows a deep and elongate alveolar trough that is backed by sets of alveolar grooves that appear to show the outlines of replacement crowns, rather than forming consistent parallel troughs (this is a non-hadrosauromorph characteristic). The alveolar trough extends back toward the posterior margin of the base of the coronoid process. The coronoid process is elongate but appears to form an obtuse angle to the long axis of the dentary ramus. The extent of post-morten distortion in this specimen (which is clearly evident in the maxilla that is described) makes it difficult to discern genuine and unique anatomy from structures that may simply reflect post-burial distortion.

Axial skeleton and appendicular skeleton. Unknown.

Typical euhadrosaur include the 'lambeosaurine' *Parasaurolophus walker* and the 'hadrosaurine' *Saurolophus osborni* and *Edmontosaurus regalis.* These have been characterised on the basis of detailed descriptions provided by Lambe (1920), Lull & Wright (1942), Ostrom (1961) and Maryanska & Osmolska (1981, 1984).

Comments on the comparative anatomy of basal ornithopod groups

Rhabdodontidae (e.g. Weishampel, et al. 2003; Godefroit, et al. 2009; Osi, et al., 2012; Butler, et al., 2008)

Rhabdodontids are medium-large (3~8 metres long) basal ornithopods (*sensu amplo*). The best-preserved and described examples of these taxa are *Zalmoxes robustus* (Weishampel, et al., 2003) and the contemporary *Z. shquiperorum* (Weishampel, et al., 2003; Godefroit, Codrea & Weishampel, 2009) from the lower Maastrichtian of Romania. Rhabdodontids, as a group, appear to be restricted to the late Cretaceous but range geographically across western Eurasia: *Rhabdodon* spp. France (Matheron, 1869; Buffetaut & Le Loeuff, 1991); *Mochlodon* spp. Hungary (Osi, et al., 2012) and Austria (Seeley, 1881). Related taxa also occur in late Lower Cretaceous of Australia (*Muttaburrasaurus* Bartholomai & Molnar, 1981, and pers. obs. 1978), South Africa (*Kangnasaurus*:

(Cooper, 1985, and pers. obs. 1993) and the Late Cretaceous of Antarctica (Unnamed taxon – Milner & Barrett in preparation and pers. obs. 2005).

Teeth and jaws. Dentary teeth are unusually large, shield-shaped and the lingual enamelled surface of the crown differs considerably in detail from that seen in *H. fittoni*. Dentary and maxillary crowns are typically clypeodont (Norman, in press a) in that they exhibit is a very prominent primary ridge, flanked upon either side by divergent sets of accessory ridges, whereas the maxillary crowns lack a prominent primary ridge labially and have a tightly packed array of apicobasally orientated accessory ridges. This general crown morphology is common to a range of basal ornithopod (clypeodont) taxa: *Hypsilophodon* spp., *Muttaburrasaurus langdoni*, *Rhabdodon* spp., *Zalmoxes* spp., *Mochlodon suessi*, *M. vorosi, Kangnasaurus coetzeei, Tenontosaurus* spp., and the unnamed Antarctic taxon (A.C. Milner & P.M. Barrett, in prep). The lower jaw is dominated by a robust dentary with a complex predentary suture that is not seen in *H. fittoni*; however, the coronoid process of the dentary is comparatively short and reclines at an obtuse angle to the long axis of the dentary, similar to that in *H. fittoni*.

Axial skeleton. The neural spines of the dorsal series are comparatively low and rectangular in lateral view, and are readily distinguished from the narrow and extremely elongate spines seen in *H. fittoni*.

Appendicular. The pectoral girdle, forelimb, pelvis and hindlimb differ in detail from the comparable elements of *H. fittoni* (Weishampel, et al., 2003; Godefroit, et al. 2009).

Tenontosaurs (e.g. Ostrom, 1970; Forster, 1990; Winkler, Murry & Jacobs, 1997; Butler, et al., 2008)

Tenontosaurs are medium-sized (5-6 metres long), basal ornithopods (‘iguanodonts’ *sensu amplo*) that range stratigraphically and geographically across the late Aptian-Albian of North America. Closer in size to *H. fittoni*, they differ substantially in their osteology from that known in *H. fittoni*.

Teeth and jaws. The salient features of the dentition of *T. tilletti* resemble those seen in rhabdodontids: dentary crowns have a prominent lingual median primary ridge while maxillary crowns lack a prominent primary ridge on the labial surface. The lower jaw is short, compact and the ramus straight, with no obvious arching of the dentary ramus anteriorly. The coronoid process is comparatively short and its axis is obtuse relative to the long-axis of the dentary. *T. dossi* Winkler, Murry and Jacobs, 1997 differs from *T. tilletti* in the possession of one premaxillary tooth.

Axial skeleton. Differs from *H. fittoni* in that the cervicals are weakly opisthocoelous (Forster, 1990: fig. 1) and the dorsals have comparatively tall centra and short, robust neural spines. The tallest neural spines in the vertebral column are to be found between the 10th – 12th caudals (Forster, 1990, fig. 5A).

Appendicular skeleton. While sharing a number of generalized anatomical similarities with *H. fittoni*, these taxa can be readily distinguished. In the forelimb the sternal bones are reniform, there is no co-ossification of the carpals, metacarpals are short and dumbbell-shaped, there is no off-set conical pollex ungual and tapering pointed unguals are present on digits I-III (Forster, 1990). The phalangeal count indicates the loss of one phalanx from digit III, a character that has been proposed as one that unites all iguanodontian ornithopods (Sereno, 1986). The pelvis is distinct in all details of its anatomy (Forster, 1990: figs 15-19). The hindlimb exhibits an elongate pendant fourth trochanter, a widely open extensor intercondylar groove and the pes is functionally tetradactyl, with narrow, pointed ungual phalanges (Forster, 1990: fig. 22).

Dryosauridae Milner and Norman, 1984 - (Janensch, 1955; Galton, 1981, 1983, Butler, *et al*., 2008)

Dryosaurids are small-medium sized (3-5 metres long) and generally lightly built (cursorial) animals that exhibit a range of distinct characters that have been used to differentiate the clade Dryomorpha from more basal ornithopods. Dryosaurids are first recognized in Callovian deposits and are also represented by un-named material that is sympatric and contemporary with *Hypselospinus*. Taxa such as *Valdosaurus* demonstrate that they persist into the Barremian-Lower Aptian (Norman, 2004, 2011b, Barrett, et al., 2011).

Teeth and jaws. The dentition exemplifies the dryomorphan configuration. The lingual surface of dentary crowns bear less prominent crown ridges with a more or less centrally positioned low primary ridge that is flanked on either side by a variable number of accessory ridges. Maxillary crowns, in marked contrast to more more basal taxa, have a labially enamelled surface that is dominated by prominent, distally offset, primary ridge. Such teeth are distinguishable in overall size and surface detail from those of *H. fittoni*. The lower jaw (dentary) differs significantly, being comparatively short and straight, while tapering anteriorly and bearing considerably fewer tooth positions than in *H. fittoni*.

Axial and appendicular skeleton. Cervical vertebrae are low and lack the strong opisthocoely exhibited in *Hypselospinus*. The dorsa vertebrae are lower, more cylindrical and exhibit relatively short neural spines. Appendicular skeleton. The pectoral girdle exhibits short, flared scapulae and the sternal bones are reniform, rather than hatchet-like. Details of the forelimb and manus structure (notably the phalangeal count) are not known. In the pelvis, the ilium and pubis are distinctive: the ilium has an elongate preacetabular process that is laterally compressed, curves gently laterally toward its anterior end and, in Valanginian forms, bears a longitudinal trough medially; the postacetabular process is shallow in lateral aspect and strongly expanded transversely, creating a broad, shallow brevis fossa. The pubic shaft is elongate and equal in length to that of the ischial shaft, which is distinct from the abbreviated shaft that is proposed for *Hypselospinus*; the prepubic process is knife-like (comparatively narrow and laterally compressed) rather than deep, plate-like and moderately distally expanded, as seen in *Hypselospinus*. The femur is bowed, slender, has a proximally positioned, pendant fourth trochanter and the extensor intercondylar groove is trough-shaped and open dorsally. The pes is functionally tridactyl, as in *Hypselospinus*, but the metatarsals and phalangeal digits are slender and the ungual phalanges are narrow and pointed.

Camptosaurus dispar Marsh, 1879 (Gilmore, 1909)

Camptosaur-grade ornithopods have been systematically reviewed in recent years (McDonald, 2011) and include *C. dispar*, *Cumnoria prestwichi* (Hulke, 1880); *Owenodon hoggii* (Owen, 1874; Norman & Barrett, 2002; Galton, 2009); *Uteodon aphanoecetes* (Carpenter & Wilson, 2008; McDonald, 2011); *Osmakasaurus depressus* (Gilmore, 1909; McDonald, 2011).

Camptosaurus dispar is chosen as a medium-sized (5-7 metres long) and reasonably well-described (Gilmore, 1909) iguanodontian and one that is closer to the size-range exhibited by *Hypselospinus*. Remains attributed to *C. dispar* are stratigraphically distributed between the Kimmeridgian and Tithonian stages and are thus substantially chronostratigraphically older than *Hypselospinus*.

Teeth and jaws. Maxillary and dentary crowns are similar in general morphology to those seen in dryosaurids and *Hypselospinus*, but the form of the dentary teeth (in particular) is distinctive. Unlike *H. fittoni,* the marginal denticles on the mesial and distal edges of the crown are not shelf-like and mammillate. The detailed structure of the primary, secondary and strand-like accessory ridges of dentary crowns are distinct: in comparison with *H. fittoni.* The lingual surface of dentary crowns in *Camptosaurus* displays a primary ridge that is offset distally on the crown surface but not strongly differentiated from a secondary ridge; the secondary ridge is not broad and mound-like and the accessory (tertiary) ridges are distributed more regularly across the crown and are straighter (apicobasally). The lower jaw (dentary) ramus is robust, straight and is both proportionally shorter as well as containing fewer tooth positions than are present in the dentary of *H. fittoni*.

Axial skeleton. Cervical centra are low (dorsoventrally compressed) and lack the strong opisthocoely seen in *Hypselospinus*. Dorsal vertebrae have low, cylindrical centra and short neural spines. Posterior dorsals and anterior caudals do not exhibit the extreme elongation of the neural spines seen in *H. fittoni*.

Appendicular skeleton. The principal shoulder bones are similar, in general shape, to those seen in *Hypselospinus*; however, the sternals are distinctive because they are reniform, rather than being hatchet-shaped (the classic ‘styracosternan’ condition). The forelimb is stout with the individual elements comparatively robust; however, the structure of the radius differs significantly in these two taxa, when the proximal and distal condyles are compared (Norman, pers. obs., 2011). The carpus and manus show some similarity in overall anatomy and phalangeal count. The carpus is co-ossified and there is a spine-like pollex ungual in both taxa; however, the metacarpals are shorter and more obviously divergent producing a broadly splayed hand in *Camptosaurus* and the non-pollex unguals of digits 2 and 3 are more pointed and claw-like (this contrasts markedly with the structures seen in *H. fittoni*). The pelvis exhibits a range of differences from that seen in *H. fittoni*: notably the pubis of *Camptosaurus* has a pubic shaft that is equal in length to that of the ischial shaft, whereas the prepubic process is laterally compressed, blade-like and has parallel dorsal and ventral margins, with no distal expansion. The femur in *Camptosaurus* is curved along its length, the shaft is stout, but its sides are not strongly angular; there is an elongate, finger-like and genuinely ‘pendant’ fourth trochanter positioned mid-shaft; and the extensor intercondylar groove is deep, but very broadly open on the extensor surface. The pes in *Camptosaurus* appears to be functionally tridactyl, but digit 1 has a small, splint-like shaft that adheres to the medial surface of metatarsal II, and has an articular distal condyle which supports a digit with three small phalanges; the unguals taper and terminate in narrow, but rounded, tips.

The status of other names applied to Wealden-aged iguanodonts
(Table 1)

Dollodon bampingi Paul, 2007

This taxonomic name was proposed on the basis of the anatomy of the Belgian ornithopod skeleton (RBINS R57 [IRSNB 1551]) that had been referred previously to *Iguanodon* (=*Mantellisaurus*) *atherfieldensis* (Norman, 1986). Norman (2012) and McDonald (2012a) independently refuted all the evidence assembled by Paul to support this new taxonomic name. The taxon *Dollodon bampingi* is a nomen dubium because it has no valid diagnostic characters and the name can be suppressed safely. The holotype material (RBINS R57) can be referred to the taxon *Mantellisaurus atherfieldensis*.

Proplanicoxa galtoni Carpenter and Ishida, 2010

This taxon was proposed on the basis of a partial skeleton (NHMUK R8649) that had previously been referred to *Vectisaurus valdensis* Hulke, 1879 by Galton (1976). Norman (1990) reviewed the holotype: a small partial associated skeleton (NHMUK R2494-R2500), and the referred material of *Vectisaurus valdensis* (NHMUK R8649 – Galton, 1976) and concluded that it was not a valid taxon and that all of the material could safely be referred to the taxon *Iguanodon* (=*Mantellisaurus*) *atherfieldensis* (Norman, 1990). McDonald (2012a) reviewed the status of the taxonomic names *Vectisaurus valdensis*, *Proplanicoxa galtoni* and the previous reference of this material to *M. atherfieldensis* by Norman (1990). He concluded that the holotype of *V. valdensis* was undiagnosable and anatomically indistinguishable from skeletal material attributable to *M. atherfieldensis* and also that the referred material (NHMUK R8649), which had been designated as the holotype of *P. galtoni,* could similarly be referred to *M. atherfieldensis*. *Proplanicoxa galtoni* was mentioned again, albeit in passing, by Paul (2012: 126). *Proplanicoxa galtoni* is a nomen dubium because it has no diagnostic characters and the name may be suppressed safely. The material attributed to *Proplanicoxa galtoni* can be referred to the taxon *Mantellisaurus atherfieldensis*.

<<INSERT TABLE 1 NEAR HERE>>

Sellacoxa pauli Carpenter and Ishida, 2010

This taxon was reviewed by Norman (2011a, 2012, 2013). The taxonomic name can be considered a nomen dubium because there are no valid diagnostic characters and the taxonomic name may be suppressed safely. The material assigned to this taxon (NHMUK R3788) is considered to be referable to *Barilium dawsoni* (Lydekker, 1888a). It can be noted, in passing, that the validity of *S. pauli* has been supported by Paul (2012: 126) on the basis of comments made on an internet ‘blog’ – these comments were apparently speculative and were withdrawn after a short period of time (Darren Naish, pers. comm. September, 2012).

Huxleysaurus hollingtoniensis Paul, 2012
Huxleysaurus fittoni Paul, 2012

These two taxa were founded upon an alleged holotype comprising a substantial quantity of unassociated skeletal material collected from different quarries: "NHMUK R1148/1629/1632/811/811b/604" (Paul, 2012: 124). All of this material has been referred to *Hypselospinus fittoni* by Norman (2010) and herein. The (*Hux. hollingtoniensis*) 'holotype' was neither described nor illustrated. The new taxon was nevertheless diagnosed using three anatomical features: "femur robust, moderately curved, 4th trochanter pendent." (Paul 2012: 124). The terms "robust" and "curved" have no discriminatory value when applied to the femora of large-bodied non-hadrosaurian iguanodontians and have no diagnostic value. The pendant 4th trochanter is not present in the femora of NHMUK R1148 (Figs 4, 18) and in fact more accurately refers to the form of this trochanter (elongate, finger-shaped and genuinely pendant) as seen in camptosaurs and more basal ornithopods. Conclusion: *Huxleysaurus hollingtoniensis* was founded on three invalid and non-diagnostic characters. Paul's diagnosis is followed by the following commentary:

> "The assignment of basal "*Iguanodon*" *hollingtonesis* [sic] to *Hypselospinus fittoni* by Norman (2010) risks creating a multitaxa chimera because of the lack of adequate overlapping material, and because of the failure to demonstrate that they are from the same level of the Wadhurst Clay Formation. Because the latter is up to nearly 80 meters thick (Anonymous, 2010) it is possible that considerable geological time passed during the deposition of the formation [sic], time sufficient to allow significant species and even genus turnover. The "*I.*" *hollingtonesis* [sic] ilium is not sufficiently complete to compare to the better preserved element of *Huxleysaurus fittoni* [another new and unjustified nomenclatural combination]; although the NHMUK R811b ilium appears to be short and deep, because it is split as [sic] midlength it could actually be

> elongated. It is possible that these are two species within the same genus." (Paul, 2012: 124).

Huxleysaurus hollingtoniensis and *Huxleysaurus fittoni* are both nomina dubia because they lack description, illustration or diagnostic characters. Both names can be suppressed safely. The holotype of *Iguanodon hollingtoniensis* NHMUK R1148 (incorporating R1629 and R1632) is referred to the hypodigm of *Hypselospinus fittoni* and the additional material (NHMUK R604, R811) has also been referred to *H. fittoni* in this article.

Darwinsaurus evolutionis Paul, 2012

This taxon was based upon an alleged holotype comprising un-associated skeletal material collected from different quarries: "NHMUK R8131[sic]/1833/1835/R1836." (Paul, 2012: 124). The diagnosis of *D. evolutionis* was as follows:

> "Dentary straight [incorrect interpretation of a fractured specimen: NHMUK R1831 – see above], elongated diastema present [incorrect], dentary shallow ventral to diastema [incorrect] and deeper astride dental battery [vague and non-diagnostic], anteriormost dentary teeth reduced [incorrect]. Forelimb very robust [non-diagnostic], olecranon process well developed [non-diagnostic], some carpals very large [non-diagnostic], metacarpals fairly elongated [non-diagnostic], thumb spike massive [non-diagnostic]" (Paul 2010: 124-125).

As should now be clear from the detailed description of NHMUK R1831 (p. XX) Paul has misinterpreted the dentary because he insists that that there is a Wealden ornithopod with a hadrosaur-like elongate diastema. It is also clear that Paul has never examined the original specimens upon which he is basing his new taxonomic proposal.

Darwinsaurus evolutionis is a nomen dubium. This taxon was not adequately diagnosed, and no attempt was made to describe or illustrate the new taxon. This new taxon was based upon 'holotype' material that comes from different quarries, and from different geological horizons: NHMUK R1831 was collected in East Sussex and is Valanginian in age, NHMUK R1836 was collected on the Isle of Wight and is Barremian in age. The name *Darwinsaurus evolutionis* can be suppressed safely and the material referred to as its 'holotype' can be referred to either *Hypselospinus fittoni* (in the case of the East Sussex material) or *Mantellisaurus atherfieldensis* (for the Isle of Wight material).

Mantellodon carpenteri Paul, 2012

This taxon is based upon a designated holotype NHMUK OR3741 (the 'Mantel-piece') that had been reviewed and re-illustrated by Norman (1993). It should be noted, in passing, that this disarticulated but associated partial skeleton possesses neither a dentary nor an emplaced dentition (Norman, 1993). Paul's diagnosis of *Mantellodon carpenteri* is as follows:

> "Dentary straight, elongated diastema present, dentary shallow ventral to diastema and deeper astride dental battery, anteriormost dentary teeth reduced. Forelimb very robust, olecranon process well developed, some carpals very large, metacarpals fairly elongated, thumb spike massive." (Paul, 2012: 125).

This diagnosis is anatomically incorrect in every respect and is identical to the diagnosis of *Darwinsaurus evolutionis* (see above). No attempt was made to describe or illustrate the new taxon. *Mantellodon carpenteri* is a nomen dubium because it has no diagnostic characters. Andrew McDonald has provided a copy of the 'missing' diagnosis of Paul:

> "Limb elements slender. Ilium deep, anterior process robust, posterior acetabular body short and very triangular, dorsal margin strongly arched." (A.T. McDonald, 5 December, 2013).

These latter characters are generalised anatomical features that are found in almost all medium-sized iguanodontian ornithopods and (allowing for post-mortem distortion, from which these specimen has clearly suffered [see Norman, 1993] for example the 'arching' of the dorsal margin of the ilium differs between the left and right ilia) do not serve to diagnose this new taxon either because they are unique, or because they form a unique character combination.

The taxonomic name *Mantellodon carpenter* is a nomen dubium and can be suppressed safely. The skeleton (NHMUK OR3741) was referred by Norman (1993) to *Iguanodon* (=*Mantellisaurus*) *atherfieldensis*. No valid justification has been presented in order to refute this latter assignment (Norman, 2013).

Wealden ankylopollexians: a taxonomical summary

Additional taxon names have been applied to a variety of Wealden-aged large-bodied ornithopod material since the latter decades of the 19th century (see Table 1): *Vectisaurus valdensis* Hulke, 1879 was reviewed by Norman (1990) and considered to be a juvenile specimen of an iguanodontian; the type material is a nomen dubium (McDonald, 2012b) and these remains were referred to *Mantellisaurus*. An additional partial skeleton referred to *Vectisaurus* by Galton (1976), which was considered also to be referable to *Mantellisaurus* (Norman, 1990) was subsequently referred to the new taxon *Proplanicoxa galtoni* Carpenter & Ishida, 2010. *Proplanicoxa galtoni* was established on the basis of a single feature on the ilium (which owes its appearance to post-mortem distortion). McDonald (2012b) reviewed this assignment, confirmed that there are no valid diagnostic characters that distinguish this material from *Mantellisaurus* and declared *P. galtoni* to be a nomen dubium and that its material should be regarded as referable to cf. *Mantellisaurus*. *Iguanodon seelyi* Hulke, 1882 and *Sphenospondylus gracilis* Lydekker, 1888a have long been regarded as a nomina dubia (Romer, 1956; Steel, 1969; Ostrom, 1970; Norman, 1980, 1986; McDonald, 2012b). *Torilion dawsoni* Carpenter & Ishida, 2010 and *Wadhurstia fittoni* Carpenter & Ishida, 2010 are junior objective synonyms of established taxa (*B. dawsoni* and *H. fittoni* respectively) and therefore both of these names can be suppressed safely (Norman, 2010, 2011a,b, 2012, 2013). *Dollodon seelyi* Carpenter &

Ishida, 2010 is a name created for the type material of *I. seelyi*; this represents an unjustifiable, and invalid, nomenclatural combination (Norman, 2011b, 2012, 2013; McDonald, 2012b).

SYSTEMATIC ANALYSIS

The recent descriptions of three new iguanodont taxa from the Wealden of south-east England (McDonald, Barrett & Chapman, 2010a; Norman 2010, 2011a, and here), add to a substantial number of publications that have appeared in recent years introducing many new iguanodonts. Within the past decade several attempts have been made to refine our understanding of the phylogenetic relationships among known large-bodied iguanodonts. The principal recent analyses have been those published by Norman (2002, 2004); Weishampel, et al. (2003); Wang, et al., (2010); McDonald, et al. (2010a) and McDonald (2012b); Wu & Godefroit (2012); Godefroit, et al. (2012) and Norman (2014). The information presented in these latter articles has been assessed here and is supplemented by consideration of the information provided in previous analyses undertaken by: Godefroit, et al. (1998); Head (1998, 2001); Kirkland (1998); Xu, et al. (2000); You, et al. (2003); as well as those of Evans & Reisz (2007) and Prieto-Márquez (2010).

Basal taxa and multitaxon groupings

The well-described basal ornithischian *Lesothosaurus* (Thulborn, 1970, 1972; Sereno, 1991; Butler et al., 2008) was chosen as an out-group for the analysis of tree topologies that could be generated for derived ornithopods. The basal neornithischian *Hypsilophodon foxii*, which was described monographically by Galton (1974), formed another taxon against which the remaining ornithopod OTUs (Appendix 2) were analysed. Four additional taxonomic groupings and one individual taxon were employed as OTUs: **rhabdodontids** (incorporating data principally from the descriptions of *Rhabdodon* Matheron, 1869; Pincemaille-Quillévéré, 2002), *Mochlodon* (Osi, et al., 2012) and *Zalmoxes* (Weishampel, et al., 2003; Godefroit et al., 2009); **tenontosaurs** (based upon the descriptions of the two well-known species: *Tenontosaurus tilletti* (Ostrom, 1970) and *T. dossi* (Winkler, Murry & Jacobs, 1997) with some additional information derived from a well-preserved skull specimen of *T*. cf. *tilletti* collected by J.R. Horner; **dryosaurids** (based upon the descriptions of the species of *Dryosaurus* (Janensch, 1955; Galton, 1981, 1983); and ***Camptosaurus dispar***, based primarily upon the original description of *Camptosaurus dispar* (Gilmore, 1909) and personal observation of the original specimens during 2001. It should be noted that the taxonomy and systematics of camptosaur-grade iguanodonts is more complex than previously assumed, following the revision of the taxonomy of the species assigned to the genus *Camptosaurus* by McDonald (2011).

Method

Previously published character-state listings have been compared, edited and added to – see Appendix 1). The revised character list was re-scored (see Appendix 2) against a range of well-described ornithopod taxa. The consolidated list of 105 characters listed in Appendix 1 can be compared with 67 (Norman, 2002, 2004), 75 (Weishampel, et al., 2003), 130 (McDonald, et al., 2010a, see also McDonald, 2012b) and 108 (Wu & Godefroit, 2012). The matrix was assembled and scored using *MacClade* 4.06 (Madison & Madison, 2003), and analysed using *PAUP** Version 4.0b10 (Swofford, 2002). The analysis was run using the HEURISTIC search option, with the branch-swapping algorithm TBR. Analyses were performed under both ACCTRAN and DELTRAN character-state optimization regimes. All characters were given equal weighting and run unordered.

Results

The analysis yielded three equally most parsimonious trees (CI: 0.578, RI: 0.782, RC: 0.452). The strict consensus tree is presented in Figure 48, which shows that the only ambiguity concerns the relationships within a comparatively weakly supported ‘iguanodontoid’ subclade (see Figs 50 - 52). In contrast to previous analyses a basal clade, named the **Clypeodonta** (‘shield-tooths’), is identified as a key point of transition from a lineage of basal neornithischians with rather simple, and similarly shaped, leaf-shaped crowns in upper and lower jaws, to clypeodontans in which the crowns in both jaws form flattened, shield-like faces; enamel is distributed unevenly: thicker on the lingual surface of dentary crowns and on the labial surface of maxillary crowns; dentary and maxillary crowns also display distinctly different morphologies). Clypeodontans are seen to split into two clades: **Hypsilophodontia** and **Iguanodontia**. More derived iguanodontians (**hadrosauromorphans**) from a succession of sister-taxa (with the possible exception of the 'iguanodontoid' sub-clade) that are gradually assembling the anatomical features that culminate in the **euhadrosaurians** of the latest Cretaceous (Fig. 52).

A REVISED PHYLOGENY AND CLASSIFICATION OF DERIVED ORNITHOPODS

Over the past two decades there has been a drive toward the adoption of a nomenclatural system derived from the PhyloCode (de Queiroz & Gauthier, 1990, 1992, 1994; Cantino, et al., 1999) in that it relies upon the topology of cladistically derived trees to generate a rank-free hierarchical classification. Some advocates of this system (Cantino, et al., 1999) go so far as to propose the abandonment of the Linnaean binomial system; the claim is that phylogenetically derived nomenclature offers greater definitional accuracy and stability. While the former is undoubtedly true, the latter is arguable, particularly in the case of fossil taxa.

Norman (2014) presented examples of nomenclatural inconsistency within attempts to systematise derived ornithopods. Phylogenetic nomenclature seeks to anchor clade names by reference to specified taxa, based on the topology of chosen cladograms. Sereno (1998) adopted this approach using a set of simplified dinosaur cladograms (Fig. 49); again it was claimed that this had the advantage of stability. However nomenclatural stability supposes that either the trees in question are stable because they are universally accepted or that they should be conserved as templates for all future work. However, cladograms (especially those based upon fossil taxa) are unstable: they are statistically-supported constructs (and are therefore subject to probabilistic error); moreover trees of this type are built by algorithms that have their own in-built logic-based parameters (which may not conform to biological reality). Systematic algorithms (particularly when applied to palaeontological data) use matrixes that comprise individually selected OTUs, subjectively chosen descriptions of characters and partial choices of character coding and scoring. As a consequence of these factors trees generated by different authors tend to differ in their topologies, which is to say the systematic literature is stacked with inconsistency, or instability.

Phylogenetic definition-based nomenclature: Iguanodontia

The clade name Iguanodontia has been defined most recently as 'the most inclusive group containing *Parasaurolophus walkeri* but not *Hypsilophodon foxii* or *Thescelosaurus neglectus*' (see discussion in Sereno, 2005). This definition is the latest iteration of definitions (Sereno, 1997, 1998; Norman, 2004) since the clade name was first proposed (Sereno, 1986)[1]. The clade Iguanodontia defined in this way is consistent with Sereno's cladogram (Sereno, 1998: fig. 5), but the latter is not only simplified, but is also topologically contentious in a number of respects. Neither *Hypsilophodon* nor *Thescelosaurus* are closely related (Weishampel, et al., 2003; Butler, et al., 2008) and may prove to belong to quite distinct clades. By definition and from the topology of the chosen tree (Sereno, 1998) reproduced as Figure 49, Iguanodontia includes *Tenontosaurus*, yet excludes *Hypsilophodon* (cf. Figs 50, 52). Iguanodontia, defined in this way, is misleading in the sense that it clusters OTUs as anatomically *dissimilar* (dentally, cranially and postcranially) as *Tenontosaurus* (and other hypsilophodontians, in the usage employed here – Figs 50, 52) with *Dryosaurus* and *Camptosaurus* that have definitively *Iguanodon*-like teeth.

This example is used simply to indicate that topological change can occur in trees resulting from different systematic analyses. Topological change

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[1] The clade name was persistently credited to Dollo (1888a) ever since Sereno (1986), but Louis Dollo only attempted to re-define the family-group name Iguanodontidae (Cope, 1869; Huxley, 1870) in that paper.

will generate nomenclatural inconsistency that compromises the technique of clade anchoring. Consistency (a universal aspiration among taxonomists) underpins the advocacy of phylogenetic definitions but can only be assured if (and when) phylogenetic trees maintain consistent relational topologies. Cladistic topologies (particularly those generated for fossil OTUs) will tend to change in response to fresh discovery and analysis. It is hoped that continued application of cladistic methodology to the analysis of relationships among fossil taxa will produce well-supported and consistent patterns of relationship and may justify nomenclatural anchoring (in this context the clades Ankylopollexia and Styracosterna are proving quite stable). However I would prefer that phylogenetically anchored locations in trees should be accompanied by sets of diagnostic characters; these latter permit an understanding of the morphological basis (bauplan) of the constituent members of such clades. Diagnoses also offer a foundation for consideration of the evolutionary implications in the morphological transitions represented by the pattern of stems and nodes within trees. The classificatory scheme outlined below adopts this dualistic approach.

A note concerning basal neornithischian taxa

“Basal ornithopods” *sensu lato* (Norman, et al., 2004), now more commonly referred to as basal neornithischians (following the usage in Butler, et al., 2008), are generally small-medium sized (1 – 3 metre long), bipedal, cursors with tapering, horn-covered beaks, five or fewer roughly conical premaxillary teeth and simple transversely compressed leaf-shaped, imbricating teeth lining the maxilla and dentary. The maxillary and dentary tooth morphology is similar to that described by Thulborn (1970) and is common to nearly all basal ornithischians (Norman, Witmer & Weishampel, 2004; Norman, et al., 2011). *Lesothosaurus* is rooted against substantially more derived neornithischian taxa. This simplification reveals a lack of consideration of the anatomical diversity within basal neornithischians (Butler, et al., 2008) but these beyond the scope of this article.

A revised ornithopod classification

The classificatory hierarchy that follows is derived from the systematic analysis that generated the trees in Figures 48, 50-52. Established clade names are used wherever possible to maintain a degree of consistency with previous literature. In a few instances new clade names have been proposed, or an existing name has had its position and composition modified. The clades listed below and shown in Figures 50 and 52 were chosen because they mark significant points of phylogenetic transition within this lineage of ornithopods.

Infraorder CLYPEODONTA 'shield-toothed' neornithischians (Norman, 2014) (Figs 50, 52).

Phylogenetic definition (node-based).
Hypsilophodon foxii, *Edmontosaurus regalis* their most recent common ancestor and all of its descendants.

A consideration of the known range of more basal neornithischian taxa is beyond the scope of this analysis so a node-based definition acts as a general phylogenetic 'place-holder'. Until the proximate sister-taxa to clypeodontan ornithopods have been identified reliably, a stem-based definition cannot be proposed.

Characters (with their numbers in parentheses so that they can be cross-referenced to Appendix I) that are supported under ACCTRAN *and* DELTRAN optimizations are unremarked. Where only one optimization identifies a character this is recognised in parentheses.

Character-based (Linnaean) diagnosis.

1. Antorbital fenestra small, subcircular with large fossa (10)
2. Broad quadrate embayment shape (29) (ACCTRAN)
3. Frontals broad and roof orbits (34) (ACCTRAN)
4. Wear facets continuous across adjacent crowns (55)
5. Dentary enamel asymmetrically distributed (57)

6. Marginal denticles tongue-shaped (58) (ACCTRAN)
7. Tooth roots longitudinally grooved (59) (ACCTRAN)
8. Dentary crowns broad and shield-shaped (60) (ACCTRAN)
9. Dentary crown develops thickened, inrolled oblique shelves (62)
10. Dentary primary ridge prominent (63) (ACCTRAN)
11. Dentary crown prominent ridge with subsidiary ridges on either side (64) (ACCTRAN)
12. Dentary crowns broader in lingual view than opposing maxillary crowns (65)
13. Alveolar trough grooves reflect the shape of successional crowns (66)
14. Maxillary crowns bear multiple labial ridges (68) (ACCTRAN)
15. Manus digit III with three phalanges (87) (ACCTRAN)
16. Postacetabular process tapers posteriorly (91) (ACCTRAN)
17. Preacetabular pubic process rod-shaped (93) (ACCTRAN)
18. Ischial shaft expanded laterally at distal end (97) (ACCTRAN)
19. Obturator process positioned midshaft (98) (ACCTRAN)
20. Femoral extensor groove broadly open (102) (ACCTRAN)

Commentary.

This deceptively substantial list reflects the fact that this derived sub-group of ornithopods is being compared to the basal ornithischian condition represented by *Lesothosaurus*. The most important features within this listing highlight the form of the dentition: shield-shaped crowns with unevenly distributed enamel; crown margins fringed by tongue-shaped denticles; the development of discrete enamel ridge patterns on the lingual side of dentary crowns and the labial sides of maxillary crowns; and the differentiation in the form of the teeth seen in the maxillary and dentary dentitions. All of these characters combine to distinguish the clypeodont condition from that seen in more basal neornithischians.

Division HYPSILOPHODONTIA (Cooper, 1985) (Figs 50, 52)

Included taxa in this analysis are: *Hypsilophodon foxii, Zalmoxes robustus* and *Tenontosaurus tilletti*. However, this clade contains additional closely similar taxa: *Zalmoxes shqiperorum, Mochlodon* sp., *Rhabdodon* sp., *Muttaburrasaurus langdoni, Kangnasaurus coetzeei* and the 'Antarctic ornithopod' (Milner & Barrett in preparation).

Phylogenetic definition (node-based).
Hypsilophodon foxii, Tenontosaurus tilletti, their most recent common ancestor and all of its descendants.

A node-based definition of Hypsilophodontia is employed until more detailed consideration has been made of a wider range of proximate taxa.

Character-based (Linnaean) diagnosis.

1. Occiput with a trapezoidal outline (1)
2. Premaxilla overlaps the Nasal posterodorsally in the midline (9)
3. Lacrimal overlaps the posteroventral margin of the prefrontal (14)
4. Lateral surface of the rostral process of the maxilla modified by a large foramen and/or a boss (16)
5. Jugal forms an anteroposteriorly abbreviated plate that forms a markedly dorsoventrally expanded plate beneath the infratemporal fenestra (18)
6. Jugal-Quadrate suture with a trough on the medioventral edge of the jugal (23)
7. Fenestration of the Quadratojugal (25) – secondarily lost in *Zalmoxes* (Weishampel, et al., 2003)
8. Lateral surface of the Quadrate shaft bears a sinuous ridge (27)
9. Quadrate (paraquadratic) foramen absent (28)
10. Quadrate (jugal wing) embayment broadly open (29)
11. Postorbital, squamosal process with a vertical indentation (37 - ACCTRAN) not present in *Hypsilophodon* (Galton, 1974)
12. Dentary tooth primary ridge very prominent (63 - DELTRAN)
13. Dentary crown dominant primary ridge flanked by variable number of subsidiary ridges (64 - DELTRAN)
14. Maxillary crown covered by an array of subsidiary ridges (68 - DELTRAN)

15. Caudal ossified tendons form a sheath (epaxially and hypaxially) around the distal caudal series (74) uncertain in *Zalmoxes* spp.
16. Rod-like preacetabular process of the pubis (93 – DELTRAN) laterally compressed in *Tenontosaurus* convergent with iguanodontians

Commentary.

The hypsilophodontian clade, as defined here, marks a fundamental morphological (and implicitly phylogenetic) division within the Clypeodonta (Figs 49-51). The most characteristic features of representatives of this clade are to be found in the dentary and maxillary tooth crowns; this is potentially valuable because teeth have a comparatively high preservational potential. The clade, if it proves to be robust when subjected to future systematic analysis, is of considerable evolutionary interest because hypsilophodontians (notably the large-bodied tenontosaurs and *Muttaburrasaurus*) exhibit convergent (homoplastic) postcranial morphologies when compared to those seen among large-bodied members of the sister-clade Iguanodontia.

Hypsilophodontians form a clade that specifically exclude *Th. neglectus* and a wide range of more basal neornithischian taxa e.g. *Agilisaurus*, *Yandusaurus*, *Jeholosaurus, Hexinlusaurus, Othnielia, Gasparinisaura, Orodromeus, Parksosaurus, Thescelosaurus* spp, *Bugenasaura* and others (Butler, et al., 2008). This fundamental change in clade composition necessitates the abandonment of previous phylogenetic definitions of the Iguanodontia (*sensu* Sereno, 2005) and prompts a re-positioning and re-definition of that clade name (as follows)

Division IGUANODONTIA (Sereno, 1986) (Figs 50, 52)

Phylogenetic definition (stem-based).

Edmontosaurus regalis and all taxa more closely related to *E. regalis* than to the taxa subtended to the clade (Hypsilophodontia) that includes *Hypsilophodon foxii* and *Tenontosaurus tilletti*.

Character-based (Linnaean) diagnosis.

1. Lateral expansion of the premaxillary rostrum (2) – convergently developed in *Tenontosaurus*, and possibly in *Muttaburrasaurus*
2. Loss of premaxillary teeth (4) – convergence among hypsilophodontians: *Zalmoxes robustus* and *Tenontosaurus tilletti*, but not in *Hypsilophodon* or *T. dossi*.
3. External naris extends posterior to the premaxillary occlusal margin (5) – convergently developed in *Tenontosaurus* spp.
4. Premaxillary posterolateral process overlaps the lacrimal (8)
5. Rostral process of the maxilla bifurcates (15 – ACCTRAN)
6. Ascending process of the maxilla forms narrow process (17 - ACCTRAN)
7. Quadrate-Pterygoid suture – pterygoid bifurcates (30)
8. Frontal shape (34 – DELTRAN)
9. Paroccipital process narrow and vertically pendant (39) convergently developed in *Tenontosaurus*
10. Predentary with denticulate oral margin (41)
11. Predentary with bifurcate ventral lobe (43) – convergently developed in *Zalmoxes*; however, this may be an example of midline 'notching' as also seen in tenontosaurs (because the lobes do not diverge strongly as they do in iguanodontians).
12. Marginal denticles (58 – DELTRAN)
13. Morphology of tooth root (59 – DELTRAN)
14. Dentary crown primary ridge modest enlargement and displaced distally (63)
15. Dentary crown ridge pattern: primary ridge with variable number of subsidiary ridges (64)
16. Maxillary crowns have a very prominent distally offset primary ridge (68)
17. Carpals (79 – ACCTRAN)
18. Postacetabular process of ilium (91 – DELTRAN)
19. Preacetabular pubic process forms a parallel-side laterally compressed blade (93) – convergently developed in *Tenontosaurus* and *Muttaburrasaurus*.
20. Shaft of ischium bowed (95) – convergently developed in *Zalmoxes*

21. Shaft of ischium cylindrical (96) – convergently developed in *Zalmoxes*
22. Distal end of ischium 'booted' (97 – DELTRAN)
23. Obturator process of ischium positioned proximally (98)
24. Metatarsal 1 lost (104 – ACCTRAN) – a specialized condition seen in dryosaurids and convergently in more derived hadrosauriformes.

Commentary.

The transition from hypsilophodontian to iguanodontian coincides with the acquisition of a suite of anatomical characters that establish the anatomical framework for the clade that produces successively more derived taxa culminating in the hadrosaurs. There is a striking contrast between the style of morphological differentiation of the dentition in hypsilophodontian and that seen in iguanodontians (which have, as is implicit in the clade name, dentary and maxillary tooth crowns that resemble those seen in the historic taxon *Iguanodon* and closely allied taxa). This differentiation suggests that an alternative morpho-functional trajectory is being followed (linked to a specific style of oral food processing). Additional characters: the development of the divergent bilobed posteroventral processes on the predentary, probably served to reinforce the dentary symphysis when the dentary rami are more widely separated from the midline; these changes in food processing ability may also be linked functionally to structural changes in the pelvis and hindlimb.

It must be noted that the node-based clade name 'Dryomorpha' was defined by Norman (2014) and a stem-based definition was indicated as being justified but not given (Sereno, 2005). This clade name occupies a position topologically equivalent to the redefined Iguanodontia. A case could be made for retaining the name Dryomorpha, however substitution of the name Iguanodontia (and its derivatives iguanodontian and iguanodont) is regarded as of greater priority because the name is used universally whereas the name Dryomorpha is rarely, if ever, used in the taxonomically relevant literature.

Subdivision ANKYLOPOLLEXIA (Sereno, 1986) (Figs 50, 52)

Phylogenetic definition (stem-based).

Edmontosaurus regalis and all taxa more closely related to *E. regalis* than to *Dryosaurus altus*.

Character-based (Linnaean) diagnosis.

1. Premaxillary margin denticulate (5)
2. Ascending process of the maxilla finger-like (17 – ACCTRAN)
3. Sinuous ventral margin of the jugal (21)
4. Frontal has narrow exposure in orbital margin (35)
5. Basipterygoid processes posteroventrally orientated (40)
6. Broadly rounded occlusal margin to the predentary (42)
7. Robust, parallel-sided dentary ramus (49)
8. Comparative crown width (dentary crowns wider than maxillary crowns) (56)
9. Dentary crown shape (60)
10. Maxillary crowns (67)
11. Neural spines of dorsal vertebrae are taller than axially elongate (72)
12. Epaxial ossified tendons form a lattice alongside the neural spines (73)
13. Scapular acromion “J-shaped” (75)
14. Forearm proportions (77)
15. Carpal structure (79 – DELTRAN)
16. Ungual phalanx of manus digit 1 (80 – ACCTRAN)
17. Metacarpal 1 is short, block-like and co-ossified to the carpals (82)
18. Ungual phalanx of digit 1 of the manus conical (85)
19. Manus digit III reduced to three phalanges (87 – DELTRAN) - convergent with tenontosaurs (unknown in rhabdodontids)

Commentary.

Very much transitional, anatomically, between the smaller dryosaurids and the larger more robustly constructed camptosaur-grade taxa exhibit: a longer a deeper skull with more powerful jaw musculature and robust dentition, and a postcranium that is essentially a scaled version of that seen in dryosaurids with the added development of the co-ossified carpals and the associated much-abbreviated (divergent) digit I of the manus that terminates in a short, conical ungual.

Infradivision STYRACOSTERNA (Sereno, 1986) (Figs 50, 52)

Phylogenetic definition (node-based).

Batyrosaurus rozhdestvenskyi, Edmontosaurus regalis their common ancestor and all of its descendants.

Character-based (Linnaean) diagnosis.

1. Occlusal margin of the premaxilla ventrally offset relative to the maxillary tooth row (3)
2. Antorbital fenestra and fossa reduced (10)
3. Maxilla-Jugal suture forms a finger-in-slot structure (20)
4. Postorbital-Squamosal contact (36 – ACCTRAN)
5. Supraoccipital excluded from the margin of the foramen magnum (38) – convergent in *Tenontosaurus* spp.
6. Rostral surface of the predentary bears divergent vascular grooves (44)
7. Modest mandibular diastema (45 – ACCTRAN)
8. Posterior dentition extends medial to the base of the coronoid process (50)
9. Marginal denticles on dentary and maxillary crowns form curved ledges with mammillations (58)
10. Dentary crowns inclined distally (61)
11. Axis neural spine dorsally and anteroposteriorly expanded (69 – ACCTRAN)
12. Cervical vertebral centrum articular surfaces opisthocoelous (72 – ACCTRAN)
13. Dorsal vertebral centrum show moderate opisthocoely in anterior part of the series (71)
14. Scapular acromion J-shaped in lateral view (75)
15. Sternal bones hatchet-shaped (76 – ACCTRAN)

16. Distal end of the radius laterally compressed and expanded (78 – ACCTRAN)
17. Compressed and discoidal phalanx 1 of digit I (81 – ACCTRAN)
18. Metacarpals II-IV closely appressed and elongate (83)
19. Manus unguals II-III flattened, twisted and hoof-like (86 – ACCTRAN)
20. Ilium, dorsal edge with transversely thickened and bevelled edge (90 – ACCTRAN)
21. Preacetabular pubic process distally expanded (93 – ACCTRAN)
22. Pubic shaft slender and shorter than than ischium (94– ACCTRAN)
23. Femoral shaft curved toward distal end (100 – ACCTRAN)
24. Femoral 4th trochanter morphology: triangular crested (101 – ACCTRAN)
25. Femoral distal extensor groove partially enclosed (102 – ACCTRAN)
26. Femoral distal condyles strongly expanded posteriorly (103 – ACCTRAN)
27. Pedal unguals elongate and bluntly truncated distally with prominent claw grooves (105 – ACCTRAN)

Commentary.

As a node-defined clade this can be distinguished from the stem-defined Styracosterna (Sereno, 1998); the strict application of the latter definition is compromised by the increased complexity of camptosaur-grade (Camptosauridae *sensu* Sereno) iguanodont interrelationships (McDonald, 2011: fig. 1) as exemplified by the positions of *Uteodon* and *Cumnoria*. It should be noted that the consistent positioning of *Probactrosaurus gobiensis* as the most basal styracosternan taxon within the topology utilized by Sereno (1986, 1997, 1998, 1999 – see Fig. 49) is no longer tenable (Norman, 2002).

‘IGUANODONTOIDS’ (Figs 50 - 52)

Proa, *Jinzhousaurus*, *Bolong*, *Barilium*, *Mantellisaurus* and *Iguanodon* form a comparatively poorly supported clade that occupies a sister-clade position relative to more derived (hadrosauriform) styracosternans (e.g.

Altirhinus and *Eolambia*). Three additional taxa basal to this subclade are *Batyrosaurus*, *Hypselospinus* and *Ouranosaurus*; these taxa all display anatomical features that are very similar to those exhibited among ‘iguanodontoids’ (see Figure 49). Modifying the tree to include these rather similar taxa increases tree length by just 3 steps (Fig. 51).

General diagnostic characters

1. Premaxillary posterolateral process extends posteriorly to contact the prefrontal (8)
2. Lacrimal-Nasal contact lost (13)
3. Squamosal process of the postorbital forms a bifurcate tip (36)
4. Coronoid process of dentary perpendicular to long axis of dentary (48). Excludes *Batyrosaurus, Hypselospinus* and *Ouranosaurus.*
5. Coronoid process expanded at apex (49). Excludes *Batyrosaurus, Hypselospinus* and *Ouranosaurus.*
6. Ungual phalanx of digit I of manus enlarged, transversely compressed and triangular in lateral view (80). Reversed in *Iguanodon* and *Mantellisaurus*
7. Preacetabular process of ilium twisted along its length so that the lateral surface comes to face dorsolaterally (88). Not seen in *Hypselospinus*.
8. Metatarsal 1 reduced and splint-like with no phalanges (104). Unreliably preserved.

Infrasubdivision HADROSAURIFORMES (emended Sereno, 1997) (Figs 50-52)

Phylogenetic definition (node-based).

Altirhinus kurzanovi, Edmontosaurus regalis their common ancestor and all of its descendants.

Character-based (Linnaean) diagnosis.

1. Antorbital fenestra closure (10)
2. Antorbital fenestra not visible laterally, probably positioned on the max-pmx suture (11)

3. At least two replacement crowns in alveolar trough (54)
4. Wear facets on dentary from a transversely broad pavement with up to three tooth crowns – one functional and two successional crowns (55 – DELTRAN)
5. Manus phalanx 1, digit 1 absent (81 – ACCTRAN)
6. Femoral head spherical [not grooved posteriorly] (99 – ACCTRAN)
7. Metatarsal 1 lost (104 – ACCTRAN)

Commentary.

The term Hadrosauriformes was originally proposed by Sereno (1997 – and later defined as: '*Iguanodon*, *Parasaurolophus*, their common ancestor and all of its descendants' Sereno, 1998: 63). This clade includes *Mantellisaurus* (as *Iguanodon atherfieldensis*, within the taxon *Iguanodon*) as its most basal representative incorporating a set of serially derived taxa culminating in definitive hadrosaurs (see McDonald, Barrett & Chapman, 2010: fig. 5; McDonald, 2011: fig. 2). In this analysis these are considered to be derived styracosternan iguanodonts (Figs 50, 52: *Altirhinus*, *Eolambia, Equijubus*) excluding members of the 'iguanodontoid' subclade. Basal members of this clade exhibit anatomical features that will become established in hadrosauromorphans and euhadrosaurs; these include loss the antorbital fenestra, increasing numbers of replacement teeth (at least two beneath the functional crown in the dentary) and the development of integrated (mutually supportive crowns) within dental magazines. There is also the gradual abbreviation of the first manual phalanx with reduction of the massive, fused carpal block seen typically in 'iguanodontoids'.

The clade name Hadrosauriformes has not been widely, or at all uniformly, adopted in the literature and is frequently confused with clades named Iguanodontoidea (Wu & Godefroit, 2012) or Hadrosauroidea (Godefroit, et al., 2012; McDonald, 2011).

Cohort HADROSAUROMORPHA (Norman, 2014) (Figs 50, 52)

Phylogenetic definition (stem-based).

Edmontosaurus regalis and all taxa positioned more closely to *E. regalis* than to *Probactrosaurus gobiensis*.

Character-based (Linnaean) diagnosis.

1. Premaxilla posterior lateral ramus elongated to contact the prefrontal (8 – ACCTRAN)
2. Jugal anterior process forms a narrow process (19)
3. Jugal-Ectopterygoid articulation reduced to small facet (22)
4. Paraquadrate foramen closed (28 – DELTRAN)
5. Quadrate embayment broad and bevelled (29)
6. Surangular foramen closed (51)
7. Lateral exposure of the surangular lost (53)
8. Dentary enamel distribution confined to lingual surface (57)
9. Angular-sided tooth roots (59)
10. Dentary crown oblique ledges reduced to thickened ridgs (62)
11. Dentary crowns reduced in size relative to mandible (65)
12. Carpals reduced (79)
13. Ungual phalanx of manus digit I absent (80)
14. Metacarpal 1 absent (82)
15. Ungual digit 1 absent (85)
16. Postacetabular process of ilium (91 – ACCTRAN)
17. Ilium brevis shelf absent (92)
18. Femoral shaft straight (100)
19. Femoral 4th trochanter forms elevated mound (101 – ACCTRAN)

Commentary.

The clade Hadrosauridae (*sensu* Weishampel, Norman & Grigorescu, 1993) is the closest topological equivalent to the stem-based Hadrosauromorpha proposed here. However, the former clade was implicitly more subjectively defined as the node-based: *Telmatosaurus transsylvanicus*, *Parasaurolophus walkeri* their common ancestor and all of its descendants. For nomenclatural familiarity the former clade name was retained in Norman (2014: fig. 2.30). Unfortunately, one consequence of such usage is that it also makes nonsense of the concept of the rank of a Linnaean family-level group (-idea). Hadrosauridae placed at a node above Euhadrosauria (Figs 50, 52) should, self-evidently, be a suprafamilial rank because it incorporates subordinate groups of superior rank and a minimum of two groupings that are of potentially equivalent rank (nominally 'Lambeosauridae' [formerly Lambeosaurinae, *sensu* Horner, Weishampel & Forster, 2004] and its sister-group that would be either 'Hadrosauridae' [formerly Hadrosaurinae, *sensu* Horner, et al., 2004] or possibly 'Saurolophidae' [formerly Saurolophinae, *sensu* Prieto-Márquez, 2010]). It may be noted that the family group name Hadrosauridae has the potential to be retained, but redefined so that it ranks at a level in the hierarchy that groups a subset of genera (ideally including the generotype *Hadrosaurus*). If this suggestion were to be adopted, Hadrosauridae could be used as a replacement for the Hadrosaurinae as it is presently used in the more widely accepted sense (Weishampel & Horner, 1990; Weishampel, et al., 1993; Horner, Weishampel & Forster, 2004). It should be noted also, in passing, that the name Hadrosaurinae has also been proposed by Prieto-Márquez (2010, 2011b, *contra* Prieto-Márquez, et al., 2006), in a completely different way to the convention: as a suprageneric 'grouping' that contains only the type genus *Hadrosaurus foulkii*. This usage not only flies in the face of Linnaean convention, but it has also been suggested that the position of *Hadrosaurus* within the phylogeny of derived hadrosauromorphans is by no means securely fixed (D.C. Evans pers. comm. May, 2013).

The sister-taxon or outgroup to Hadrosauromorpha, *Probactrosaurus gobiensis,* displays important anatomical differences that distinguish this and all more basal iguanodontian taxa from hadrosauromorphans: dentary crowns retain an asymmetrical aspect when viewed lingually, and bear accessory ridges running parallel to the distally off-set primary ridge, a surangular foramen is present and the quadrate has a semi-circular embayment in the jugal wing rather than the shallow embayment seen in hadrosauromorphans such as *Tethyshadros* (Dalla Vecchia, 2009). The acromion process of the scapula of *Probactrosaurus* is J-shaped in lateral view, rather than forming an overhanging promontory-like structure that lies parallel to the main axis of the scapular blade in hadrosauromorphans.

In the forelimb, the radius, ulna and metacarpals are elongate and slender in *Probactrosaurus* as well as hadrosauromorphans, which is suggestive of a general trend toward gracility in this part of the skeleton and a greater dependence upon bipedality. However, *Probactrosaurus* retains a small, conical pollex, which *implies* the presence of an at least partially competent and ossified carpus (Norman, 2002). The ilium of *Probactrosaurus* has a modestly everted dorsal margin (Norman, 2002), but there is no evidence of either strong eversion or development of a pendule, as seen in *Tethyshadros*. The unguals of the pes of *Probactrosaurus* are comparatively elongate and truncated at their tips (Norman, 2002).

Bactrosaurus and *Telmatosaurus* retain a consistent topology in many different analyses (Prieto-Márquez, 2010, 2011b; Wang, et al. 2010; McDonald, 2012b; Wu & Godefroit, 2012) as successive out-group taxa to the well-established node-based clade (Euhadrosauria) represented in this analysis by *Parasaurolophus* (*Saurolophus* + *Edmontosaurus*).

Subcohort EUHADROSAURIA (Weishampel, et al., 1993) (=Hadrosauridae of others [see also Norman, 2014] – Figs 50, 52)

P*hylogenetic definition (node-based)*.

Parasaurolophus, Saurolophus, Edmontosaurus, their most common ancestor and all of its descendants.

Character-based (Linnaean) diagnosis.

1. Premaxilla extends posteriorly to contact prefrontal (8)
2. Lacrimal-Nasal contact absent (13)
3. Jugal anterior process dorsoventrally expanded and bluntly truncated (19)
4. Quadrate articular condyle transversely compressed and spherical (32)
5. Frontal abbreviated and broad (34 – ACCTRAN)
6. Frontal excluded from the orbital margin (35 – ACCTRAN)
7. Postorbital-Squamosal ramus bifurcated (37)

8. Mandibular diastema enlarged (45 – DELTRAN)
9. Coronoid process of dentary expanded dorsally and inclined anteriorly (48 – DELTRAN)
10. Dentary crown shape, small and diamond shape (61 – ACCTRAN)
11. Dentary primary ridge median, but reduced in height (63)
12. Dentary subsidiary ridges absent (64 – DELTRAN)
13. Maxillary tooth labial ridge, median and low (68)
14. Dorsal vertebral centra are all moderately opisthocoelous (71)
15. Dorsal flange on ilium forms a 'pendule' (90 – DELTRAN)
16. Preacetabular process of pubis deeply expanded and laterally compressed (93 – DELTRAN)
17. See also Prieto-Márquez (2010:457-461)) for an extended consideration of the character states that may be used to diagnose his concept of Hadrosauridae (= Euhadrosauria in this account).

Comment. The status of the restrictively defined clade named Euhadrosauria (=Hadrosauridae of others) has been the subject of critical discussion (e.g. Prieto-Márquez, 2010: 456) and need not be considered further.

STRATIGRAPHY AND ANATOMICAL TRENDS

A stratigraphically calibrated phylogeny (Fig. 52) demonstrates the degree to which the topology of the most resolved tree matches the known estimates of stratigraphic occurrence of individual taxa in the fossil record. Given the known imperfections of the fossil record, striking congruence is improbable. Most strikingly incongruent is the ghost lineage (cross-hatched) for hypsilophodontians (*Hypsilophodon*, rhabdodonts and tenontosaurs). It is the case that larger rhabdodonts and tenontosaurs exhibit anatomical convergence with respect to that seen in the larger-bodied iguanodontians. Iguanodontians are predicted to have diverged from hypsilophodontians during the Callovian at the latest and are succeeded by ankylopollexians in the late Callovian-early Oxfordian.

Styracosternans appear in the Valanginian and their earliest known representatives, to date, are the lower Wealden European taxa *Hypselospinus* and *Barilium*. The appearance of styracosternans heralds the assembly of skeletal anatomy that becomes a template for the evolution within the euhadrosaur 'stem-lineage'. Styracosternans (iguanodontoids and hadrosauriforms in the usage employed here) become abundant and geographically widespread during the Aptian-Cenomanian interval; their cranial anatomy becomes, in a quasi-evolutionary sense, 'experimental' while their body sized generally trends toward large size (8 metres or more in length). Skeletally these forms are generally robustly constructed; this skeletal design coincides with the widespread adoption of a facultatively quadrupedal stance and gait and extremely robust forelimbs and pedal modifications to the manus to permit weight support using the forelimb. The notable ghost lineages of *Batyrosaurus* and *Ouranosaurus* stand out as incongruent. Batyrosaurus is notably 'primitive' in its overall morphology and may even represent a relict. Ouranosaurus though typically iguanodontoid in its overall anatomy exhibits a few interesting anatomical convergences with later euhadrosaurs (notably in relation to the structure of its jaws and snout).

Hadrosauromorphans first appear during the Cenomanian-Turonian interval and initially represent a craniologically 'conservative' range of gracile-bodied and primarily bipedal forms. Definitive hadrosaurs (the Euhadrosauria) do not seem to arise before the mid-Campanian.

CONCLUSIONS

The lower Wealden styracosternan ornithopod dinosaur *Hypselospinus fittoni* (Lydekker, 1889) is diagnosed and described in detail for the first time. Its history has been very much obscured by the limited, and piecemeal, description of material collected from the Wadhurst Clay Formation during the latter half of the 19th century. All the material that can be assigned justifiably to this taxon has been examined and a considerable proportion of it has now been illustrated and described. It has proved necessary to examine and describe the history of the original discoveries their description and their subsequent taxonomic assignments in order to arrive at an understanding of the hypodigm.

In recent years, attempts to subdivide taxonomically the hypodigm of *H. fittoni* in an attempt to create greater ornithopod diversity in the Wealden can be rejected safely. *Wadhurstia fittoni* (Lydekker, 1889 – Carpenter & Ishida, 2010) is a junior objective synonym of *H. fittoni* (Lydekker, 1889); *Huxleysaurus hollingtoniensis* (Lydekker, 1889 – Paul, 2012), *Huxleysaurus fittoni* (Lydekker, 1889 – Paul, 2012) and *Darwinsaurus evolutionis* (Paul, 2012) are nomina dubia.

Hypselospinus fittoni is a medium-to-large sized (7-8 metre long) styracosternan member of the Iguanodontia. It has a large, shallowly arched dentary that houses an incipient magazine of large, shield-shaped teeth. Dentary crowns bear a distinctive pattern of enamelled ridges on their lingual surface. The dorsal and anterior caudal regions of the vertebral column are notable for the development of extremely tall, narrow neural spines. The forelimb is stoutly constructed and has a large, laterally compressed pollex ungual that articulates against a massive, co-ossified carpometacarpus (some examples exhibit fusion of the pollex to the carpometacarpal block). Metacarpals II-IV are bunched together and bound by ligaments; these metacarpals are comparatively short, and the manus unguals (II, III) are twisted and flattened to form hoof-like structures used for weight-support/locomotion. The pelvis has an ilium whose morphology contrasts strikingly when compared to that of its sympatric contemporary *Barilium dawsoni*. The hindlimb has a notably robust femur with angular sides and a curved shaft that appears to be indistinguishable from that of the latter taxon.

Systematic analysis of a range of ornithopods suggests that *Hypselospinus* is one of the earliest known representatives of the clade Styracosterna. Furthermore there appears to have been a basal dichotomy within a derived clade of neornithischians, the Clypeodonta, that created two distinct clades: Hypsilophodontia and Iguanodontia; these clades diverged in late Middle Jurassic times. These two clades evolved anatomically convergently toward large body size. The iguanodontian lineage demonstrates the sequential acquisition of anatomical features that anticipate the appearance of the most abundant and diverse ornithopod dinosaurs that ever existed, the euhadrosaurians.

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FIGURE LEGENDS

Fig. 1. The location of the town of Hastings within the county of East Sussex in the UK. Quarries and location names indicate sites that are known to have yielded *Iguanodon*-like ornithopod remains (most of which were collected by either Samuel H. Beckles or Charles Dawson). The ambiguity surrounding the location of ‘Hollington Quarry’ is genuine and reflects inconsistencies and vagueness introduced (probably by Dawson) when the documentation of these collections was being assembled in the late 1880s.

Fig. 2. Stratigraphy of the Wealden of southern England. Abbreviations: Fm – Formation; L.T.W. Sand Fm – Lower Tunbridge Wells Sand Formation; U.T.W. Sand Fm – Upper Tunbridge Wells Sand Formation; Lower Grnsd – Lower Greensand. Stratigraphic chart based upon Batten (2011: text-fig. 2.1) with the approximate stratigraphic distribution of the principal large-bodied ornithopod taxa indicated using solid vertical bars.

Fig. 3. Comparative ilia. A. *Iguanodon (=Hypselospinus) fittoni*. NHMUK R1635, holotype in lateral view; B, NHMUK R1635 in medial view; C, *Iguanodon (=Barilium) dawsoni* NHMUK R802, holotype in lateral view; D, NHMUK R802, holotype in medial view. Abbreviations: ?brf – brevis fossa non-existent (the area forming a smoothly curved overhang; brf – brevis fossa; lr – lateral ridge that demarcates the brevis fossa; ?mr – medial ridge (much reduced); mr –medial ridge very prominent and forming an overhanging ledge; prp – preacetabular process; srf – sacral rib facet (prominent medially and clearly visible laterally). Scale bars: 10 cm.

Fig. 4. *Iguanodon hollingtoniensis (=Hypselospinus fittoni)* Holotype. NHMUK R1148. A, femur (right) nearly complete but crushed, as illustrated by Lydekker (1890*a*); B, C, the original specimen as preserved (May 2011) in dorsal and ventral views respectively – the ventral view reveals the extent of longitudinal crushing *post-mortem*. Abbreviations: 4t – fourth trochanter; at – anterior (lesser) trochanter; cr – crushing of the dorsal part of the medial condyle; icg – anterior intercondylar groove.

Scale bar: 10 cm.

Fig. 5. *Iguanodon (=Hypselospinus) fittoni*. Holotype. NHMUK R1635. The ilium as illustrated in Lydekker (1890*a*: fig. 1C). A, lateral; B, ventral portion of the postacetabular process. The original illustration indicates the existence of a separate anterior portion of the preacetabular process; this latter part has not been found in the collections of the NHMUK since it was first looked for in 1974. C, teeth with the same registered number as the holotype and, though not mentioned before, presumably associated: 1. The stump of a heavily worn dentary tooth; 2, 3. Worn maxillary crowns in labial view. Abbreviations: brf – brevis fossa; prp – preacetabular process. Scale bar: 10 mm.

Fig. 6. A generalized outcrop map for the Weald of south-east England to show the distribution of the Hastings Group and Weald Clay Group. Hastings Group shown in even tone, Weald Clay Group shown in textured tone. Boundary of the Weald District indicated in thick solid line and county boundaries shown using a thinner line.

Fig. 7. *Iguanodon (=Hypselospinus) fittoni*. Holotype NHMUK R1635. Partial sacrum. A, dorsal; B, lateral; C, ventral. Abbreviations: k – ventral keel, ln – aperture for lateral spinal nerve; na – broken base of the neural arch positioned supra- rather than intervertebrally on the last sacral centrum; sr – sacral rib remnants. Scale bar: 10 cm.

Fig. 8. *Iguanodon (=Hypselospinus) fittoni* Holotype NHMUK R1635. Anterior-middle caudal centrum in: A, anterior; B, lateral; C, posterior; views. Abbreviations: cf – chevron facet; cr – caudal rib (eroded basal portion). Scale bar: 10 cm.

Fig. 9. *Iguanodon (=Hypselospinus) fittoni* Holotype NHMUK R1635. Ischium (right) proximal end, eroded. Abbreviations: ac – acetabular margin; obt – obturator process (eroded base).
Scale bar: 10 cm.

Fig. 10. *H. fittoni*. Holotype NHMUK R1635. Ilium illustrated in A, lateral; B, dorsal; C, posterior; D, medial views. Abbreviations: brf – brevis fossa; ip – ischiadic peduncle with laterally stepped surface; lr – lateral ridge that demarcates the brevis fossa; pth – probable pathology; srf – sacral rib facets; sy – scarred area for attachment of the sacral yoke. Shading: cross-hatching indicates broken surfaces. Scale bar: 10 cm.

Fig. 11. *Hypselospinus cf. fittoni* (Holotype: *I. hollingtoniensis*) NHMUK R1148. A-D, left metatarsal III in dorsal, ventral, proximal and distal views; E-H, left metatarsal II (R1629) in dorsal, ventral, proximal and distal views; I-N, proximal pedal phalanx (?1-IV) in lateral, medial, dorsal, ventral, distal and proximal views respectively. Abbreviations: lig – scarred surfaces for ligament attachment; sc – scarred surface; tab – flap-like tab on the dorsolateral margin of mt II; tab.sc – corresponding scarred and indented surface on the medial edge of the shaft of mt III for the attachment of the tab on mt II. Shading: even tone - proximal metatarsal surface; hatching – broken surfaces. Scale bar: 10 cm.

Fig. 12. *Hypselospinus cf. fittoni* [*I. hollingtoniensis* Holotype]. NHMUK R1148. A,B: dorsal centra as preserved in lateral view. A1, centrum A illustrated and pseudo-articulated with a neural arch; A2, centrum and neural arch in ventral view; B1, similar pseudo-articulation and B2, ventral view of the same. Hatching indicates broken surfaces. Scale bars: 10 cm.

Fig. 13. *Hypselospinus cf. fittoni* [*I. hollingtoniensis* Holotype] NHMUK R1148 (R1629). Scapula (left) missing distal end of blade and some damage proximally. A, A1, medial view; B, B1, lateral view. Abbreviations: ar – acromial ridge; co.s – coracoid suture; gl – margin of humeral glenoid; hr – recess to accommodate the excursions of the lateral shoulder of the humerus; m/l.sc – muscle and ligament scars on the surface of the scapula. Hatching – broken surfaces. Scale bar: 10 cm.

Fig. 14. *Hypselospinus cf. fittoni* [*I. hollingtoniensis* Holotype] NHMUK R1148 (R1629). Radius and ulna (right). A, lateral view sketched from

originals (ulna crushed and distorted); B, medial view; C, medial view sketched. Abbreviations: m.sc – muscle scars; ra.f –facet (partially preserved) for articulation of the proximal end of the radius; rug – prominent rugose striations on the mediodistal surface of the radius; ul.f – ligament scarred ridge that was attached to the dorsal edge of the distal ulna. Scale bar: 10 cm.

Fig. 15. *Hypselospinus cf. fittoni* [*I. hollingtoniensis* Holotype] NHMUK R1148 (R1629). Pollex (right). A, medial; B, lateral view; C-F, interpretative sketches of the original specimen in medial, posterior, anterior and lateral views. Abbreviation: c.gr – claw groove running along the posterior edge (a less well-defined and irregular groove may be present on the anterior edge). Hatching indicates broken bone. Scale bar: 10 cm.

Fig. 16. *Hypselospinus cf. fittoni* [*I. hollingtoniensis* Holotype] NHMUK R1148. (R1629). Ilium (right preacetabular process). A, A1, lateral view; B, B1, medial view. Abbreviations: mr – medial ridge, m.sc – blister-like strip of muscle scarring on the lateral surface beneath the dorsal edge; srf – sacral rib facet. Hatching indicates broken bone. Scale bar: 10 cm.

Fig. 17. *Hypselospinus cf. fittoni* [*I. hollingtoniensis* Holotype] NHMUK R1148. (R1629). Ischium proximal portion (left). A, A1, lateral view; B, B1, medial view. Abbreviations: m.sc – muscle scars on lateral surface of shaft; obt – broken base of the obturator process; ri – prominent curved ridge that extends from the base of the obturator process to the posterior margin of the shaft distally. Hatching indicates broken and/or filled surfaces. Scale bar: 10 cm.

Fig. 18. *Hypselospinus cf. fittoni* [*I. hollingtoniensis* Holotype] NHMUK R1148. (R1629). Femur (left). A, anteromedial view; B, posterolateral view. Abbreviations: 4t – fourth trochanter; at – anterior (lesser) trochanter; br – broken base of the posterior lateral buttress; h – head of the femur; icg – anterior intercondylar groove; mb – medial posterior

articular buttress; pig – posterior intercondylar groove. Crushing and plaster infill are clearly visible. Scale bar: 10 cm.

Fig. 19. *Hypselospinus cf. fittoni* [*I. hollingtoniensis* Holotype] NHMUK R1148 (R1632). Cervical vertebrae. A-C: anterior cervical vertebra in lateral, dorsal and anterior views respectively (N.B. image A is of the right-hand side and has been reversed). D-F: more posterior cervicals, demonstrating the increasing depth of the centrum and the enlargement of the parapophyseal facet. Abbreviations: dia – diapophysis; k – thick midline keel; par – parapophysis; poz – posterior zygapophysis; prz – anterior zygapophysis. Hatching indicates broken bone. Scale bar: 10 cm.

Fig. 20. *Hypselospinus* cf. *fittoni*. NHMUK R604. 1st or 2nd dorsal. A, lateral; B, anterior; C, ventral. Abbreviations: dia – diapophysis; k – midline keel; ncs – neurocentral suture; ns – neural spine; par – parapophysis; poz – posterior zygapophysis; prz – anterior zygapophysis. Scale bar: 10 cm.

Fig. 21. *Hypselospinus* cf. *fittoni*. NHMUK R604. 3rd dorsal. A, A1, lateral (A is a reversed image of the right side); B, ventral; C, anterior. Abbreviations: dia – diapophysis; k - midline keel; ncs – neurocentral suture; ns – neural spine; par – parapophysis; poz – posterior zygapophysis; prz – anterior zygapophysis; rs – rugose surface for ligamentous attachment of the neck of the rib. Scale bar: 10 cm.

Fig. 22. *Hypselospinus* cf. *fittoni*. NHMUK R604. 4th dorsal. A, lateral; B, ventral; C, anterior. Abbreviations: dia – diapophysis; k – midline keel; par – parapophysis; poz – posterior zygapophysis; prz – anterior zygapophysis; rs – rugose surface for ligamentous attachment of the neck of the rib. Scale bar: 10 cm.

Fig. 23. *Hypselospinus* cf. *fittoni*. NHMUK R604. Middle dorsals (range: 7-10). A. [7th] Lateral; A1, ventral; A2, anterior. B, [9th] lateral; B1, ventral; B2, anterior. Abbreviations: dia – diapophysis; k – midline keel; par –

parapophysis; rs - rugose surface for ligamentous attachment of the neck of the rib. Scale bar: 10 cm.

Fig. 24. *Hypselospinus* cf. *fittoni*. NHMUK R604. Posterior dorsals (range: 14-16). A, A1, A2, 14th dorsal in lateral, ventral and dorsal views respectively. B, B1, B2, 15th dorsal in lateral, ventral and dorsal views respectively C, C1, C2, C3, 16th [last free dorsal] in lateral, anterior, ventral and dorsal views respectively. Abbreviations: dia – diapophysis; k – midline keel; par – parapophysis; prz – anterior zygapophysis. Scale bar: 10 cm.

Fig. 25. *Hypselospinus* cf. *fittoni*. NHMUK R604a. Dorsal ribs. A, right anterior; B, right middle; C, right middle-posterior; D, right posterior. Abbreviations: ar – anterior curved ridge (for intercostal ligaments/muscles); cap – capitulum (rib head); n – neck of the rib; tub – tuberculum. Scale bar: 10 cm.

Fig. 26. *Hypselospinus* cf. *fittoni*. NHMUK R604. Anterior caudals (range: 1-4)). A, A1-A4, lateral, anterior, posterior, ventral and dorsal views respectively. B, B1, B2, lateral, anterior and posterior views respectively. Abbreviations: cf – chevron facet; cr – caudal rib; poz – posterior zygapophysis; prz – anterior zygapophysis. Hatching indicates broken bone. Scale bar: 10 cm.

Fig. 27. *Hypselospinus* cf. *fittoni*. NHMUK R604. Anterior caudal (range: 3-5). A, A1-A4, lateral, anterior, posterior, ventral and dorsal views respectively. Abbreviations: asr – anterior slot-and-ridge margin to the neural spine; cf – chevron facet; cr – caudal rib; poz – posterior zygapophysis; prz – anterior zygapophysis; psr – posterior slot-and-ridge margin to the neural spine.

Scale bar: 10 cm.

Fig. 28. *Hypselospinus* cf. *fittoni*. NHMUK R604. Anterior-middle caudals (range: 7-13). A, A1, A2, lateral, anterior and ventral views respectively; B-D: lateral views of typical anterior-middle caudal vertebrae. Caudal ribs

and chevron facets well-developed, ventral surface of the centrum convex transversely. Abbreviations: asr – anterior slot-and-ridge margin to the neural spine; cf – chevron facet; cr – caudal rib. Scale bar: 10 cm.

Fig. 29. *Hypselospinus* cf. *fittoni*. NHMUK R1632. Middle and posterior caudals. A, A1, A2, middle caudal centrum in lateral, ventral and anterior views respectively. B, C, posterior caudal centra in lateral, ventral and anterior views. Abbreviations: cf – chevron facet; sul – midline sulcus. Scale bar: 10 cm.

Fig. 30. *Hypselospinus* cf. *fittoni*. NHMUK R811. A. Sacrum in ventral view. B, C. NHMUK R811b. The left ilium in lateral and medial views respectively (corrected from Norman 2010). Note: the two broken and laterally flattened ilium portions are positioned slightly too close together. Abbreviations: ip – ischiadic peduncle (crushed remains of); k – ventral midline keel; mr – medial ridge (poorly preserved); m.sc – blister-like strip of muscle scarring on the lateral surface beneath the dorsal edge; s1-5 – numbered sacral vertebrae; sd – sacrodorsal centrum; sr – sacral rib (base of).
Scale bars: 10 cm.

Fig. 31. *Hypselospinus* cf. *fittoni*. NHMUK R811. A. Pubis partial (right, this is a reversed image) in lateral view. B. Ischium complete (left) in lateral view. Abbreviations: ac – acetabular margin; ap – anterior blade of the pubis; ib – ischial ‘boot’; il.p – iliac peduncle; obt – obturator process; obt.c – obturator channel; pp – pubic peduncle; p.pu – posterior ramus of the pubis. Scale bar: 10 cm.

Fig. 32. *Hypselospinus* cf. *fittoni*. NHMUK R33. Dentary teeth. A. Partially worn right tooth with well-developed root; B. Partially worn left crown; C. Unworn [anterior] right crown and partial root. Abbreviations: ch – channels in the root to accommodate adjacent replacement teeth; cin – ‘cingulum’; cr – eroded base of the root caused by growth of a replacement crown; dm – marginal denticles; inr – inrolling of the distal

margin of the crown; p – primary ridge; st – strand-like subsidiary ridges. Scale bars: 10 mm.

Fig. 33. *Hypselospinus* cf. *fittoni*. NHMUK R33. A, dorsal vertebra (middle – reversed image) in lateral view, showing the base of a narrow, oblique neural spine. B, caudal vertebra (anterior-middle) with partial narrow neural spine. Abbreviations: asr – anterior slot and ridge margin to the neural spine; cf – chevron facet; cr – caudal rib (broken base); dia – diapophysis; ns – neural spine; par – parapophysis; poz – posterior zygapophysis; prz – anterior zygapophysis. Scale bar: 10 cm.

Fig. 34. *Hypselospinus* cf. *fittoni*. NHMUK R33. Caudal vertebrate in ventral view. A, anterior-middle caudal showing transversely rounded surface between chevron facets, with vascular foramina; B, C, middle caudals with sulcate ventral surfaces. Abbreviations: cf – chevron facet; cr – caudal rib (base of); sul – midline sulcus; vf – vascular foramina. Scale bar: 10 cm.

Fig. 35. *Hypselospinus* cf. *fittoni*. NHMUK R1627, R1636. Fragmentary portions of the ilium. A, NHMUK R1627, a central portion of the iliac blade of robust build collected from Brede; the dorsal margin of the blade is narrow and flat-topped and there is a distinct blister-like strip of scarring just below the dorsal margin; the preacetabular blade is comparative narrow at its base and there is not large medial ridge. B, NHMUK R1636 a central portion of the ilium collected from Shornden and illustrated by Lydekker (1890*a*). Slightly more complete the dorsal margin of the blade is laterally compressed and flat-topped and there is a similar blister-like strip of scarred tissue that runs parallel to the dorsal margin; the preacetabular process is laterally compressed and concave externally and has a very reduced medial ridge. Abbreviations: ac – margin of the acetabulum; m.sc – blister-like strip of muscle scarring; pp – pubis peduncle (only partially eroded); sac – supra-acetabular crest. Scale bar: 10 cm.

Fig. 36. *Hypselospinus* cf. *fittoni*. NHMUK R1831. Dentary right with teeth preserved *in situ*. A, medial. B, lateral. C, dorsal views. Abbreviations: am – alveolar margin; br – badly broken portion of the dentary; cp – coronoid process; ds – dentary symphysis; m – matrix; mgr – Meckelian groove; pr – anterior lateral process of the dentary; sl – 'slot-and-lip' portion of the dentary symphysis; tf – tooth fragments in alveolar bone; vc – vascular channel. Scale bar: 10 cm.

Fig. 37. *Hypselospinus* cf. *fittoni*. NHMUK R1831. Teeth. A, dentary tooth in lingual view (isolated specimen on stub of matrix); B, maxillary tooth in labial view. C-E, dentary replacement crowns embedded in the alveolar bone of the dentary. Abbreviations: m – mammillae on the marginal denticles; p – primary ridge; r – minor ridges; st – strand-like ridges.

Fig. 38. *Hypselospinus* cf. *fittoni*. NHMUK R1831 (R1832). Radius, ulna, pollex and partial carpus (right) in lateral view. Abbreviations: II-IV – articular facets for metacarpals II-IV; abs – abscess-like depression; c.gr – ungual claw groove; ls – lateral shelf; MCB – metacarpo-carpal block; mf – medial flange; ol – olecranon process; PO – pollex; RA – radius; rf – facet for attachment of radius; uf – facet for attachment of the ulna; UL – ulna. Scale bar: 10 cm.

Fig. 39. *Hypselospinus* cf. *fittoni*. NHMUK R1831 (R1832, R1833), R33. Digits II-IV of the manus reconstructed. A, metacarpals II-IV (right) reconstructed in articulation (dorsal view). B, NHMUK R33. Metacarpal III (uncrushed, right) showing natural width for comparison with: C. NHMUK R1831, which is transversely compressed. D, digit II (left, inverted), ungual phalanx somewhat distorted; E, digit III (left, inverted), distal end (only) of mc III appears to be relatively uncrushed, penultimate phalanx missing and ungual phalanx distorted; F, digit IV (apparently complete). G, digit V (possible morphology) penultimate phalanx missing. H, H1, NHMUK R33: ungual phalanx of digit III of manus in dorsal and ventral view respectively – showing the expected asymmetric shape expected – as in Norman (1986, figs 50, 51). Abbreviations: art – articular facet for penultimate phalanx; c.gr – ungual claw groove. Scale bar: 10 cm.

Fig. 40. *Hypselospinus* cf. *fittoni*. NHMUK R1831 (R1832/R1833). Reconstructed antebrachium and manus in lateral view. Abbreviations: mcI/mcIII – metacarpals; MCB – metacarpo-carpal block; ol – ossified ligaments; PO – pollex ungual; RA – radius; UL – ulna. Scale bar: 10 cm.

Fig. 41. *Hypselospinus* cf. *fittoni*. NHMUK R1831 (R1833). Pedal unguals in A,B, dorsal; A1,B1, ventral views. Abbreviations: art – articular facet for penultimate phalanx. Scale bar: 10 cm.

Fig. 42. *Hypselospinus* cf. *fittoni*. NHMUK R1831 (R1833). Pubis (right) in lateral view. Abbreviations: ac – acetabular surface; ap – anterior ramus of the pubis; il.p – iliac peduncle; p.pu – posterior ramus of the pubis. Scale bar: 10 cm.

Fig. 43. *Hypselospinus* cf. *fittoni*. NHMUK R1831 (R1835). Sternal apparatus. A, external (ventral); B, internal (dorsal). Abbreviations: apr – apron area of sternal blade; con – condylar area for attachment of dorsal rib cartilage; co.s – coracoid suture; 'h' – sternal handles; iso – intersternal ossification; k – midline keeled structure traversed by strands of bony tissue; lf – lateral fingers of ossified tissue; st – sternal bone. Scale bar: 10 cm.

Fig. 44. *Hypselospinus* cf. *fittoni*. NHMUK R1834. Dentary (left, partial). A, medial (lingual); B, lateral (labial); C, dorsal. Abbreviations: am – alveolar margin; alv – alveolar trough; dias – margin forming a diastema; ds – dentary symphysis; mgr – Meckelian groove; sa.s – surangular suture; sl – posterior 'slot-and-lip' portion of the dentary symphysis. Scale bar: 10 cm.

Fig. 45. *Hypselospinus* cf. *fittoni*. NHMUK R1834. Vertebrae. A-C. Representative dorsal centra. D, NHMUK R1635 (holotype) caudal vertebra. E, NHMUK R1834. Caudal vertebral centrum. Abbreviations: cf – chevron facet; cr – caudal rib (base of).
Scale bar: 10 cm.

Fig. 46. *Hypselospinus* cf. *fittoni*. NHMUK R1834. Ilium (right, nearly complete). A, lateral; B, ventral view of postacetabular process; C, dorsal; D, medial. Abbreviations: ac – acetabulum; bl – abnormally truncated preacetabular process; brf – brevis fossa; fdm – flattened, narrow dorsal margin of the iliac blade; ip – ischiadic peduncle; lr – lateral ridge; mr – medial ridge; m.sc – blister-like strip of rugose tissue running parallel to the dorsal margin of the ilium; pp – pubic peduncle; prp – preacetabular process; th – dorsoventral thickening of the blister-like muscle scar. Scale bar: 10 cm.

Fig. 47. *Hypselospinus fittoni.* A preliminary reconstruction of the skeleton based upon the type and referred material described in this article. N.B. Forelimb relative to hindlimb length, and proportions, are currently unknown. Scale bar: 1 metre.

Fig. 48. Topology of a tree generated using using the taxon-character matrix scored as in Appendix 2. This tree represents a strict consensus of the 3 MPTs created when the matrix was analysed with character scoring unordered and without weighting. The only ambiguity concerns the internal relationships between the taxa within the subclade referred to in Figures 49-50 as ‘iguanodontoids’. Statistical support: CI: 0.578, RI: 0.782, RC: 0.452. Tree length: 313 (minimum possible: 181, maximum possible: 786).

Fig. 49. The tree used for Sereno’s (1998, 2005) stabilised ornithopod clade nomenclature. Is this a stable tree? Specific points of contention include the status of: Hypsilophodontidae (status disputed, widely regarded as paraphyletic – Butler, et al., 2008), Iguanodontia (constituent taxa and topographic position of *Tenontosaurus* disputed - here), Camptosauridae (status and constituent taxa uncertain – McDonald, 2011), *Probactrosaurus* (topographic position disputed – Norman, 2002, 2004; Wang, et al., 2010; Wu & Godefroit, 2012), Iguanodontidae (family status disputed and inconsistent constituent taxa – here, Norman, 2004; Wu & Godefroit, 2012), Hadrosauriformes (constituent taxa disputed –

here, Norman, 2004; McDonald, Barrett & Chapman, 2010), Hadrosauroidea (topographic position of *Ouranosaurus* disputed – Norman, 2004; McDonald, Barrett & Chapman, 2010; Wang, et al., 2010; Wu & Godefroit, 2012).

Fig. 50. A tree based upon the analysis that generated Figure 48, with particular nodes and stems named (see text for discussion/explanation).

Fig. 51. A tree ‘adjusted’ (using the MacClade 4 tree window editor) by the addition of three OTUs (*Batyrosaurus*, *Hypselospinus* and *Ouranosaurus*) that lie immediately basal to the ‘iguanodontoid’ subclade into the stem of that subclade (compare with Figure 49). Tree length: 316 (CI: 0.57, RI: 0.78).

Fig. 52. A phylogeny derived from Figure 49 calibrated, by reference to known stratigraphic ranges of individual taxa plotted, against the geological timescale. Approximate age ranges of known taxa are indicated by black rectangles, and where there are implied stratigraphic ranges these are indicated by connecting tramlines. In instances where implied divergence events have occurred and generated substantial ghost-ranges, these are indicated by cross-hatching.

TABLE LEGEND

Table 1. A summary listing of the taxonomic names that have been proposed for large-bodied Wealden ornithopods. Left column represents the taxonomy that is consistent with that advocated by Norman (2010, 2011b, 2012, 2013) and McDonald (2012b, and pers. comm.). The column on the right lists the variety of taxonomic names that have been proposed for various remains recovered from SE England since the 1820s, and an assessment [in square backets] of the status of each (emended from Norman, 2013). The asterisk denotes the name created for a specimen recovered from Maidstone in Kent (strictly-speaking outside the geographic area described as the Weald). Abbreviations: jos – junior objective synonym; jss – junior subjective synonym; nd – nomen dubium; v – valid taxonomic name

APPENDIX 1. CHARACTERS USED: DESCRIPTIONS AND SCORING

1. Occiput outline in posterior view: rectangular (0), trapezoid (width between quadrate condyles exceeds the width of the squamosals (1).

2. Premaxillary rostrum, dorsal aspect: margins converge to a blunt tip (0), modest rounded expansion (1), occlusal margin is broad and rounded in dorsal view such that its overall width approaches that of the skull roof (2), flared occlusal margins that form a 'spoon-bill' structure in dorsal view (3) - (emended from Norman, 1986).

3. Premaxilla: level of occlusal margin relative to that of the maxillary tooth row: not at all (or slightly) ventrally offset from alveolar margin of the maxilla (0), strongly ventrally offset (1) - (emended from Sereno, 1986).

4. Premaxillary teeth: present (0), absent (1) - (emended Milner & Norman, 1984)

5. Premaxilla, marginal denticulations: absent (0), present (1). (Norman, 1990; Weishampel, et al., 2003:7).

6. External naris: confined to area above oral margin of premaxilla (0), posterior margin extends posteriorly to lie above the maxilla (1). (Norman, 2002:6).

7. Premaxilla, anterolateral margin of the narial fossa above the occlusal edge of the premaxilla is reflected dorsally to form a distinct rim: absent (0), present (1). (Norman, 2002:3).

8. Premaxilla-Lacrimal contact: absent (0), present (1) posterolateral premaxillary process extends posterodorsally to also contact/overlap the prefrontal (2) – (emended from Milner & Norman, 1984).

9. Premaxillary dorsal process and its suture with the nasal: dorsal process of the premaxillary process overlaps the nasal (0), anterior tip of nasal overlaps the dorsal process of the premaxilla (1).

10. Antorbital fenestra perimeter, when viewed laterally: large and subtriangular (0), small and irregularly subcircular (1), forms a

posteromedially directed canal (2), not visible in lateral view (3) – (emended from Milner & Norman, 1984).

11. Antorbital fenestra location: between lacrimal and maxilla (0), on anterodorsal margin (premaxillary suture) of maxilla and therefore not visible in lateral view of the fully articulated skull (1). (Weishampel, Norman & Grigorescu, 1993; Norman, 1998).

12. Orbit shape: circular in outline (0), anteroventral corner of the orbit forms an approximate right angle (1) - (emended from Weishampel, et al., 2003:4)

13. Lacrimal-Nasal contact: present (0), absent (1). (emended from Milner & Norman, 1984; Norman 2002:12).

14. Lacrimal-Prefrontal suture: prefrontal overlaps the dorsal margin of the lacrimal (0), lacrimal overlaps the posteroventral margin of the prefrontal (1).

15. Maxilla, anterior process structure: single tapering anterior process that wedges into the posteromedial margin of the premaxilla (0), bifurcate anterior process (1) – (emended from Sereno, 1986).

16. Maxilla, anterior process, lateral surface adjacent to the premaxilla: unmodified lateral surface (0), modified with enlarged foramen and/or a supplementary boss (1).

17. Maxilla, dorsal (ascending) process morphology: low mound-like structure (0), narrow, finger-like process (1), laterally flattened subtriangular plate (2) - (emended from Norman, 2002:11).

18. Jugal shape: elongate and strap-like with long posterior extension (0), anteroposteriorly shortened and the portion of the jugal beneath the infratemporal fenestra forms a markedly dorsoventrally expanded, sub-rectangular plate (1).

19. Jugal, anterior process: tapering to a point (0), expanded and laterally compressed (1), expanded and abruptly truncated anteriorly (2). (Norman, 2002:14)

20. Jugal-Maxilla suture: elongate scarf joint (0), ‘finger-in-recess’ [oblique finger-like process of the maxilla fits into a slot formed in

the medioventral surface of the anterior ramus of the jugal] (1), butt-jointed against a broad facet on the lateral surface of the ascending process of the maxilla (2) - (emended from Norman, 2002:15).

21. Jugal, free ventral margin: either straight or describes a very slight undulation (0), sine wave-like with a pronounced ventral deflection where it approaches the quadrate (1) - (emended from Norman, 2002:16).

22. Jugal-Ectopterygoid contact: present (0), absent (1). (Head, 1998: 6; Norman, 2002:17).

23. Jugal-Quadratojugal suture: scarf-like, with the jugal overlapping the quadratojugal (0), ventral margin of jugal forms a trough-like recess to receive the anteroventral margin of the quadratojugal (1).

24. Jugal contribution to the ventral half of the infratemporal fenestra: jugal contributes to the margin (0), jugal forms the entire ventral margin by overlapping and excluding the quadratojugal (1) – (emended from Butler, et al., 2008).

25. Quadratojugal fenestration: absent (0), present (1). (Norman, 1986).

26. Quadrate shaft morphology: mid-shaft gently concave, transversely rounded, posterior margin (0), shaft straight, or has a slightly posteriorly convex mid-section that is also carina-like [transversely compressed] (1).

27. Quadrate lateral surface: relatively smooth and unmodified by ridges (0); subdivided by a prominent sinuous ridge (1).

28. Quadrate (paraquadratic) foramen between quadratojugal and quadrate: present (0), absent (1). (Norman, 2002:20).

29. Quadrate embayment on anterolateral (jugal) wing: small notch on the margin of the quadrate wing (0), relatively small with a semi-circular boundary (1), broad embayment the rim of which is marked by a bevelled sutural surface for the quadratojugal (2) - (emended from Norman, 1990: Node 1:3; Prieto-Márquez, et al., 2006:40)

30. Quadrate-Pterygoid articulation: fan-like overlap (0), bifurcate pterygoid wing, with discrete dorsal and ventral portions.

31. Quadrate: posterior margin of the shaft: concave posteriorly with the dorsal (condylar buttress) also strongly tilted posteriorly (0), straight (1).

32. Quadrate-Articular condyle: transversely expanded, subrectangular in distal view (wider laterally than medially) with a trochlear-like articular surface (0), triangular in distal view, with its base facing laterally and a ventrally off-set sub-spherical lateral condyle (1) - (emended Norman, 2002:21; McDonald, et al., 2010:64).

33. Palpebral [supraorbital] bone(s): present (0), absent [or potentially fused to orbital margin] (1). (Norman, 2002:13).

34. Frontal shape: arched, narrow (embayed dorsal to the orbit) and elongate (0), flat profile and extend laterally to roof the orbital cavity (1) anteroposteriorly abbreviated and consequently very broad relative to length (2) – (emended Norman, 2002: 18).

35. Frontal forms part of the dorsal margin of the orbit: forms a major part of the orbit margin (0), reduced to small exposure in the dorsal margin (1), excluded from the orbital margin by contact between prefrontal and postorbital (2). (Norman, 2002:19)

36. Postorbital-Squamosal contact: postorbital forms a tapering finger-like ‘squamosal process’ the overlaps the squamosal (0), squamosal process of the postorbital develops a bifurcate tip (1) – (emended from McDonald, et al., 2010:52).

37. Postorbital, squamosal process: the external surface of the process is not indented (0); the process is flattened or slightly convex dorsoventrally externally and indented posterior to a ridge that runs vertically behind the orbital margin (1), postorbital inflated into a pouch-like structure (2).

38. Foramen magnum, dorsal margin: supraoccipital exposed in the dorsal margin (0), supraoccipital excluded from the dorsal margin by

a bar formed by fusion of the exoccipitals (1). (Sereno, 1986; You et al., 2003:23).

39. Paroccipital process shape: horizontal bar that is dorsoventrally expanded distally (0), pendant distal tip (1). (Weishampel, et al., 2003:13).

40. Basipterygoid process orientation: anteroventral (0), posterolateral (1) – (emended from Butler, et al., 2008:83).

41. Predentary occlusal margin: smooth-edged (0), denticulate (1). (Weishampel, et al., 2003:19).

42. Predentary profile [in occlusal view]: subtriangular (0), arcuate (1), broad and subrectangular (2) - (emended from Weishampel, et al., 2003:18).

43. Predentary medioventral lobe: median tab [maybe 'notched' on its posterior edge in the midline] (0), posterior margin is deeply incised in the midline producing bifurcated lobes (1) – emended from Weishampel, et al., 2003:20).

44. Predentary rostral surface: smooth curved surface [puckered by small neurovascular openings] (0), bearing a pair of oblique grooves, on either side of midline, that converge dorsally (1), single midline groove (2) – (emended from McDonald, et al., 2010:6).

45. Mandibular diastema [the gap between the posterior end of the predentary and the first dentary alveolus]: absent (0), present but modest [>2 crown widths] (1), 'elongate' [greater than five crown widths] (2) – emended from Norman, 2002:22).

46. Dentary ramus shape in lateral view: straight (0), arched along its ventral edge (1). (Norman, 2002:23).

47. Dentary ramus [tooth-bearing portion] shape: tapers anteriorly (0), parallel dorsal and ventral borders (1), deepens anteriorly (2) – emended from Norman, 2002:24).

48. Coronoid process inclination: principal axis of the coronoid process is obtuse relative to the long-axis of the dentary (posterodorsal inclination) (0), perpendicular to the long-axis of the dentary (1),

subtends an acute angle relative to the long axis of the dentary anterodorsal inclination (2) – (emended from Norman, 2002:25).

49. Coronoid process apex: dorsal portion is unexpanded anteroposteriorly (0), expanded (1) – (emended from Norman, 2002:26; McDonald, et al., 2010:21).

50. Coronoid process position on the dentary ramus: laterally offset and dentition [alveoli] curve laterally into its base (0), posterior dentition extends to a position approximately medial to the middle of the coronoid process, leaving a tapering shelf between the alveolar margin and the base of the coronoid process (1), posterior dentition extends to the posterior edge of the coronoid process, or beyond, and there is a continuous horizontal shelf that separates the base of the coronoid process from the alveolar margin (2). (Norman, 2002:26).

51. Surangular foramen: present (0), absent (1). (Weishampel, et al., 1993:27).

52. Surangular-Angular suture: obliquely inclined (0), horizontal (1) – emended from McDonald, et al., 2010:26).

53. Angular [lateral exposure]: visible laterally (0), not visible laterally [sutured to a facet on the medial surface of the surangular] (1). (Norman, 2002:28).

54. Replacement crowns in the alveolar trough: present: One (0), two (1), three or more (2). (Weishampel, et al. 1993:32).

55. Wear facet distribution on dentary and maxillary crowns: irregular and discontinuous distribution on individual crowns (0), wear facets continuous across adjacent crowns, producing a uniformly narrow cutting surface (1), oldest and other successional crowns contribute to the wear surface to varying degrees, thereby forming a transversely broad cutting/grinding occlusal surface (2).

56. Relative crown width: maxillary crowns equal in width to dentary crowns (0), narrower than dentary crowns (1), equal in width to

dentary crowns, but ‘miniaturized’ (2) – (emended from Norman, 2002:34).

57. Enamel surface distribution: equally distribution on labial and lingual sides of crown (0), asymmetrical distribution (thicker on one surface of the crown) (1), enamel restricted exclusively to either the lingual or labial side of the crown (2). (Sereno, 1986; Norman, 2002:30).

58. Marginal denticle shape: simple cones (0), tongue-shaped (1), curved ledges with mammillae along edges (2), denticles absent or reduced to small and irregularly distributed papillae along the mesial and distal coronal margins (3) – (emended from Norman, 2002:31).

59. Tooth roots: tapering cylinders (0), longitudinally grooved to accommodate relatively closely packed teeth (1), highly angular-sided (hexagonally prismatic) roots that indicate close packing of the teeth to form a functionally integrated polytooth magazine (2) – (emended from Norman, 2002:32).

60. Dentary teeth, crown shape in lingual view: coarse beech leaf-shaped profile (0), broad and shield-like (1), coronal margin, in unworn examples, is truncated and exhibits a distinct ‘shoulder’ mesial to the tip of the crown formed at the intersection of the primary ridge with the coronal margin (2), mesiodistally compressed, mesial and distal coronal and apical margins converge and create an approximately diamond-shaped outline for the exposed, enamelled, tooth surface (3) – (emended from Norman, 2002:29).

61. Dentary teeth, crown shape 2: the midline axis of the crown in lingual view is straight (0), the entire enamelled crown face is inclined posterodorsally (1), the upper half of the crown face is distally recurved (2).

62. Dentary teeth, presence of oblique, thickened inrolled ridges along the lower (apical) margins of the enamelled lingual face: absent (0), present (1), reduction of the rolled ridges to form a simple, thickened enamelled edge (2).

63. Dentary teeth, primary ridge: absent (0), mesial/median position and prominent (1), distally offset and modestly developed (2).

64. Dentary teeth, ridge pattern: simple median swelling (0), prominent primary ridge with variable number of parallel subsidiary ridges (1), parallel primary and secondary ridge divide crown face into three zones (2), dominant median primary ridge, flanked by secondary ridges (3), median primary ridge alone (4).

65. Dentary teeth size, relative to the alveolar trough: small and leaf-shaped in profile (0), large and shield-shaped (1), miniaturized (2) – (emended from Norman, 2002:29)

66. Dentary, lateral alveolar wall tooth grooves: reflect the shape of successional dentary crowns (0), narrow, parallel-sided grooves (1). (Norman, 2002:33).

67. Maxillary teeth shape: approximately equal in width to dentary crowns (0), narrower and more lanceolate than opposing crowns (1), lanceolate and equal in width to opposing dentary crowns (2) – (emended from Norman, 2002:34).

68. Maxillary teeth, labial surface morphology: simple median swelling framed by the denticulate margins (0), array of subsidiary ridges (1), distally offset enlarged primary ridge (2), single, low, median primary ridge (3).

69. Axis vertebra, neural spine shape: low and sloping (0), dorsally and anteroposteriorly expanded (1). (McDonald, et al., 2010:93).

70. Cervical vertebrae, centrum articular surfaces: amphiplatyan (0), opisthocoelous (1). (Butler, et al., 2008:134).

71. Dorsal vertebrae, centrum articular surfaces: anterior dorsals amphiplatyan (0), anterior dorsals ‘cervicalized’ and display moderate opisthocoely, before becoming more regularly amphiplatyan about one-third of the way along the dorsal series (1), entire dorsal series displays moderate opisthocoely (2).

72. Dorsal vertebrae (middle to posterior) neural spine proportions: low and rectangular, axial length similar to height (0), tall and narrow, axial length <30% of height (1); ‘extreme height’, in excess of 10x

the axial length of the spine and expanded distally (2), elongate but very narrow (3).

73. Epaxial ossified tendons: arranged in linear bundles (0), form a layered lattice against the neural spines (1) - (emended from Weishampel, et al., 2003:42).

74. Ossified tendons form a posterior caudal sheath: absent (0), present (1).

75. Scapular acromion: prominent thickening restricted to the proximodorsal margin of scapula (0), occupying a median position on the external surface of the proximal scapular blade, and curves toward the dorsal edge of the blade creating a distinctly 'J-shaped' structure (1), developed into a raised promontory that overhangs the proximal lateral surface of the scapula and not curved toward the dorsal border (2).

76. Sternal morphology: reniform (0), hatchet-shaped (1), pronounced elongation of the 'handle' of the hatchet (2). (Norman, 2002:35).

77. Forearm (radius and ulna) proportions: slender, bowed bones that are sub-equal to the length of the humerus (0), robust bones that are straight and have pronounced (expanded) proximal and distal articular surfaces (1), slender, elongate bones that taper distally and exceed the length of the corresponding humerus: proximal and distal articular surfaces show little or no expansion) (2).

78. Radius distal end morphology: expanded and circular in distal view (0), laterally compressed and expanded dorsoventrally (1), narrow and tapered (2).

79. Carpals: fully ossified and separate (0), fused together to form a carpometacarpal I block (1), reduced to two small ossicles (2) – (emended from Norman, 2002:48).

80. Ungual phalanx of manus digit I (morphology): narrow and claw-like (0), conical spike (1), enlarged and laterally compressed spine (2), small, narrow spine (3), absent (4).

81. Manus phalanx 1 of digit I (morphology): normal phalangeal proportions (0), discoidal plate (1), absent (2).

82. Metacarpal I: elongate 'dumb-bell' shaped (0), short, block-like and fused against carpals (1), absent (2). (Norman, 2002:49).

83. Metacarpals II-IV: capable of forming a broad 'spreading' palm (0), robust, compressed against adjacent metacarpals (1), slender and elongate (2). (Norman, 2002:50).

84. Manus digit I: present (0), absent (1). (Norman, 2002:51).

85. Ungual of manus digit I: claw-like (0), sub-conical (1), absent (2). (Norman, 2002:52).

86. Unguals of manus digits II & III: claw-like (0), flattened, twisted and hoof-like (1). (Norman, 2002:53).

87. Manus digit III: four phalanges (0), three phalanges (1). (Sereno, 1986).

88. Ilium, preacetabular process: long, laterally compressed (0), axially twisted so that lateral surface faces dorsolaterally (1) - (emended from Weishampel, et al., 2003:56).

89. Ilium, profile of dorsal edge: horizontal-to-slightly arched, no significant notch posterodorsal to the ischiadic peduncle (0), sinuous profile (1). (Norman, 2002:55).

90. Ilium, dorsal margin development: no transverse thickening of the dorsal edge in the region above the ischial peduncle (0), transversely thickened, bevelled edge (1), thickened dorsal edge developed into a rolled edge (2), discrete bulbous boss present posterodorsal to the ischiadic peduncle (3), prominently everted and downturned (flap-shaped) pendule that overhangs the ischiadic peduncle region of the ilium (4) – (emended from Norman, 2002:56).

91. Ilium, postacetabular process in profile: vertical plate with rounded edge (0), generally triangular, tapering posteriorly (1), laterally compressed and relatively narrow, rectangular bar (2), upturned plate (3) – (emended from Norman, 2002:57).

92. Ilium, brevis fossa: arched recess on the ventral surface of the postacetabular process of the ilium enclosed laterally by a ridge (0), shallow brevis fossa no lateral ridge (1), postacetabular blade narrow and no brevis fossa present (2).

93. Pubis, prepubic process shape: short, deep and blunt (0), rod-shaped (1), laterally compressed parallel-sided blade (2), expanded distally (3), deeply expanded distal portion (4). (Norman, 2002:58).

94. Pubis, pubic shaft: terminates bluntly adjacent to distal end of ischium (0), slender, shorter than ischial shaft and tapers to a point (1). (Norman, 2002:59).

95. Ischium, shaft morphology: straight (0), bowed (1). (Norman, 2002:60).

96. Ischium, shaft morphology 2: compressed and blade-like along length of shaft (0), cylindrical central shaft (1), narrow, angular-sided shaft (2).

97. Ischium, shaft morphology 3: distal end unexpanded (0), distal end expanded into 'boot' (1), distal end laterally expanded, rather than expanded anteroposteriorly (2).

98. Ischium, obturator process: absent (0), positioned near mid-shaft (1), positioned close to pubic peduncle from which it is separated by a well-defined embayment (2). (Norman, 1986).

99. Femoral head, articular surface bears a prominent groove posteriorly: present (0), absent (1).

100. Femur, curvature of shaft: distal half of shaft curved caudally (0), straight (1). (Norman, 2002:62).

101. Femur, 4th trochanter: pendant (0), large, with a triangular profile (1), large, with a profile that is smoothly convex, laterally compressed ‘eminence’ (2). (Norman, 2002:63).

102. Femur, distal extensor groove: absent (0), very broad V-shaped trough (1), narrower U-shaped trough (2) partially enclosed by expansion of adjacent anterior condyles (3), edges of trough meet to form a fully-enclosed canal (4) – (emended from Norman, 2002:64).

103. Femur, distal condyles: moderately expanded anteroposteriorly (0), strongly expanded and partly occluding flexor channel (1).

104. Metatarsal I: well-developed metapodial that articulates with a proximal phalanx and supports a pedal digit (0), slender, small and splint-like by comparison with mtII (1), absent (2). (Norman, 2002:66).

105. Pedal ungual phalanges, shape: dorsoventrally flattened, but elongate and pointed (0), elongate, bluntly truncated tip with prominent claw grooves retained (1), anterior margin broadly rounded in dorsal view, lateral claw grooves either indistinct or entirely absent (2). (Norman, 2002:67).

Notes:

- All characters were run in the analyses as *unordered*.
- No characters were weighted.
- All characters were parsimony-informative.

APPENDIX 2. DATA MATRIX

Lesothosaurus diagnosticus	000000001000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Hypsilophodon foxii	1000000001000101010000?0101120000000?00000000000000000101000011111010000010000000000000000001000010000000
Rhabdodontids	100100000101010101000?11?1112?00?10?100001120010000100111111011111111001?10010?????????1001111111000010?0
Tenontosaurs	110001000101010101??0?10111120100110111011000010000000101111011111011001110011000000001000302100210101000
Dryosaurids	01010101110010?010000000000011000100001010100000000000101111012211020000000000?0000?00?000102011120002010
Camptosaurus dispar	01011101110000?0?0001000000??1000110001111100010000000111112012211120001101010110100101000102011120001000
Mantellisaurus atherfieldensis	0111110212001010100110000000110001120111111111111101001112121122111211111011111211101111101103102120113111
Iguanodon bernissartensis	0111110212001010100110000000111001120111111111111101001112121122111211111011111211101111112103111120113111
Ouranosaurus nigeriensis	0211111112000010201110000000110001110111112112120010000111212112211121111210111112111011100111411112?1131??
Altirhinus kurzanovi	0111110113100010200110000000110001110?1?11111211110001211212112211112?????0111112?11011100111310102?11???1
Eolambia caroljonesa	?111110???????102011100000001?00?11?01?1??1?102101000121121211231122??11??111113?11011?101113?1112111131?1
Jinzhousaurus yangi	0111110213101010?0001?000000110?01220?1?11111110?10000?112?20122111211?1101111121110111?01112?0112?1131??
Hypselospinus fittoni	??111001???0?1121211221112?1131?111112111011?0011031111201131?1
Barilium dawsoni	??1111???0?1121211221112?1?11?11111211101??101013111?201131?1
Equijubus normani	0111110113101010?0001?0100001110?111011?11111111?1010121121211221112111??0????????1????0011??11??????????
Probactrosaurus gobiensis	011111011?1?1010?00?1001?00?1?00?11?011?1111121111010121121211231122?111?0122213?12011?0011131111120113121
Bactrosaurus johnsoni	011111011310?01020111100000?2100111011112111112121111222222122322221111?01222?422212??0031231111121223122
Tethyshadros insularis	01111102131010?0?0100?0100022?0001110?1?11111111111111??2222?2232?2311?11012222422212?100422311202?2??121
Parasaurolophus walkeri	0111110213100010202211000002210112222111121?22121211122223231234222311211022222422212110142241111121224122
Saurolophus osborni	0311111213101010202211010002211112222111121?201212111222232312342223112110222224222121101422410202122412 2
Edmontosaurus regalis	031111121310001020221101000221111110211112 1?20121210122223231234222311211022222422212110142241020212241 22
Telmatosaurus transsylvanicus	?111110??31?1??0??011????0022?10?112011???1??011121102222323211322221111??2?2?????????????????????12141??
Bolong yixianensis	011111021?101010?00???0????????0???0?11111?11?001???0211212112211121??1?01?1112111111110322??1112?11?1?1
Proa valdearinnoensis	?111110??200????20?0????000?2?10?11??11?1011111111???021121211221112???????????????????1031121????01141??
Gilmoreosaurus mongoliensis	?1??1???31?1??02012110??0022?10????0???11?1111??2????22221322142?12?121??22?22?42?1????0132231111212231?1
Batyrosaurus rozhdestvenskyi	???????????0?????00110???00?1?0??11??1?11111?010010100?1121211221012??1????2?????????011?????????????????
Levnesovia transoxiana	0???????????????1?12?1??????2?000110?11112111111011????12222122211 12?1?1?????2???????????1??3????????3???2

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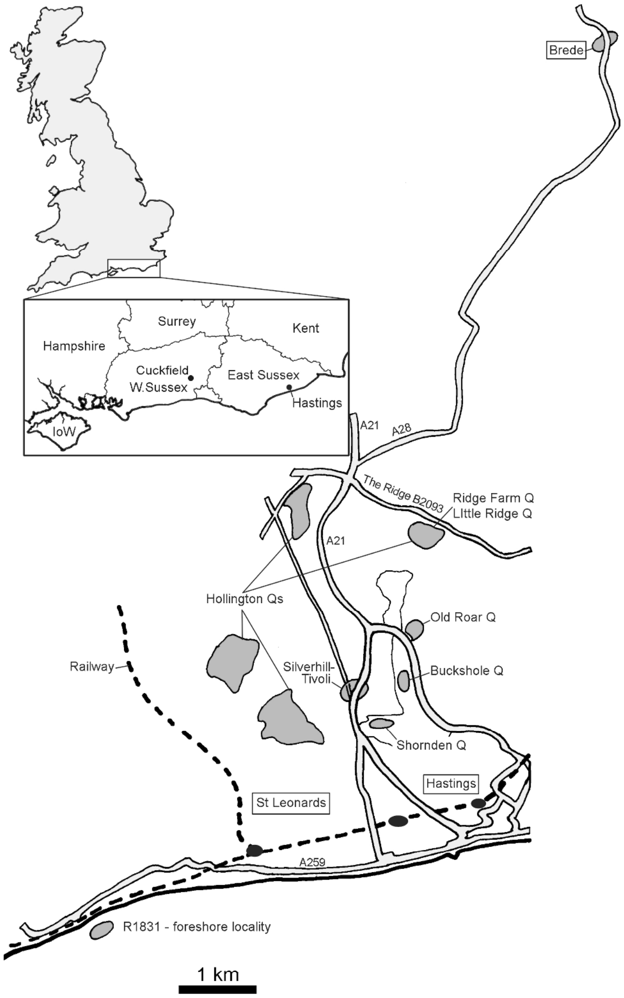
Fig. 1



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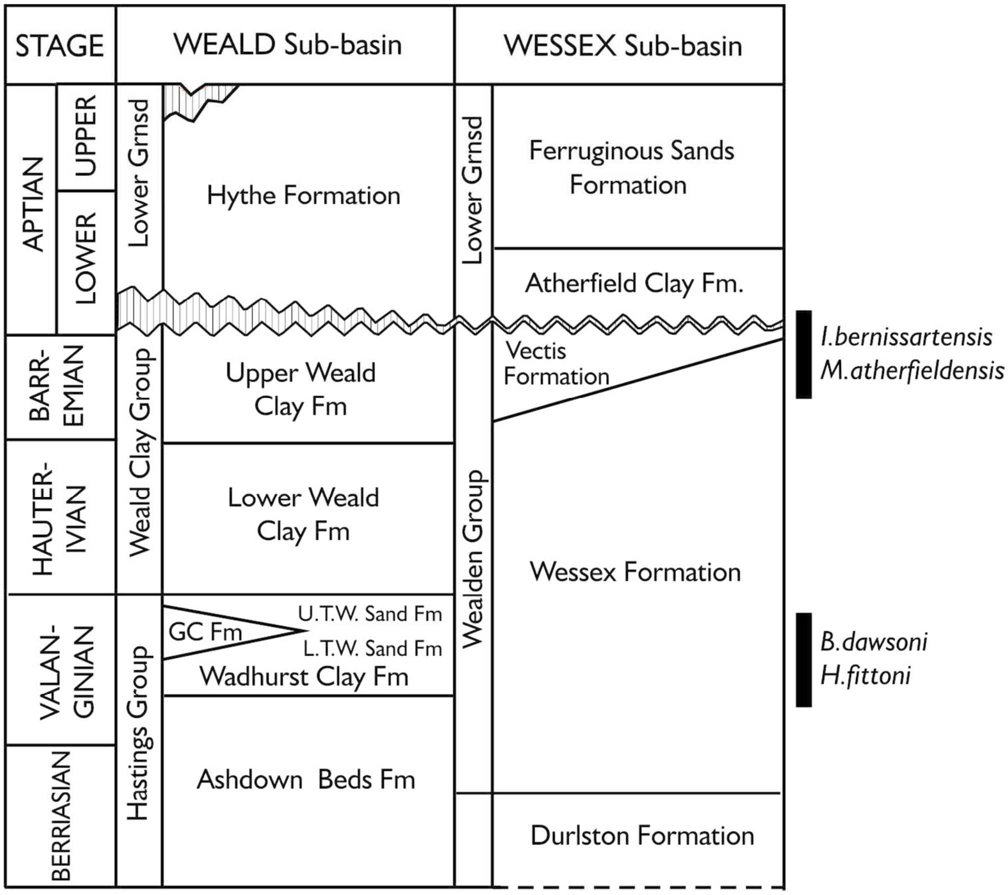

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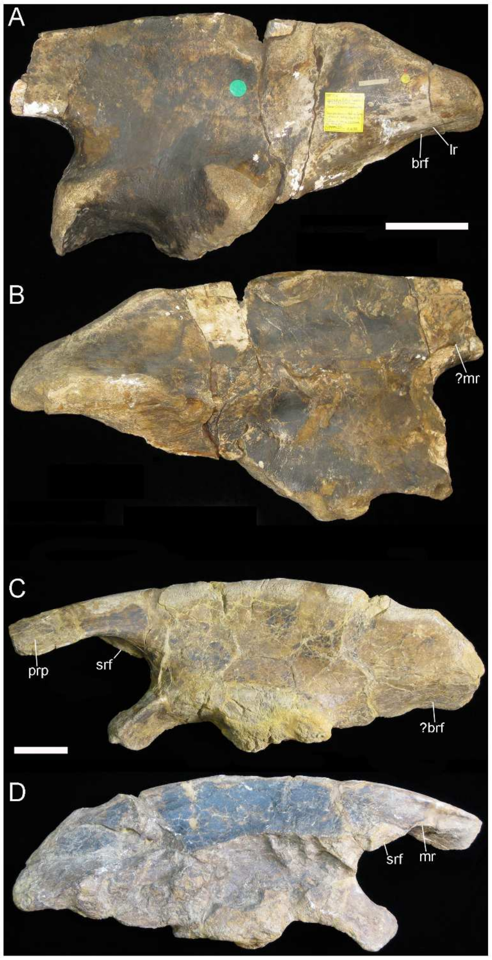
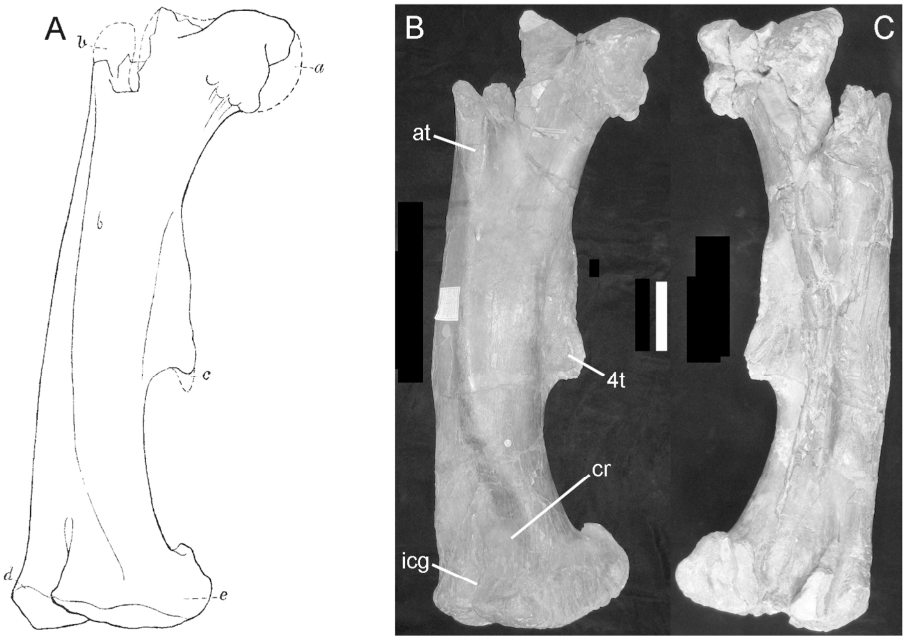
Fig. 3



209x297mm (300 x 300 DPI)

Fig. 4



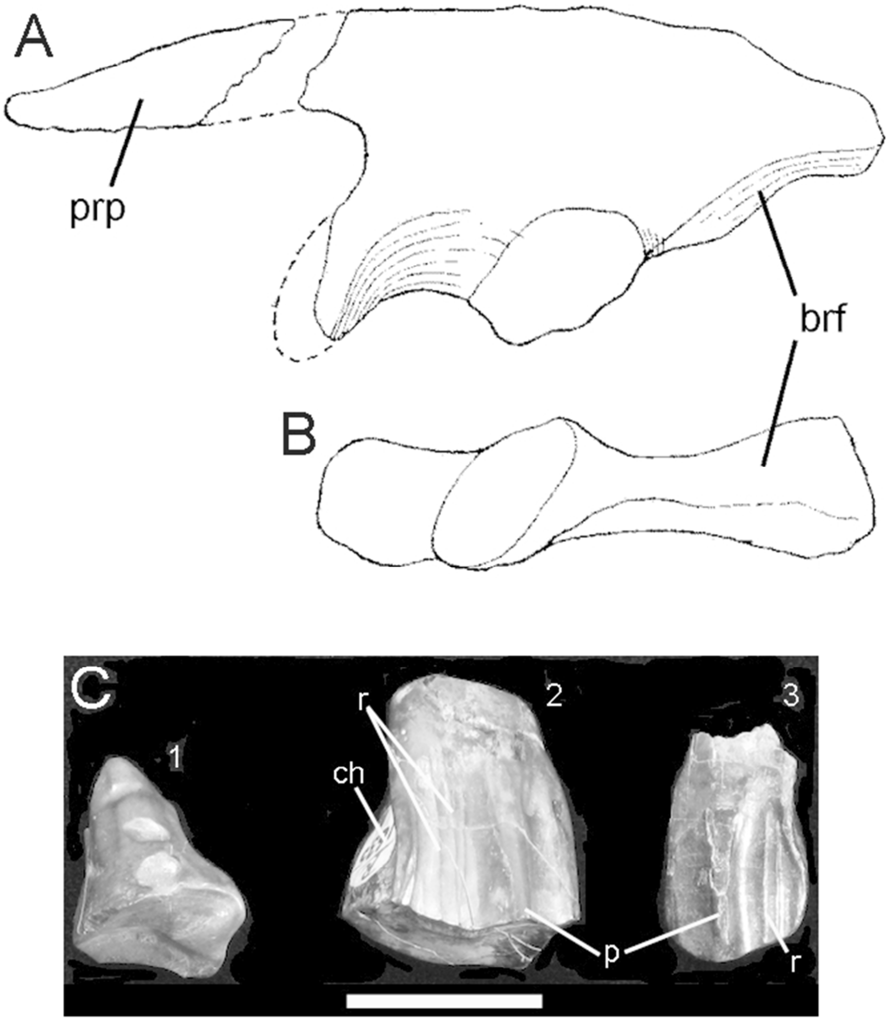
[redacted]

[redacted]

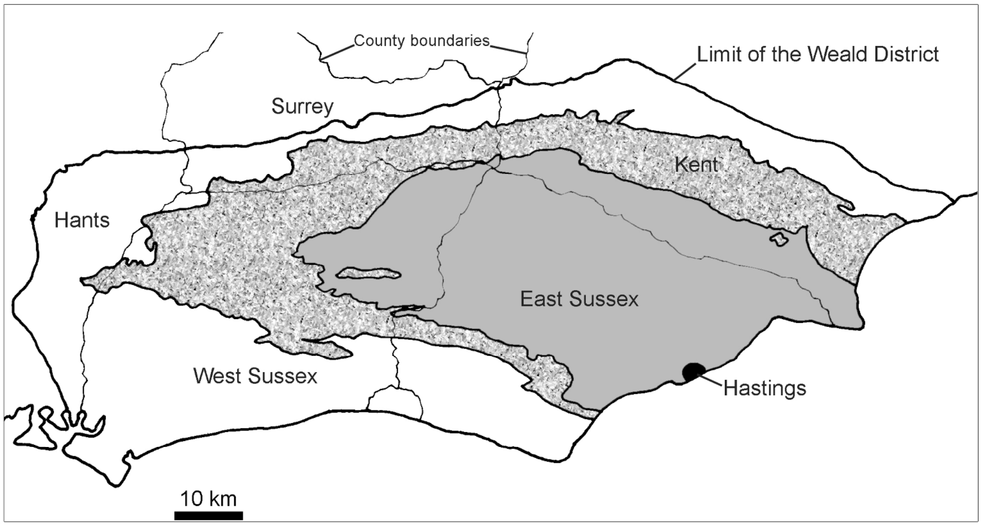
[redacted]

155x125mm (300 x 300 DPI)

Fig. 5

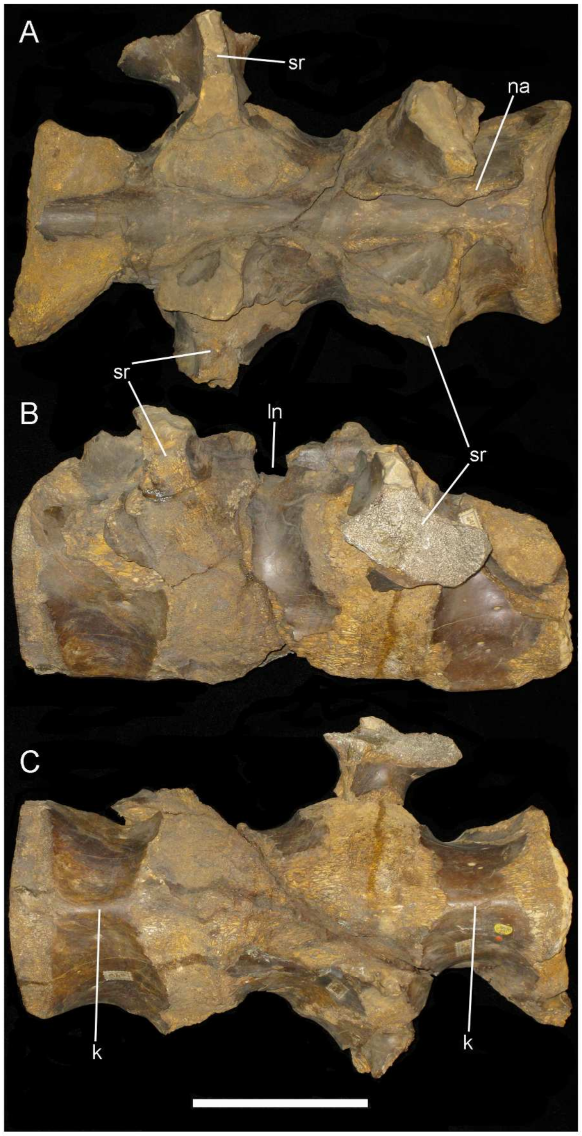


105x127mm (180 x 180 DPI)



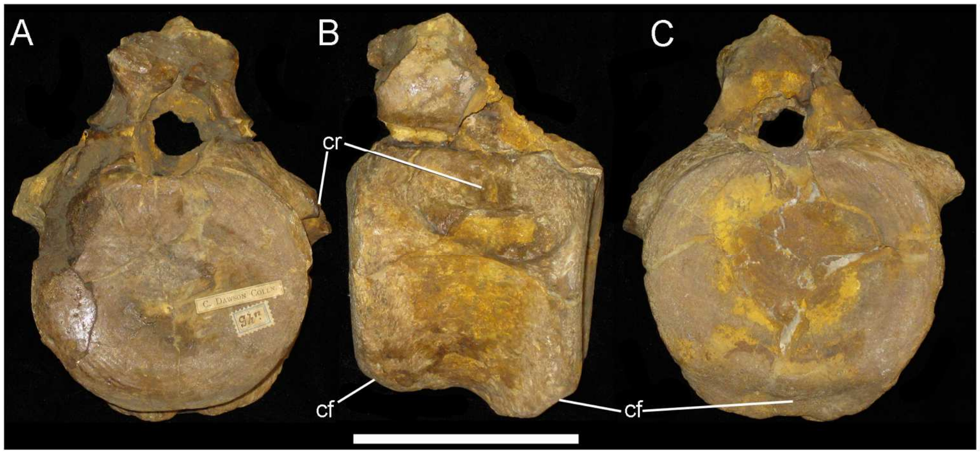
197x107mm (300 x 300 DPI)

Fig. 7



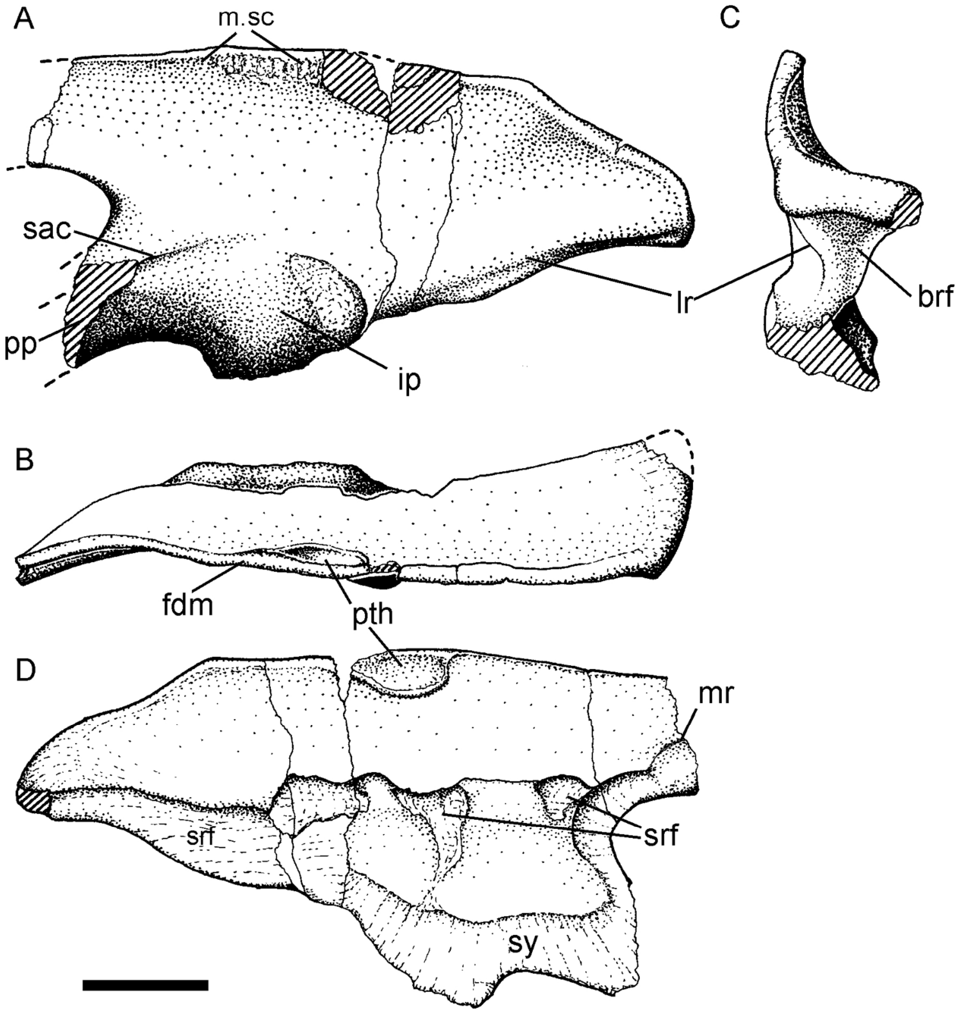
129x250mm (300 x 300 DPI)

Fig. 8



178x92mm (300 x 300 DPI)

Fig. 9

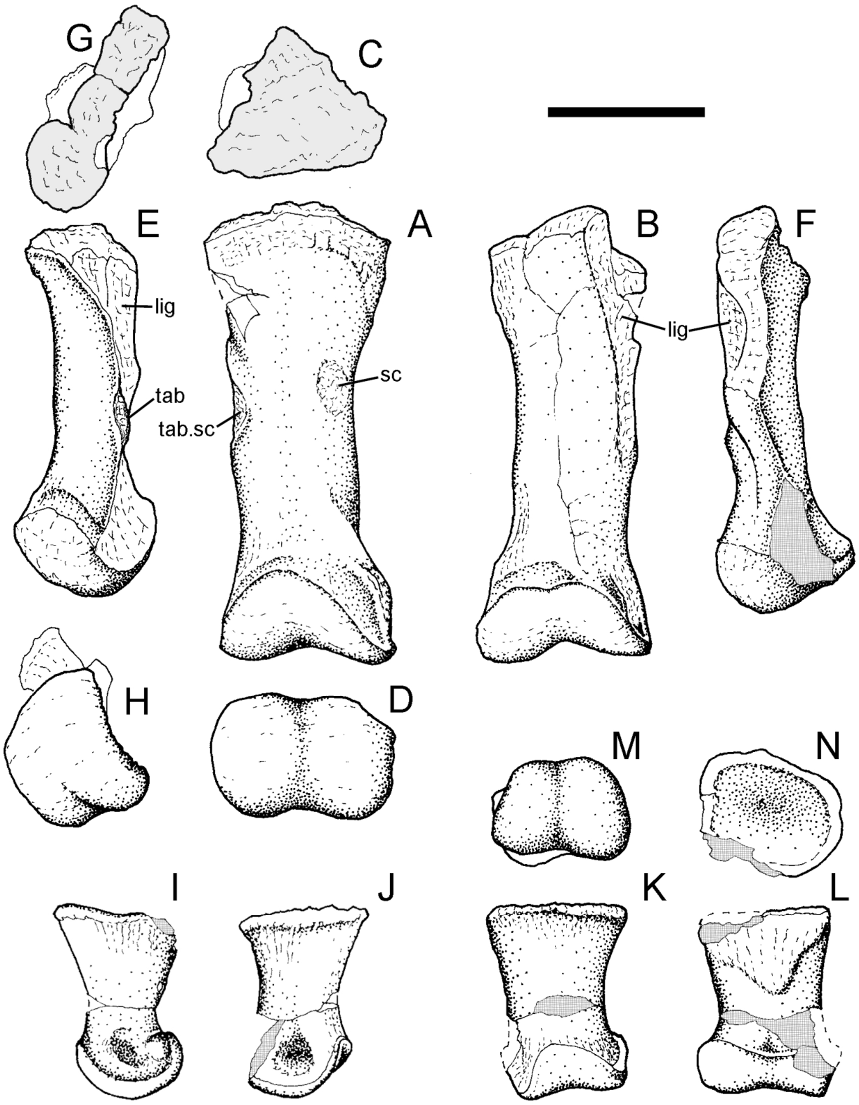


159x177mm (300 x 300 DPI)

Fig. 10

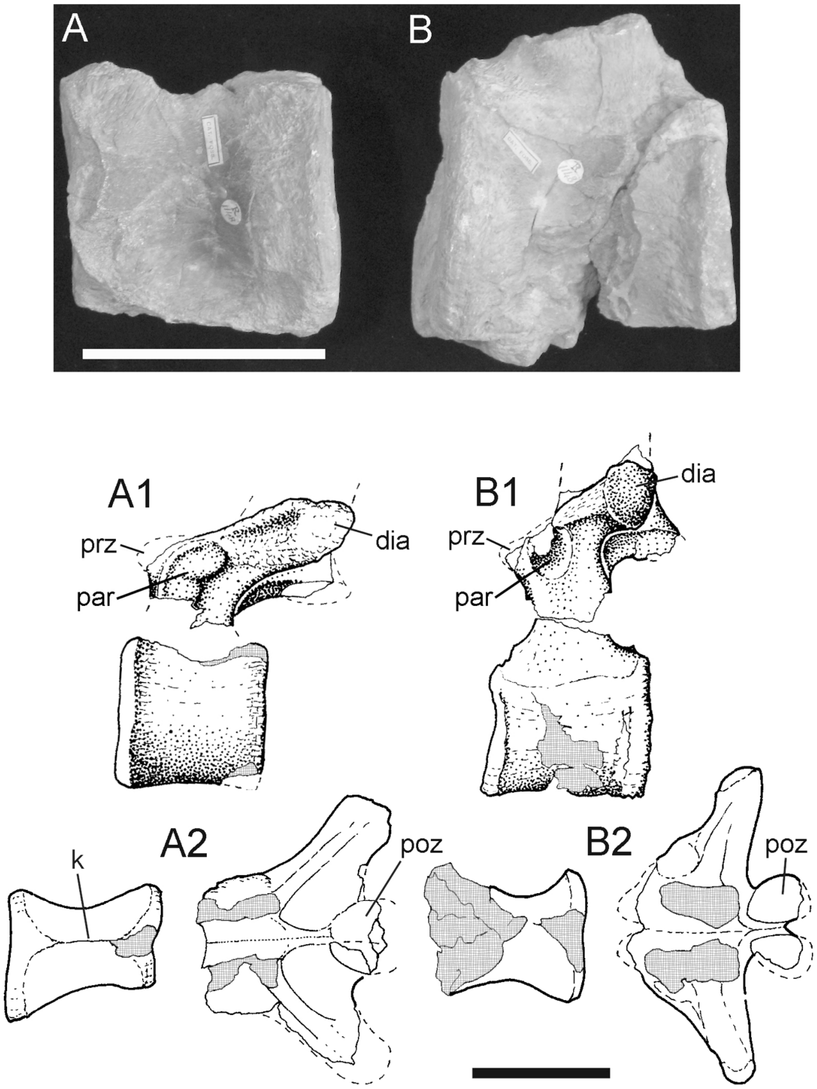
105x161mm (300 x 300 DPI)

Fig. 11



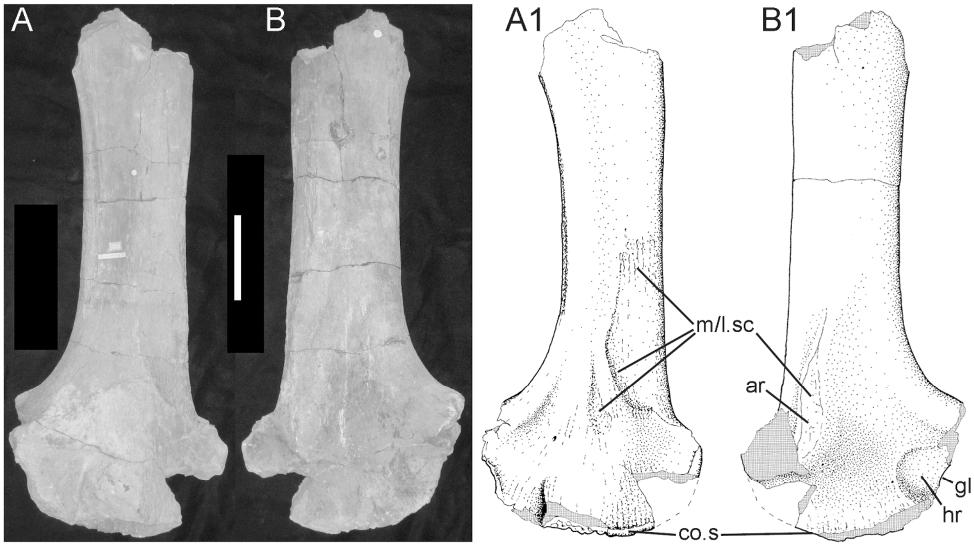
152x201mm (300 x 300 DPI)

Fig. 12



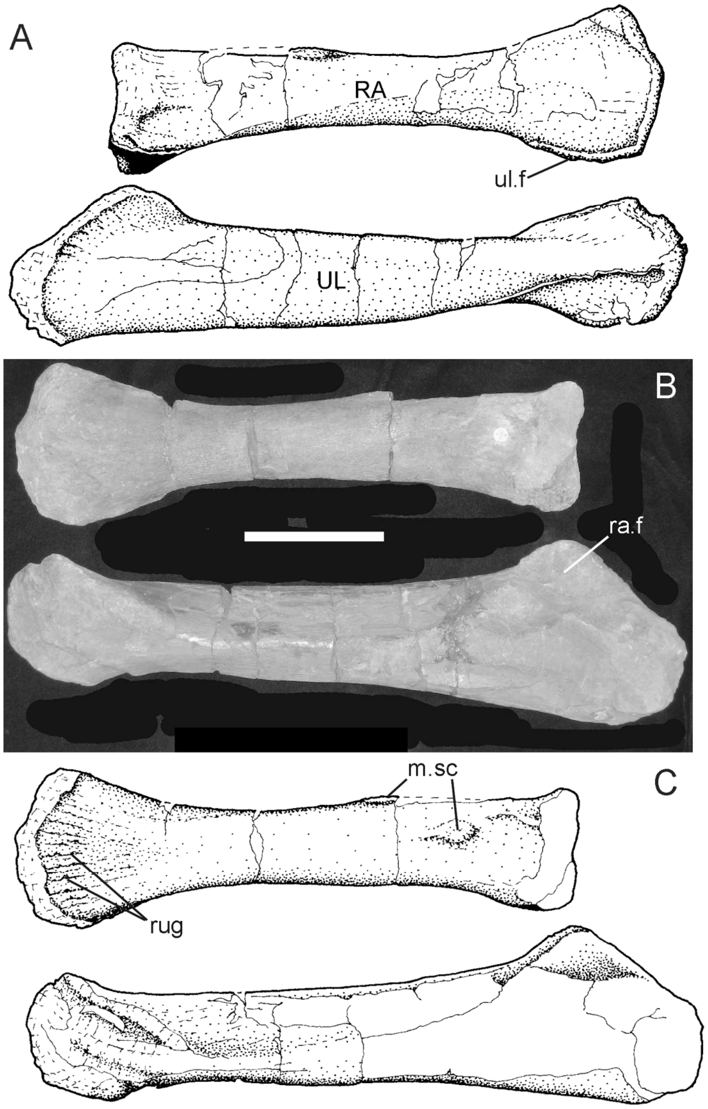
143x192mm (300 x 300 DPI)

Fig. 13



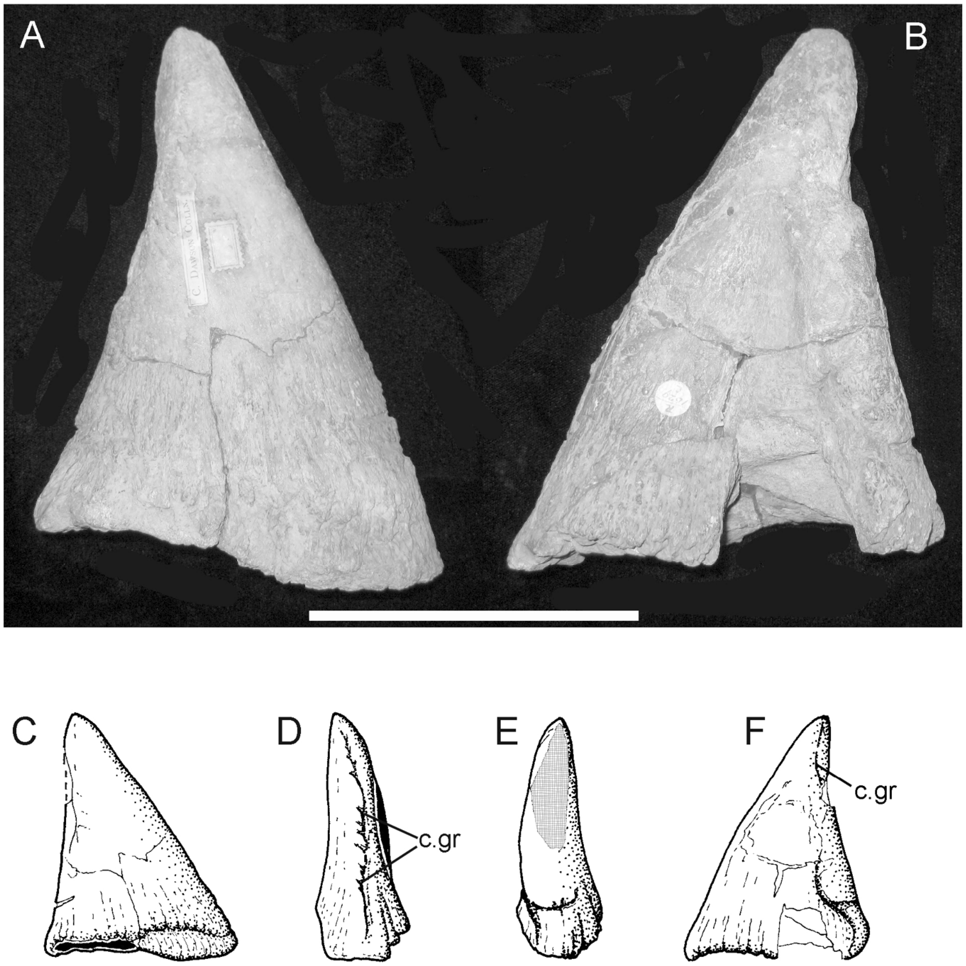
192x125mm (300 x 300 DPI)

Fig. 14



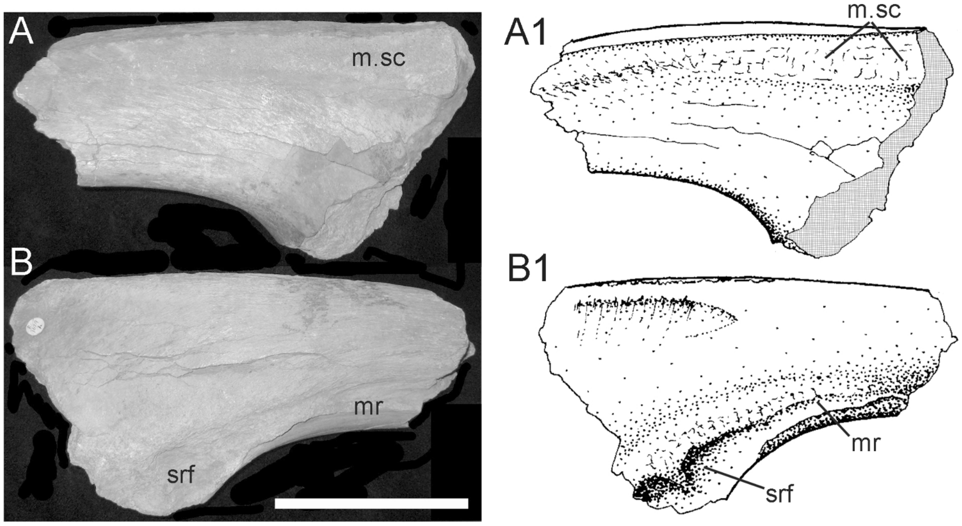
140x216mm (300 x 300 DPI)

Fig. 15



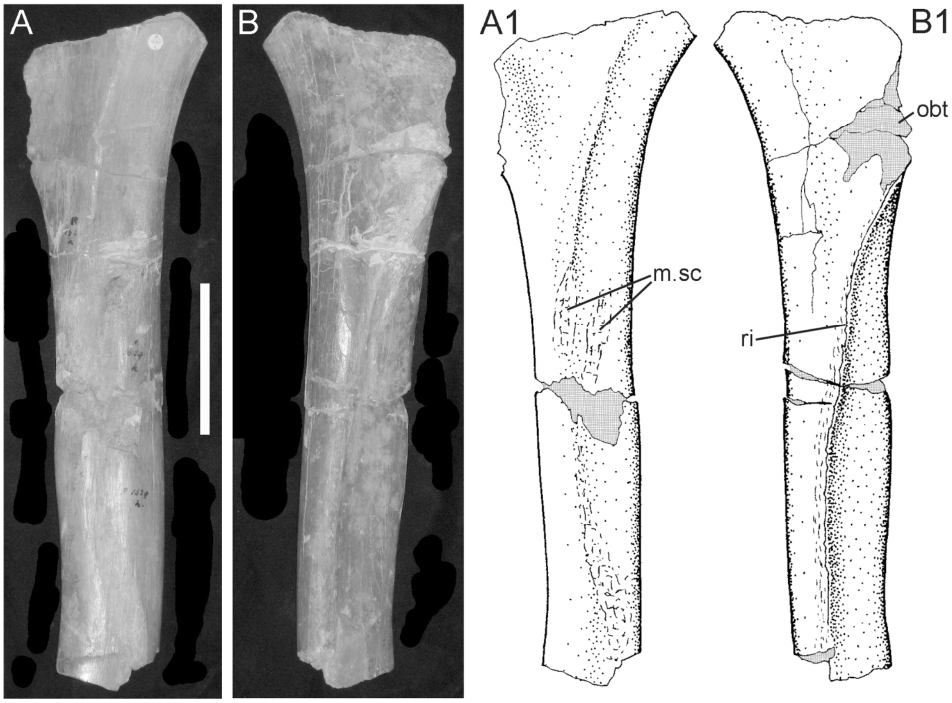
166x177mm (300 x 300 DPI)

Fig. 16



167x105mm (300 x 300 DPI)

Fig. 17

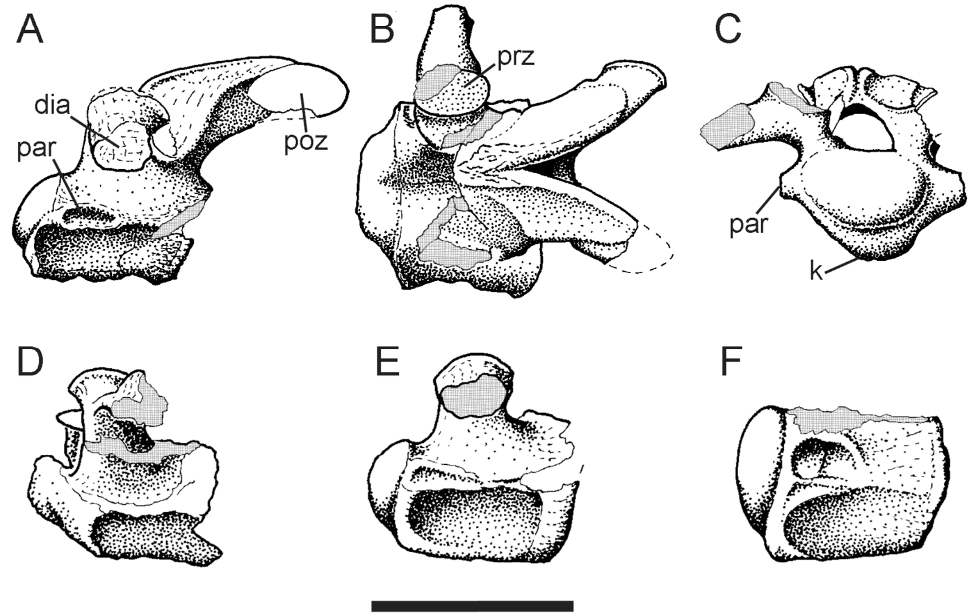


183x145mm (300 x 300 DPI)

Fig. 18

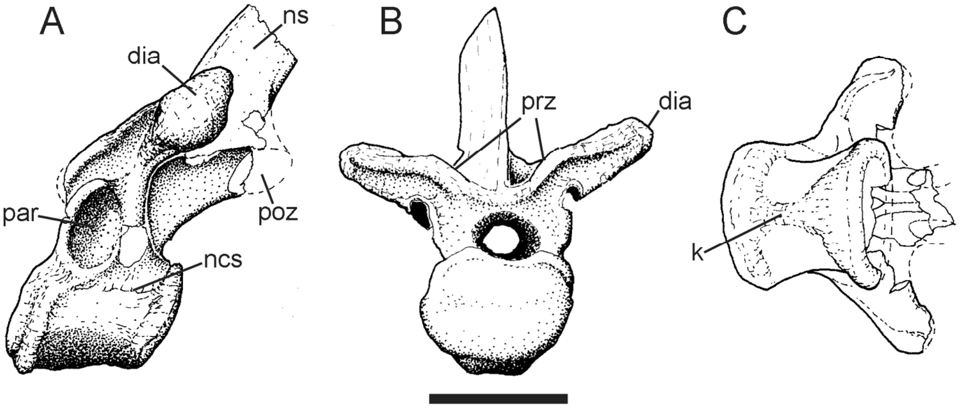
128x178mm (300 x 300 DPI)

Fig. 19



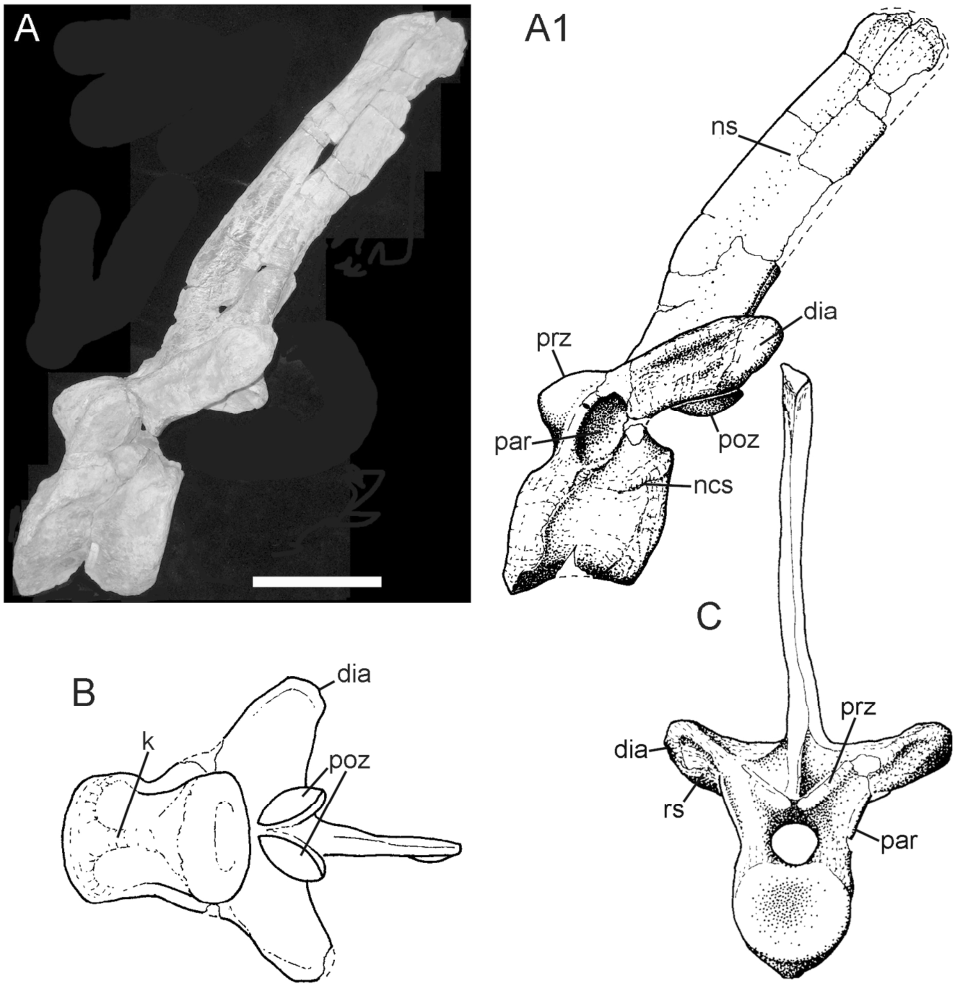
154x115mm (300 x 300 DPI)

Fig. 20



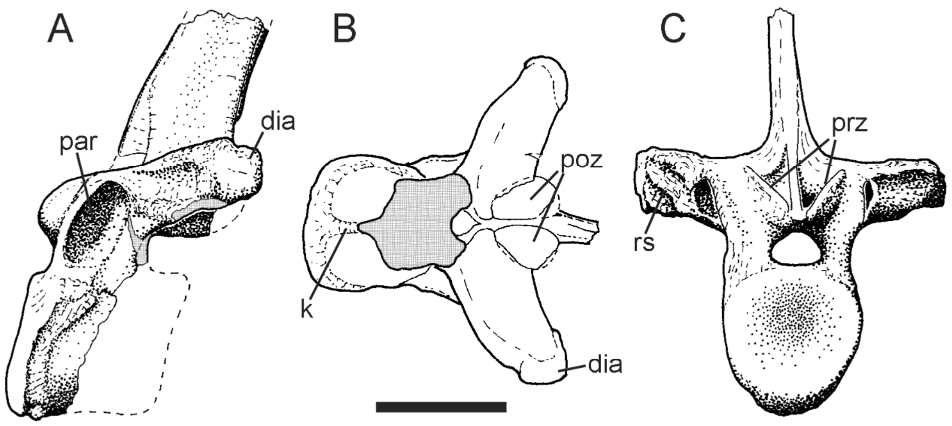
168x93mm (300 x 300 DPI)

Fig. 21



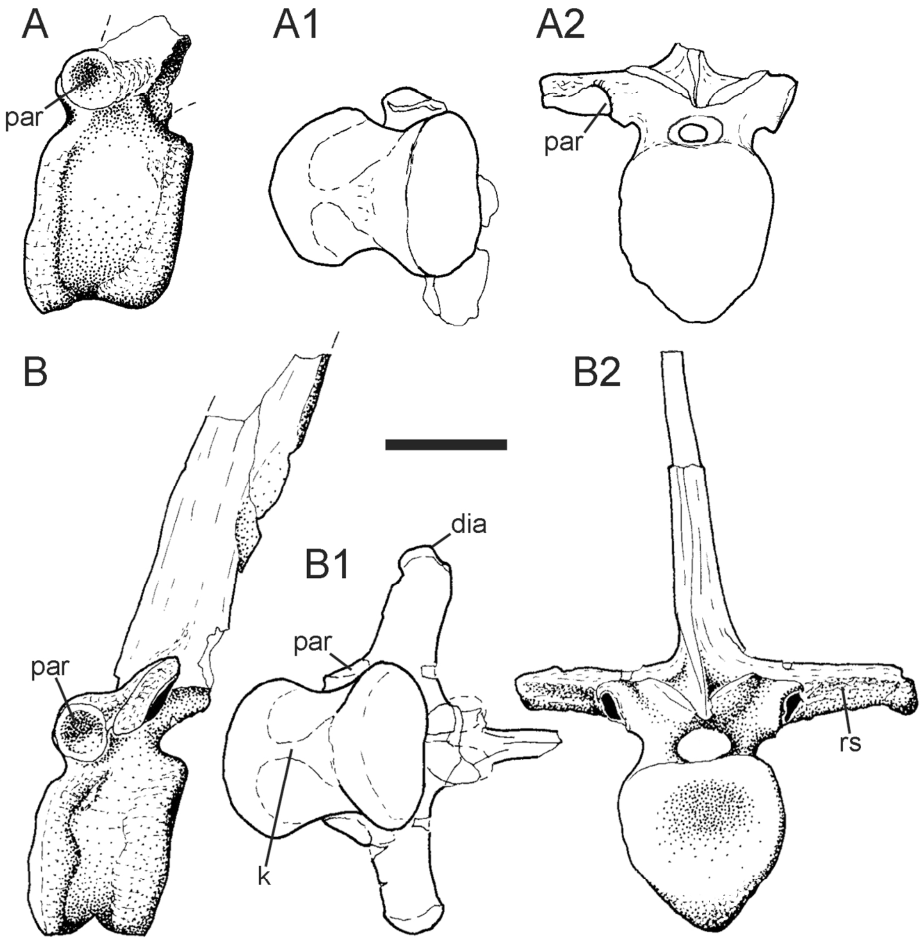
164x178mm (300 x 300 DPI)

Fig. 22



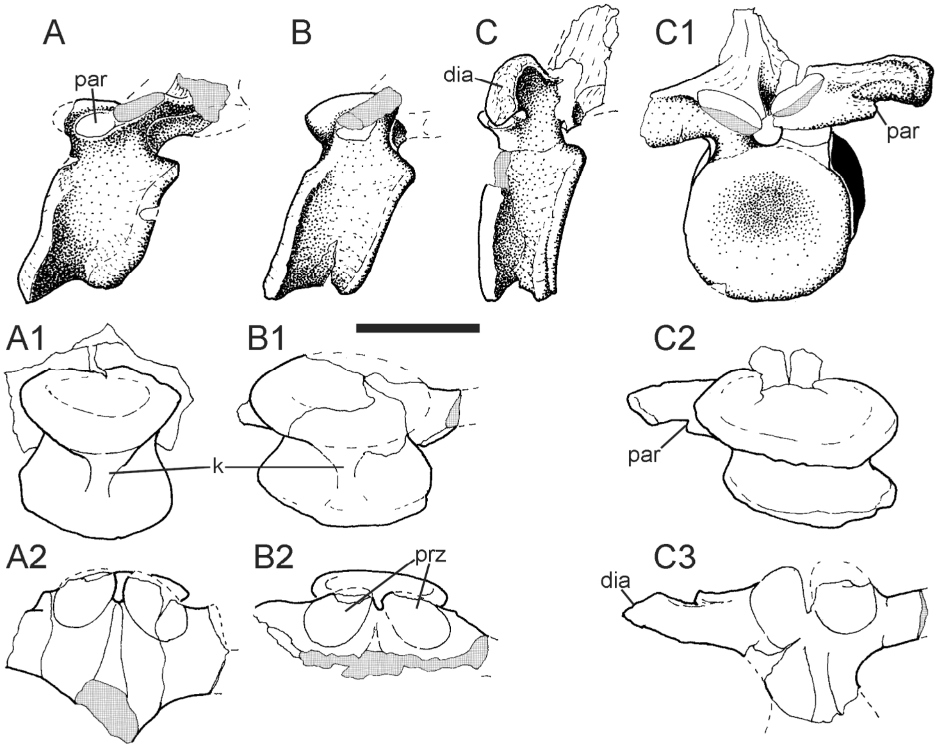
160x92mm (300 x 300 DPI)

Fig. 23



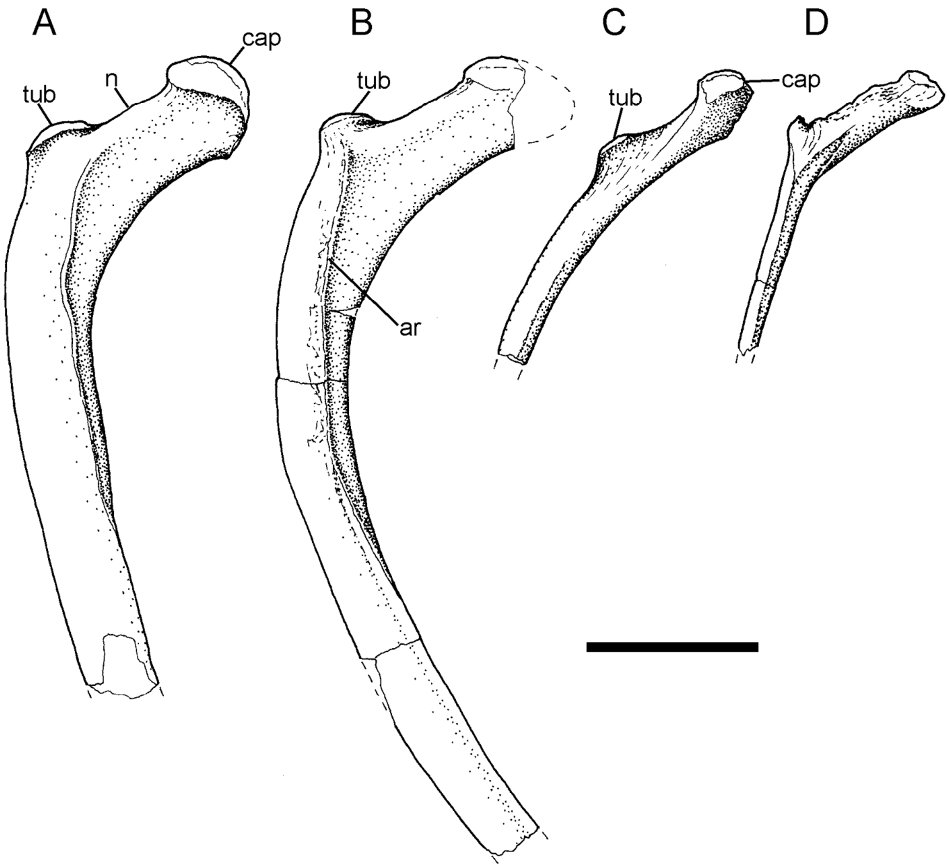
155x168mm (300 x 300 DPI)

Fig. 24



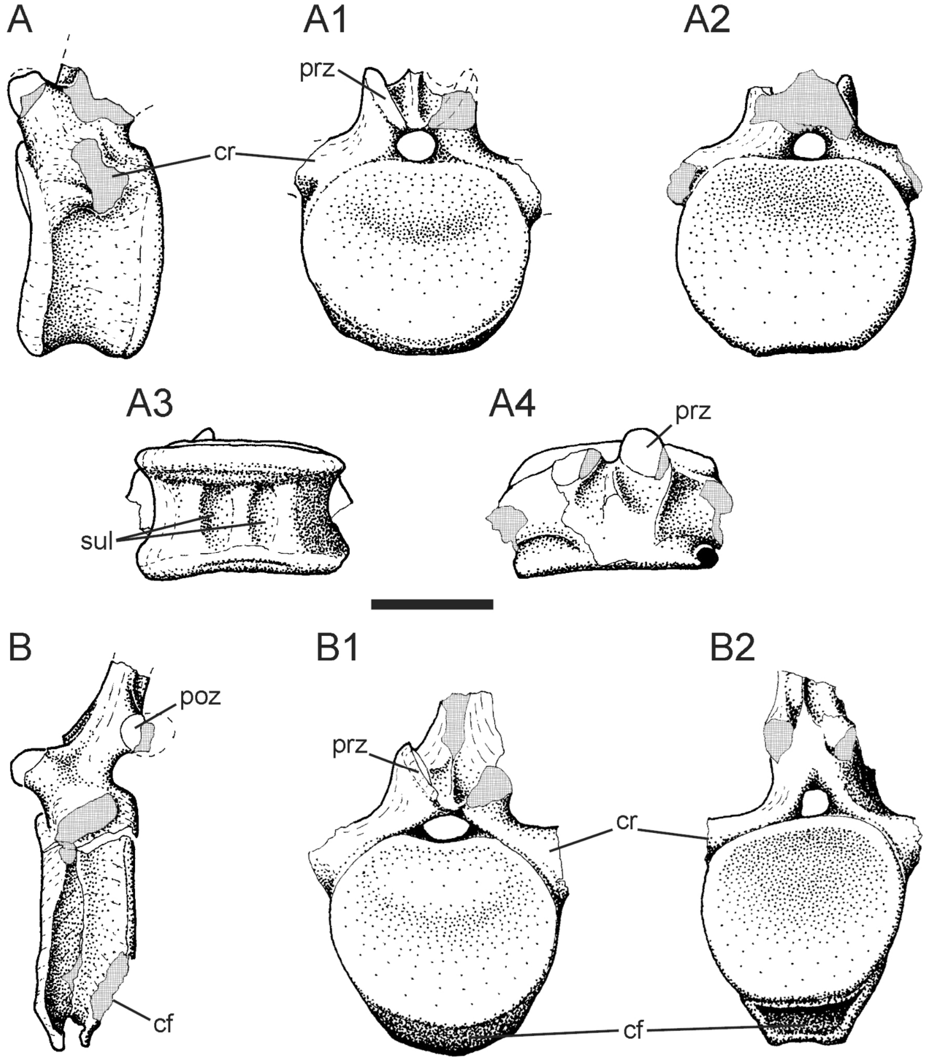
186x162mm (300 x 300 DPI)

Fig. 25



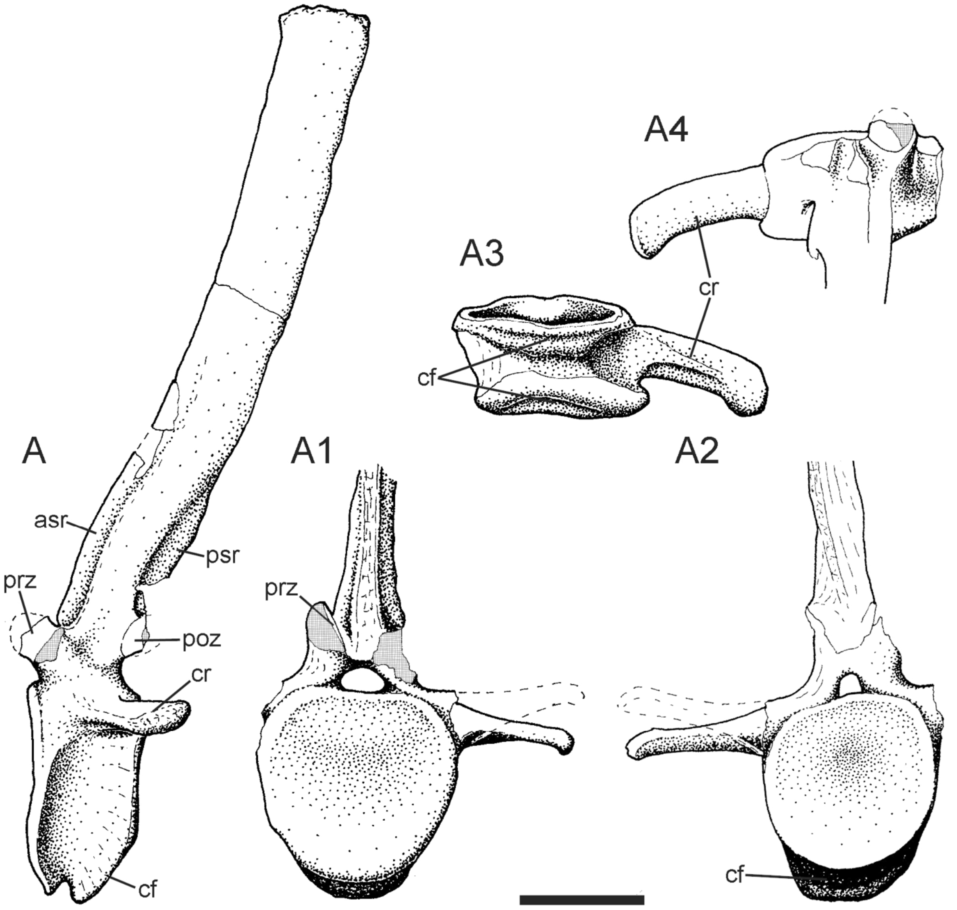
173x170mm (300 x 300 DPI)

Fig. 26



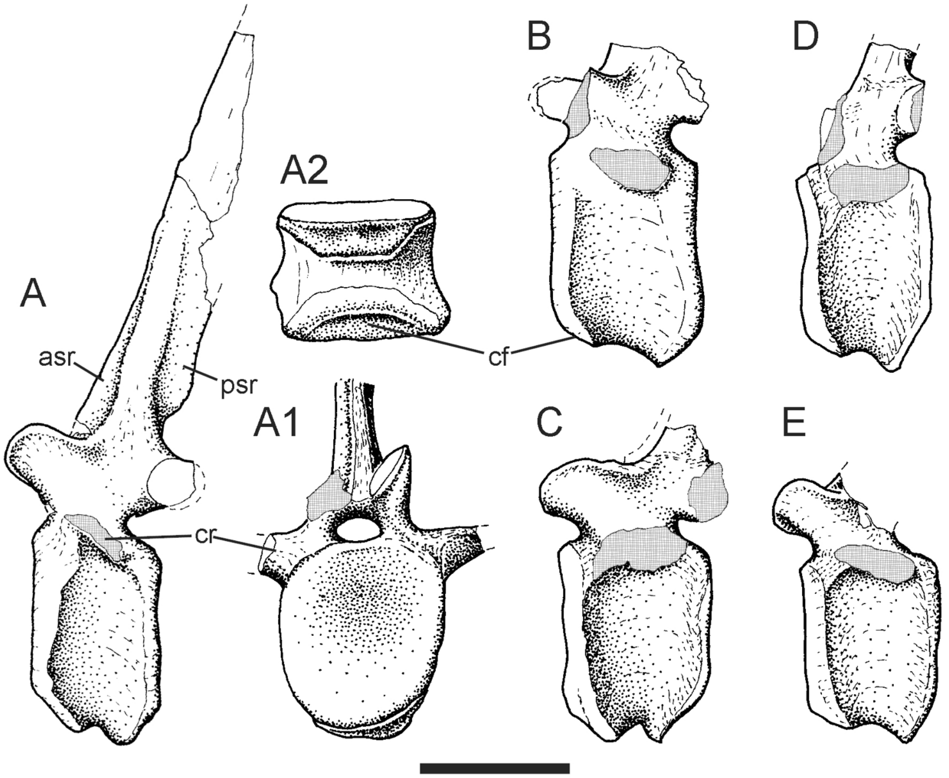
163x193mm (300 x 300 DPI)

Fig. 27



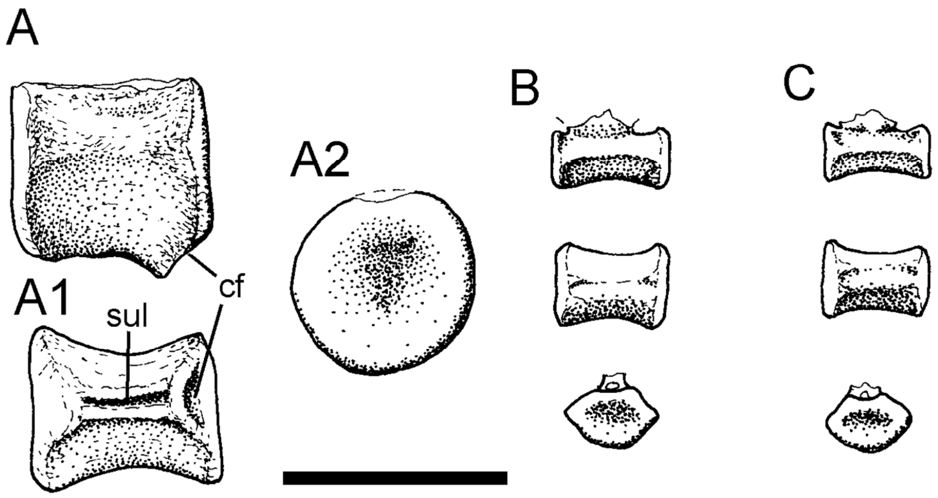
173x177mm (300 x 300 DPI)

Fig. 28



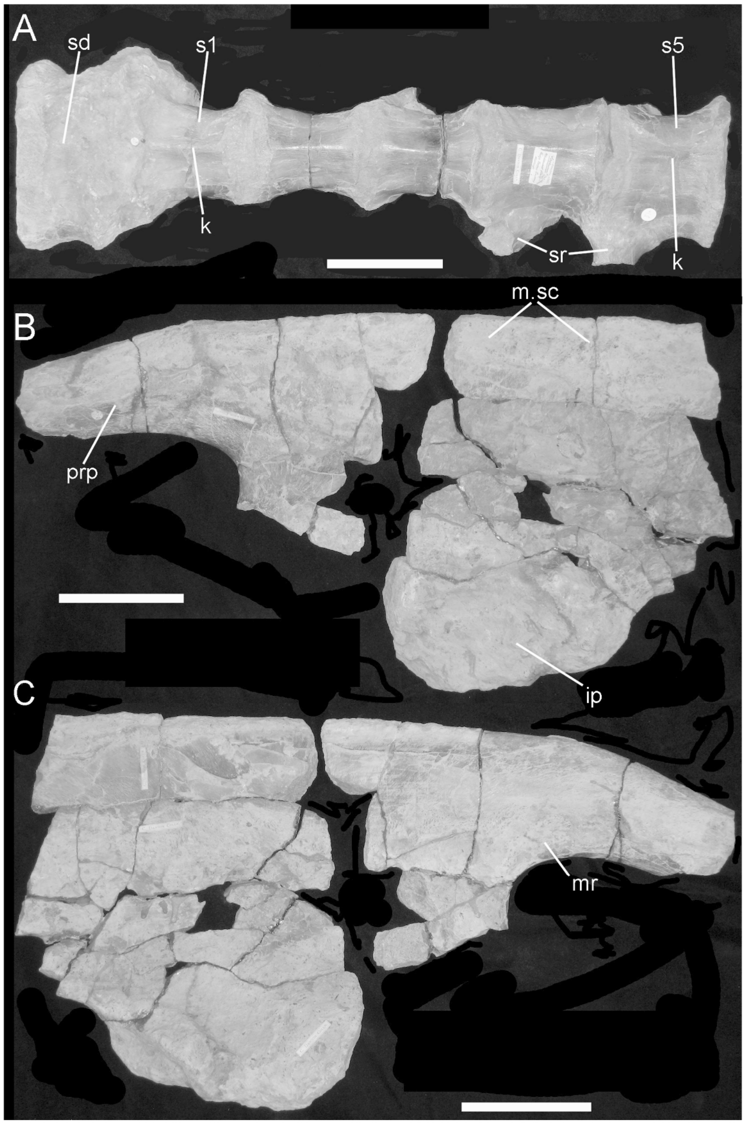
158x140mm (300 x 300 DPI)

Fig. 29



127x84mm (300 x 300 DPI)

Fig. 30



[redacted]

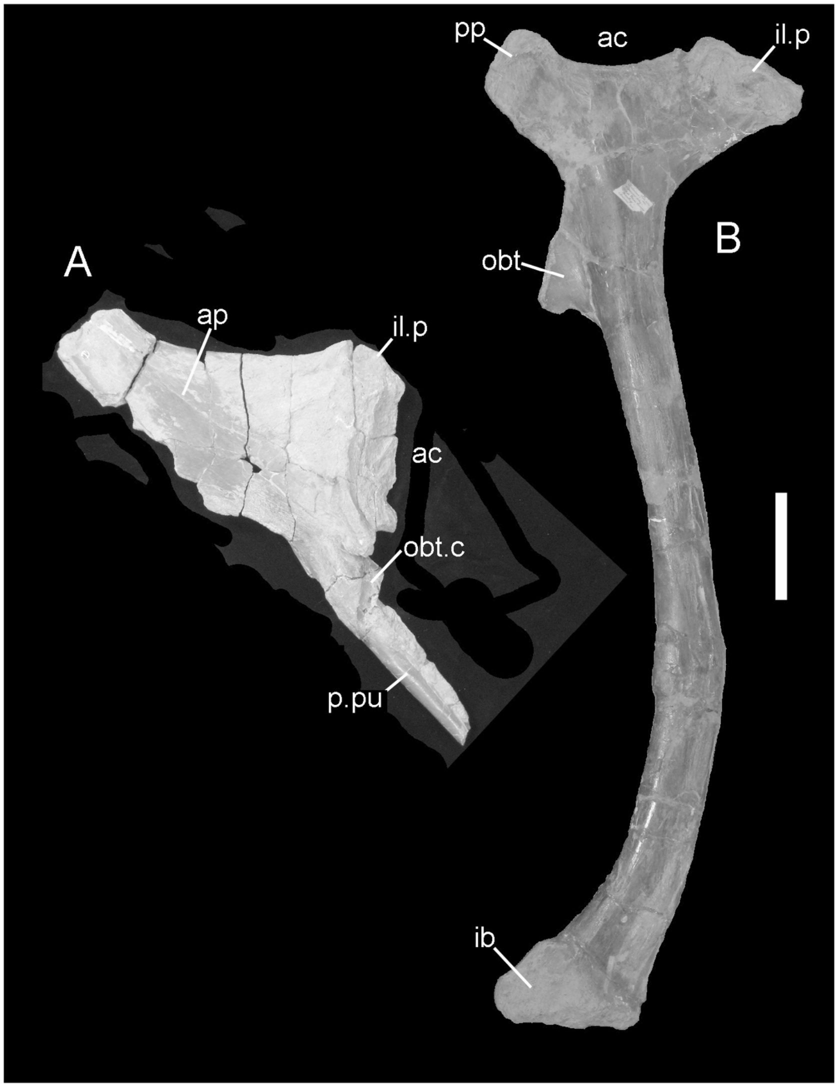
[redacted]

[redacted]

[redacted]

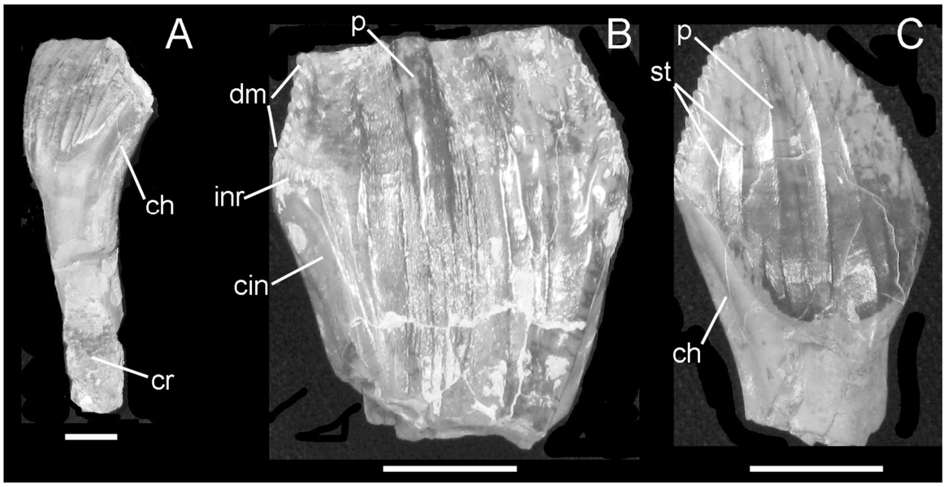
148x229mm (300 x 300 DPI)

Fig. 31



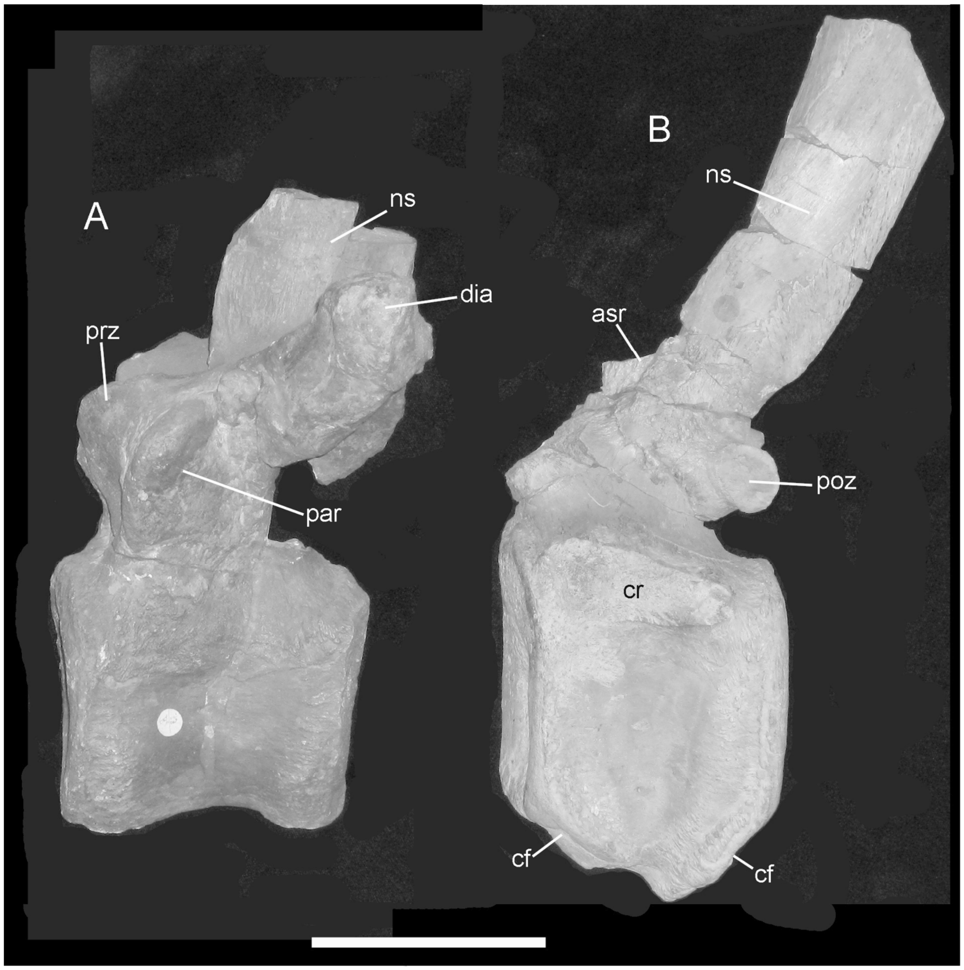
131x178mm (300 x 300 DPI)

Fig. 32



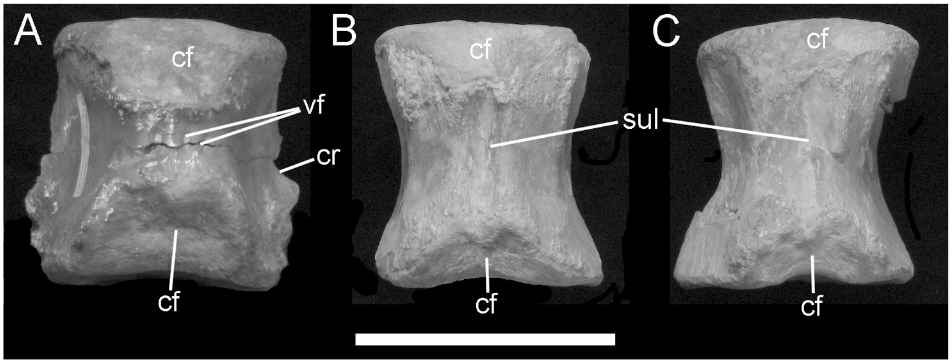
151x91mm (300 x 300 DPI)

Fig. 33



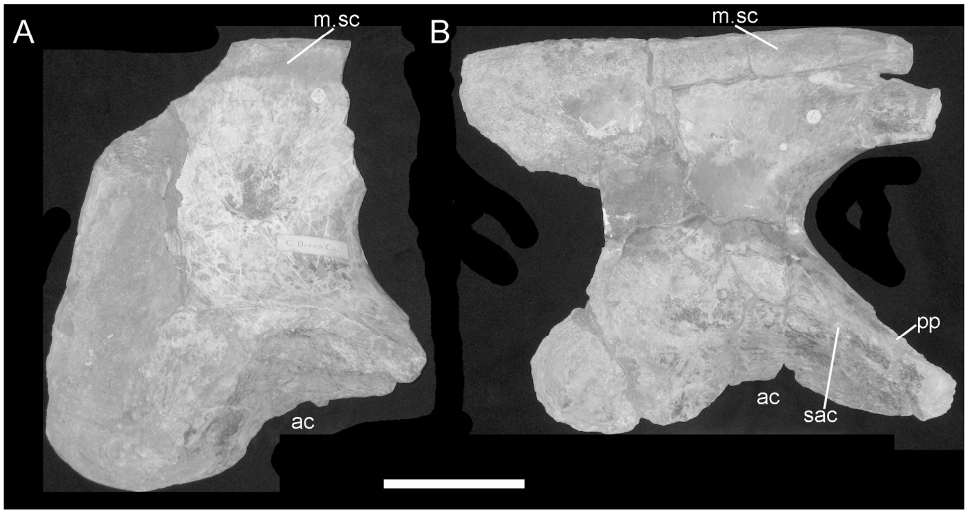
169x180mm (300 x 300 DPI)

Fig. 34



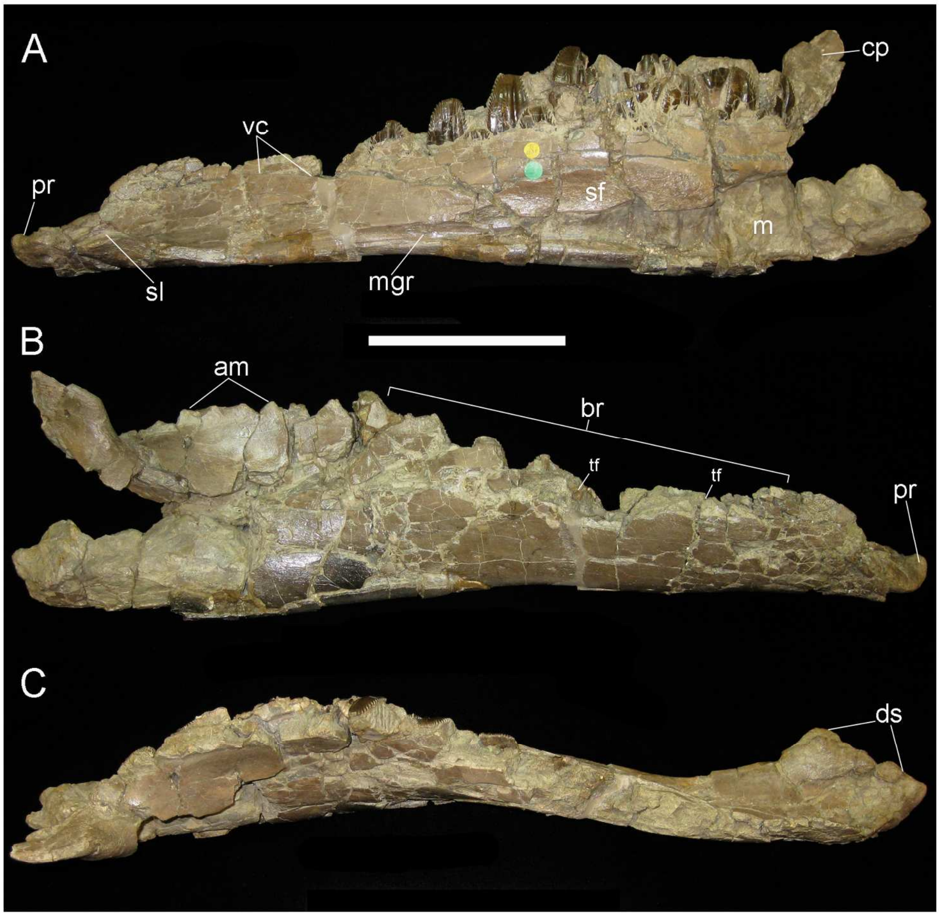
147x70mm (300 x 300 DPI)

Fig. 35



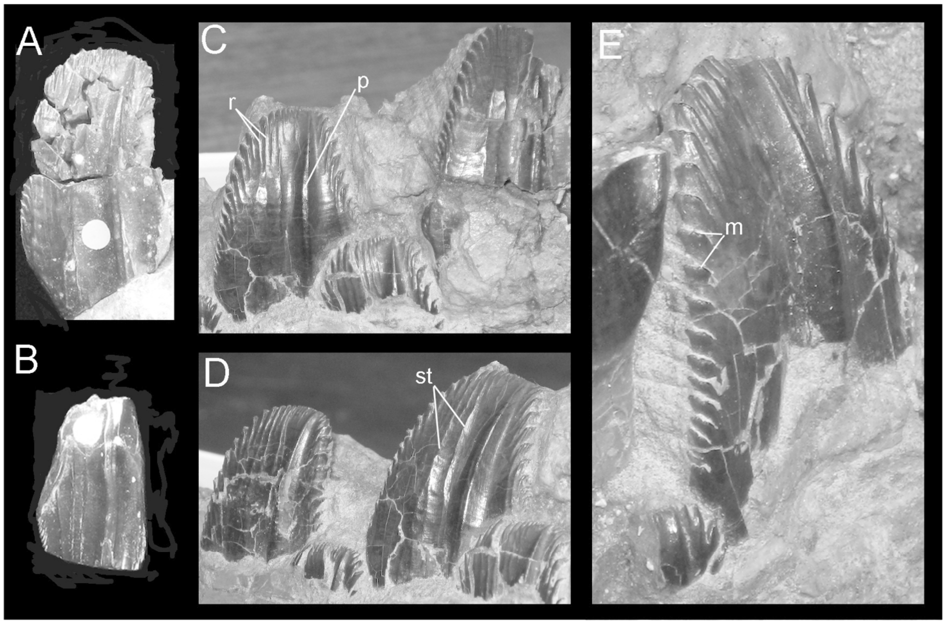
194x116mm (300 x 300 DPI)

Fig. 36



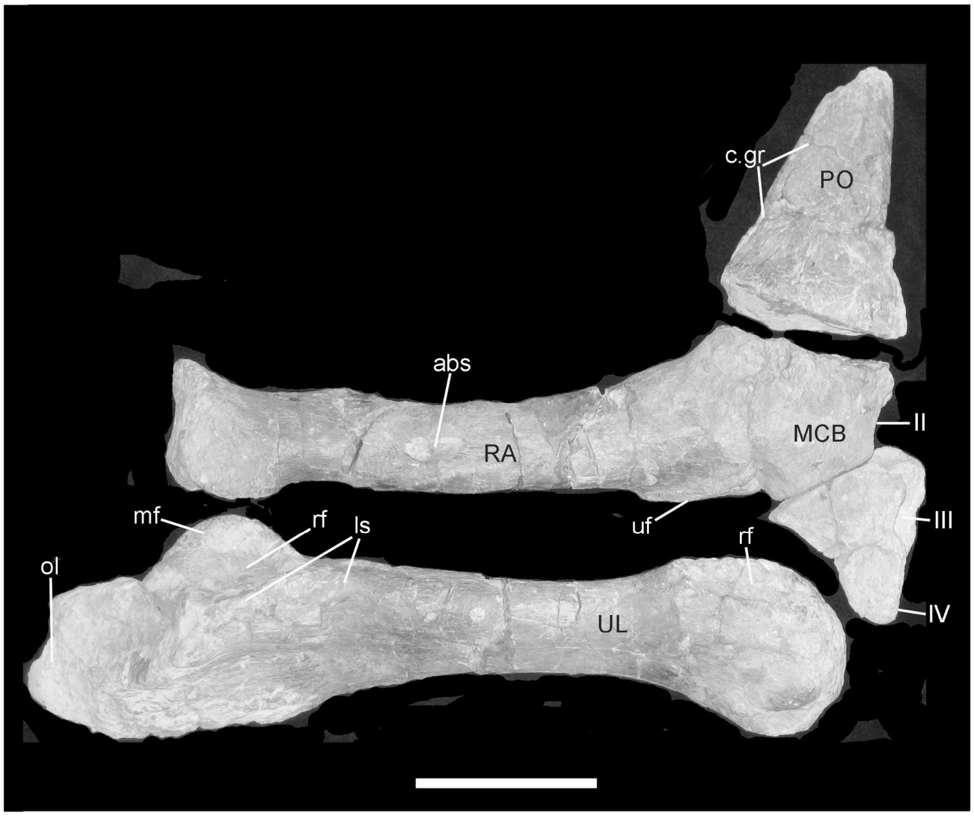
160x163mm (300 x 300 DPI)

Fig. 37



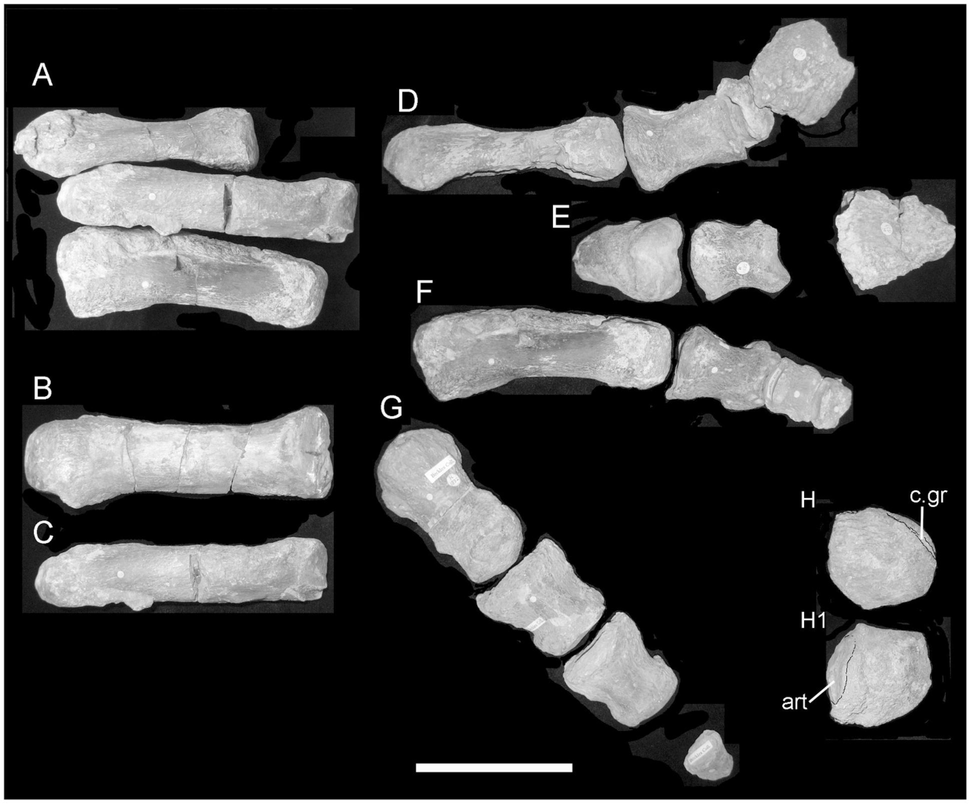
159x116mm (300 x 300 DPI)

Fig. 38



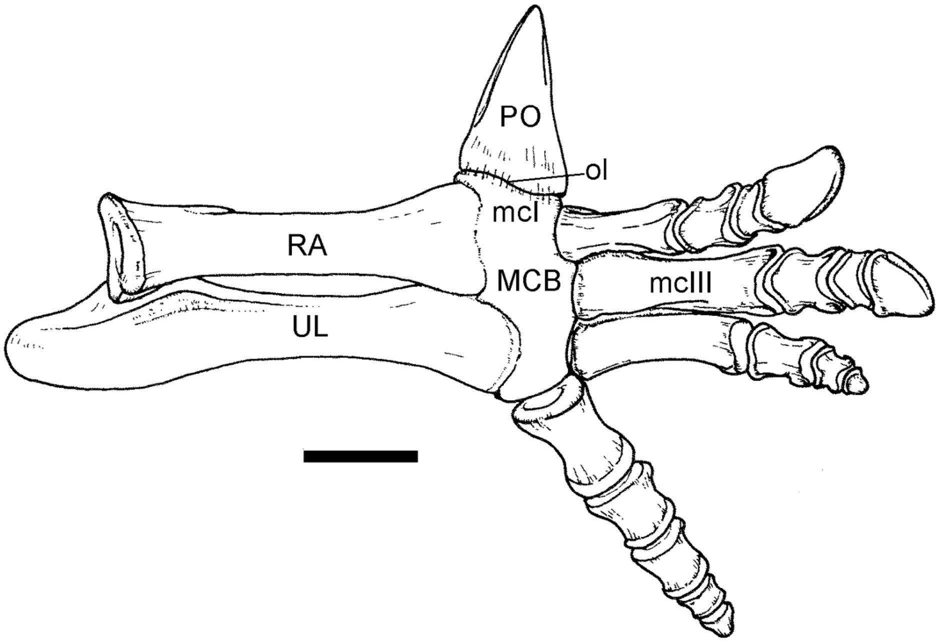
176x156mm (300 x 300 DPI)

Fig. 39



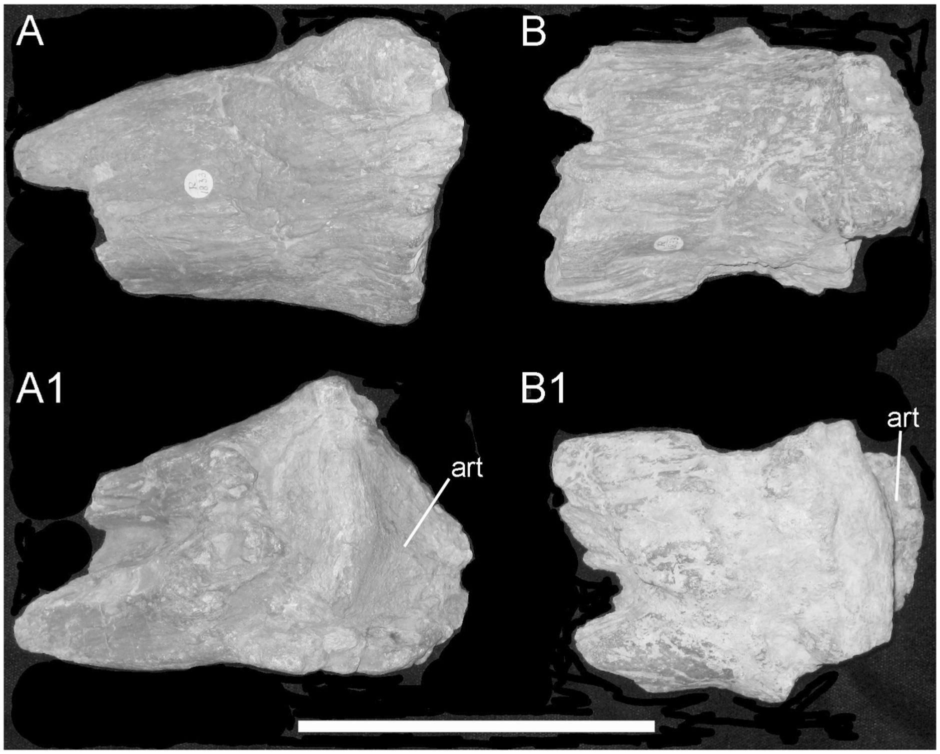
187x166mm (300 x 300 DPI)

Fig. 40



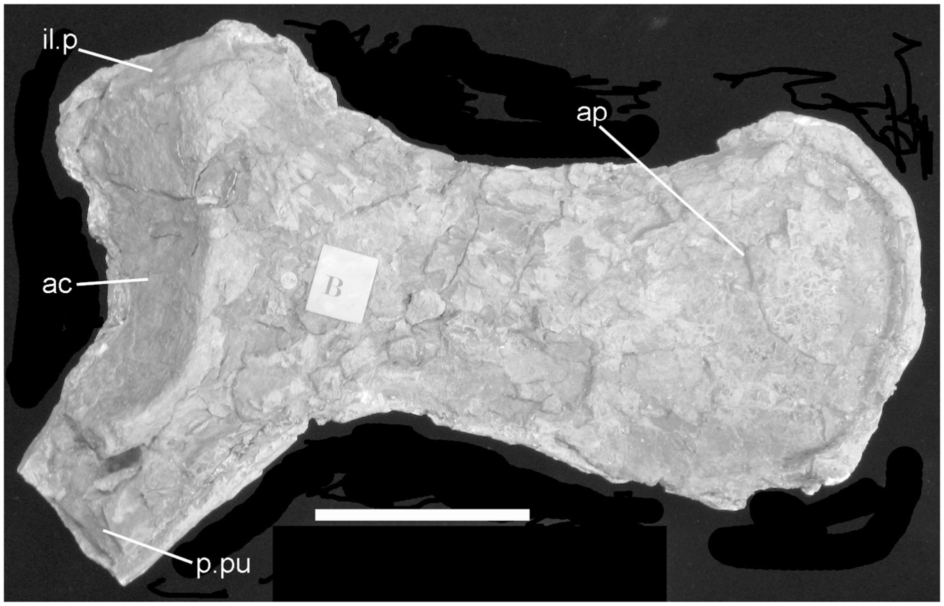
143x110mm (300 x 300 DPI)

Fig. 41



150x129mm (300 x 300 DPI)

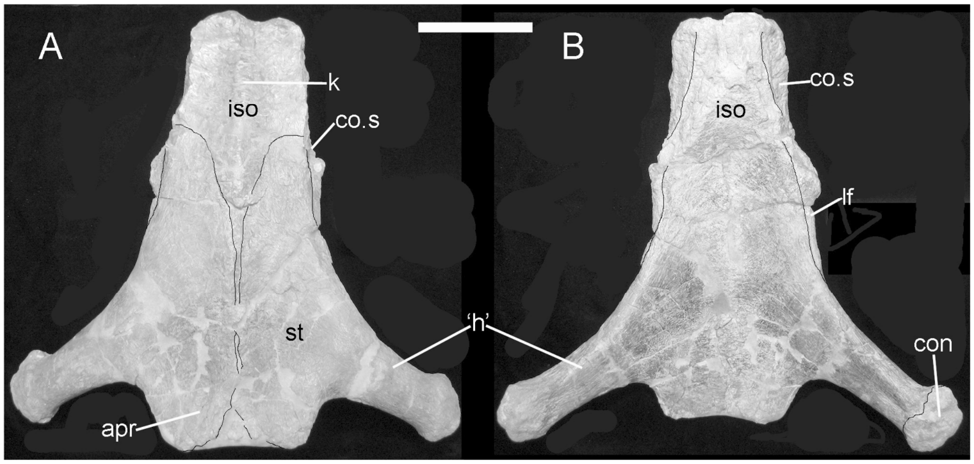
Fig. 42



[redacted]

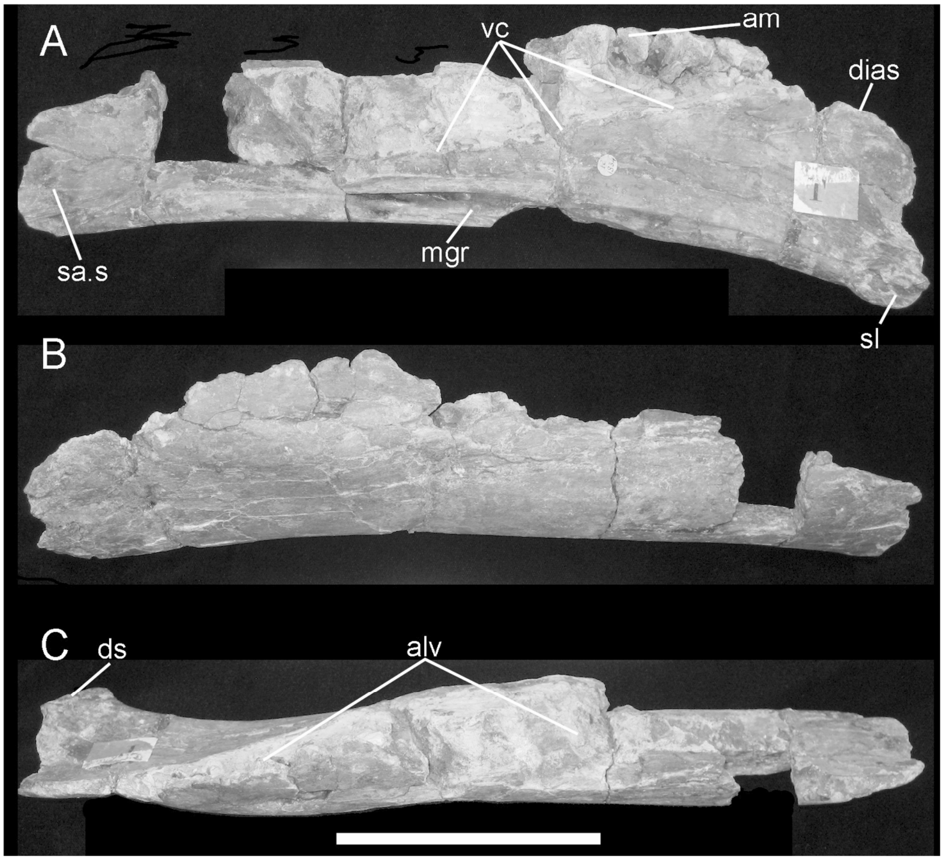
149x107mm (300 x 300 DPI)

Fig. 43



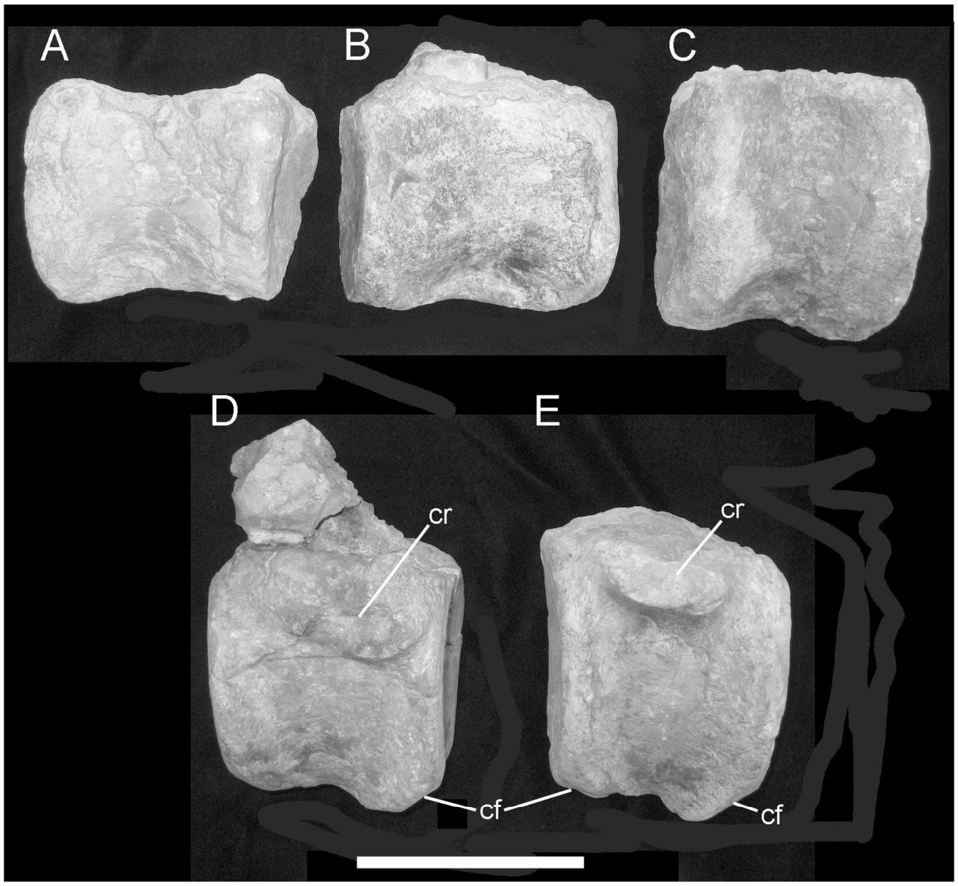
173x98mm (300 x 300 DPI)

Fig. 44



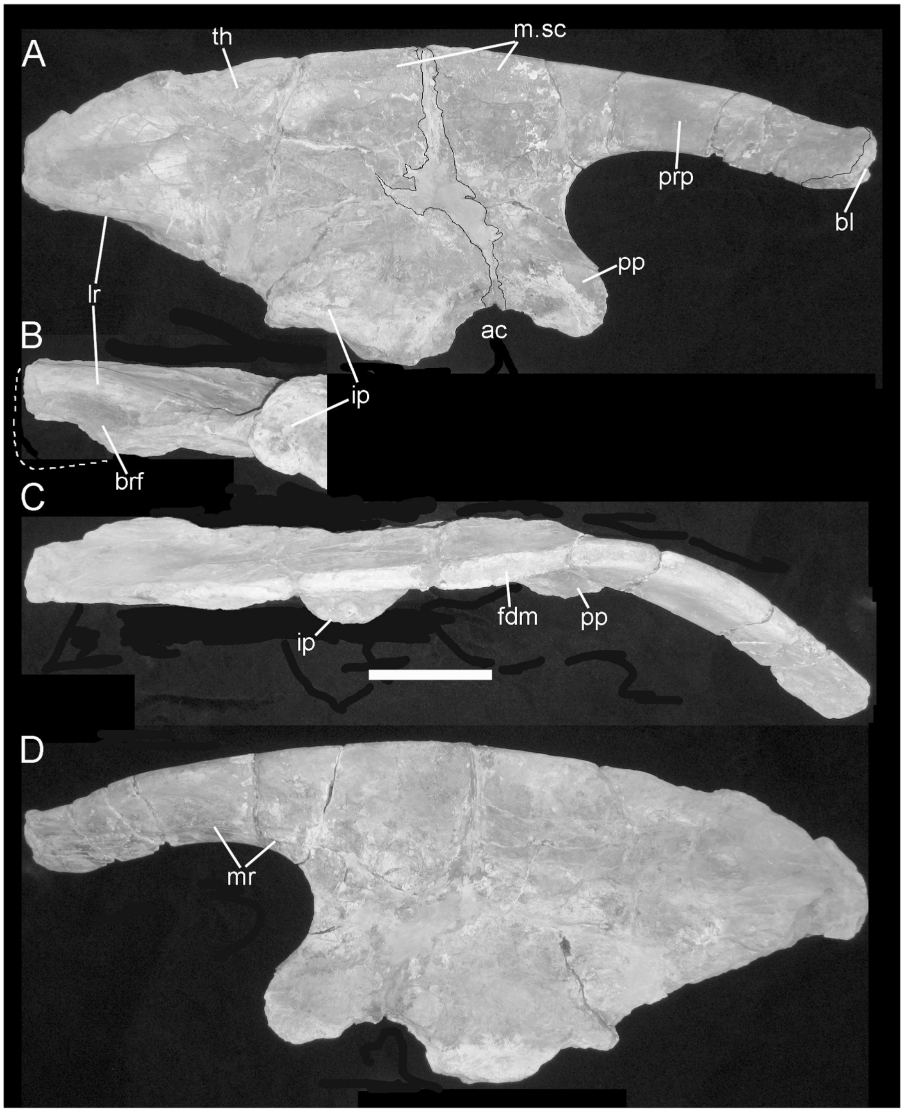
150x145mm (300 x 300 DPI)

Fig. 45

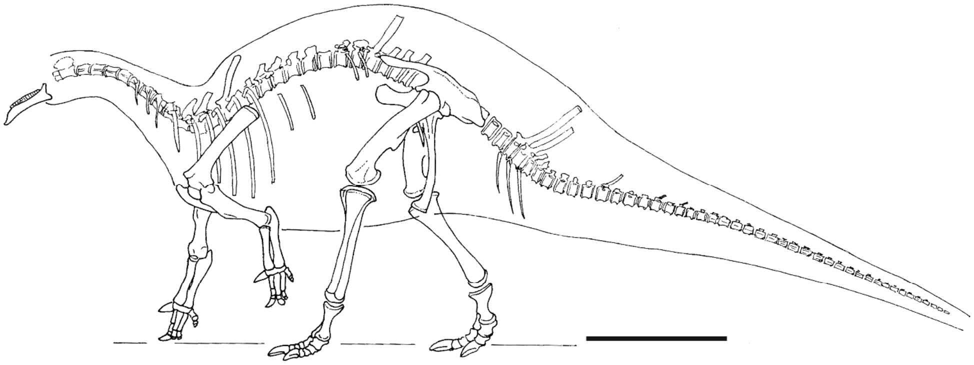


147x147mm (300 x 300 DPI)

Fig. 46

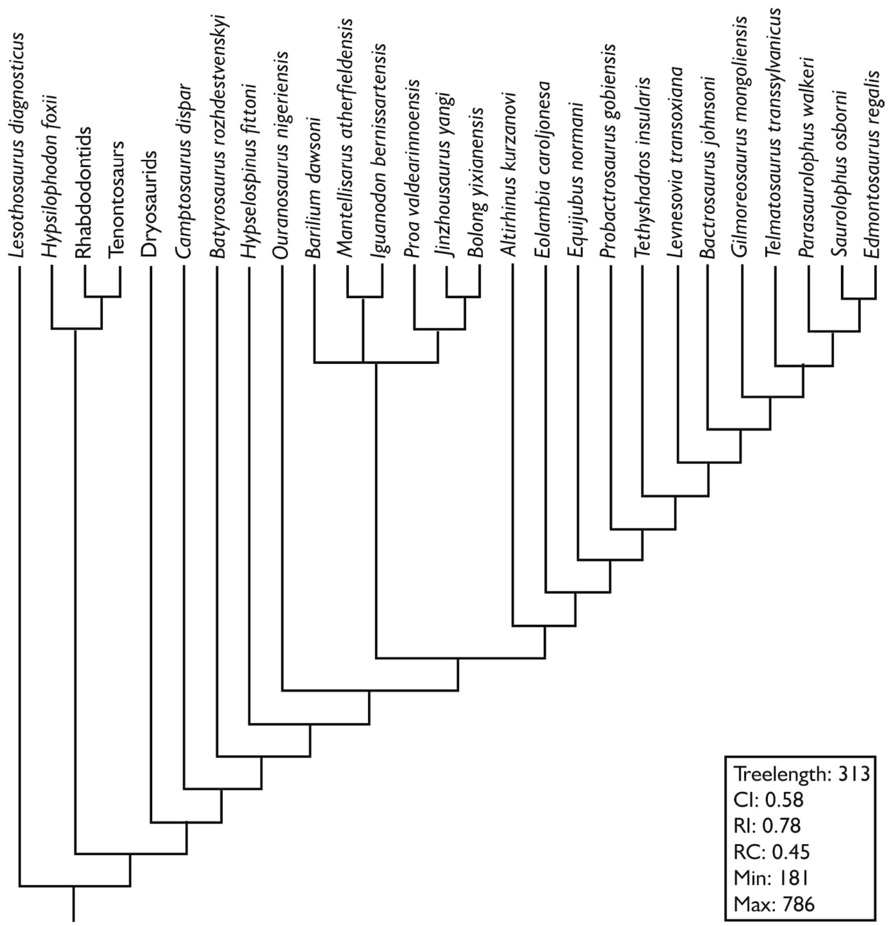


162x204mm (300 x 300 DPI)



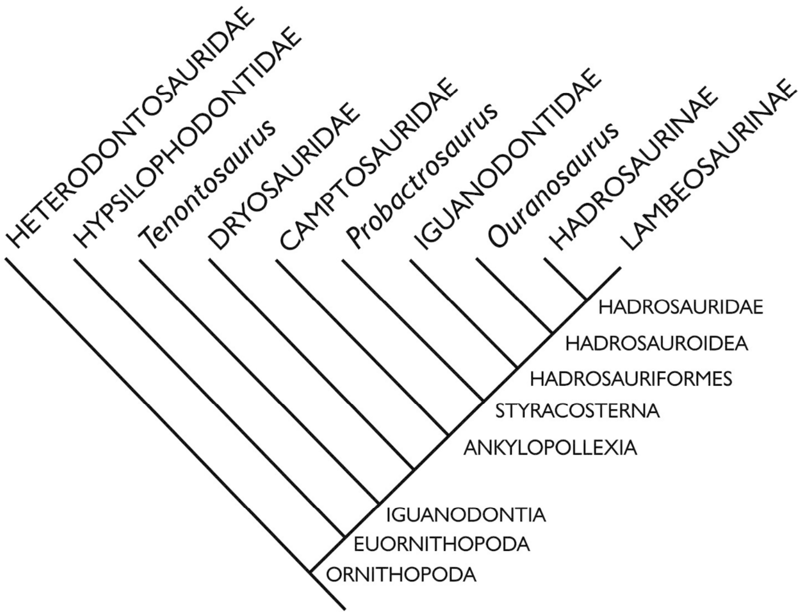
281x110mm (300 x 300 DPI)

Fig 48



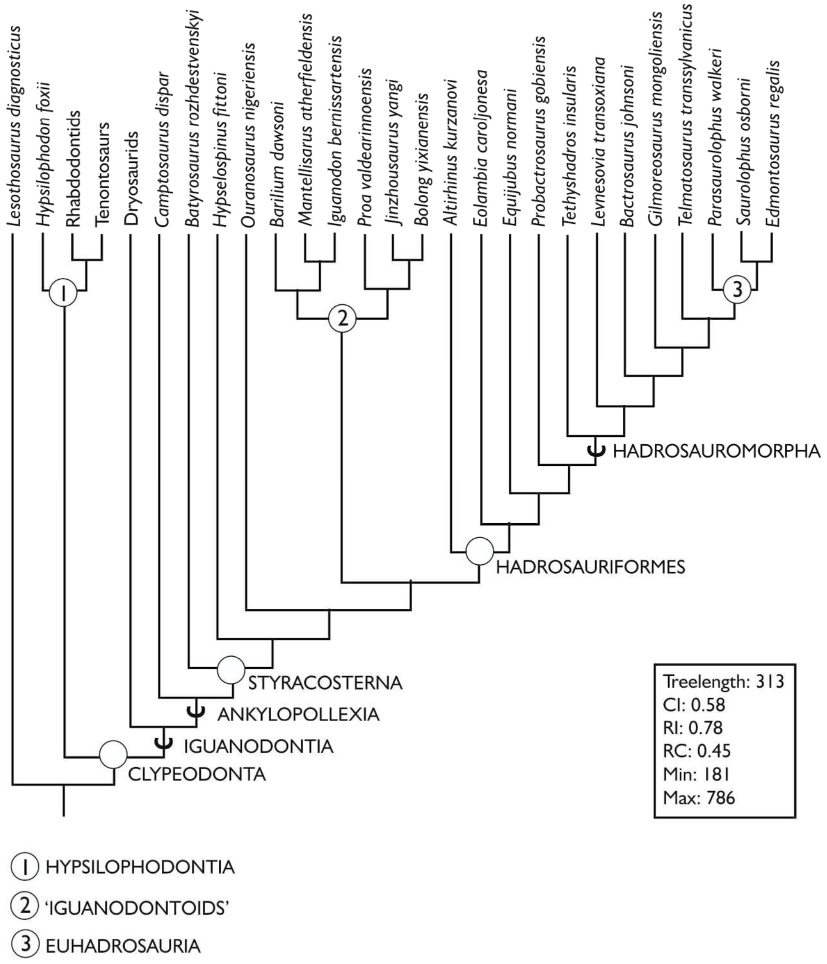
180x231mm (300 x 300 DPI)

Fig 49



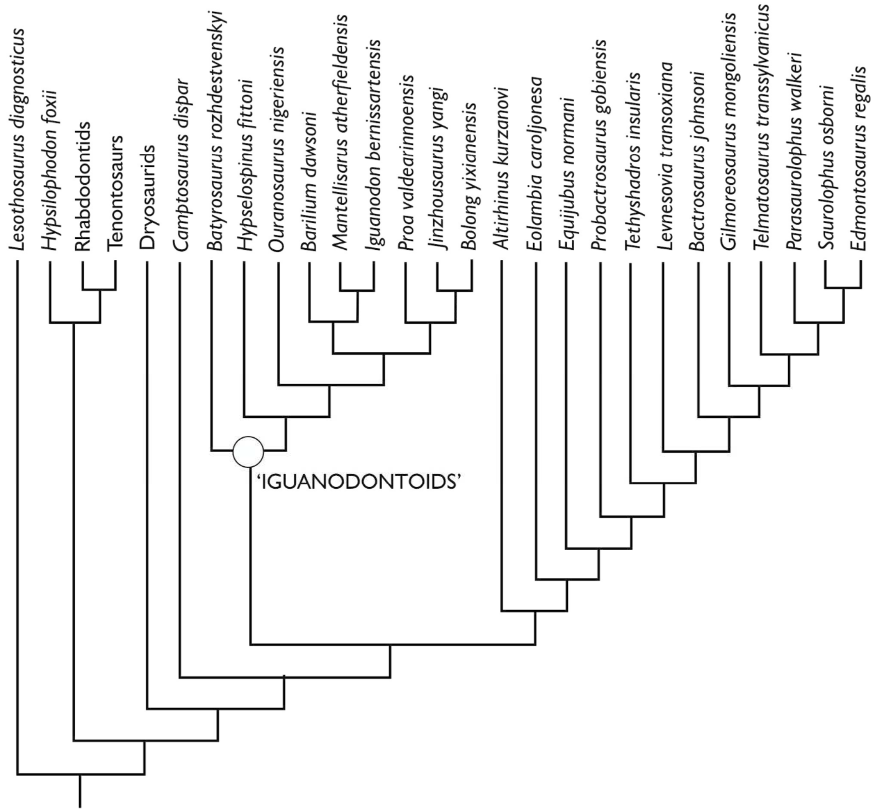
153x174mm (300 x 300 DPI)

Fig 50



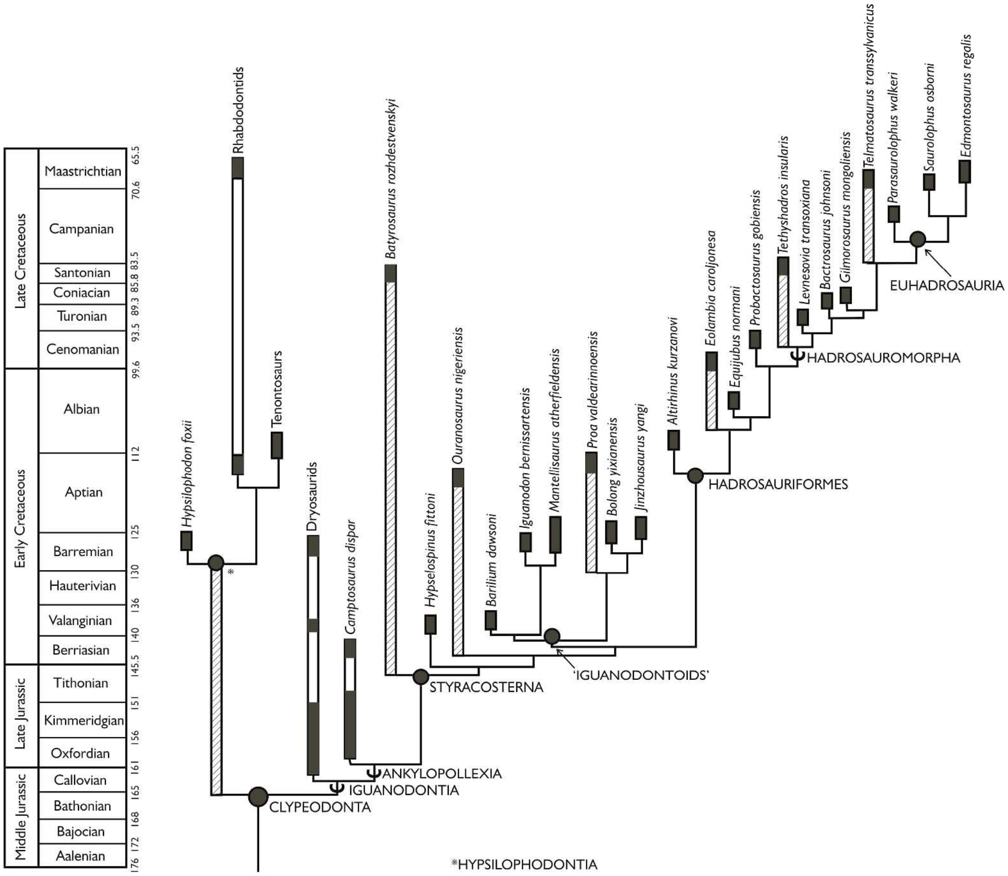
177x261mm (300 x 300 DPI)

Fig 51

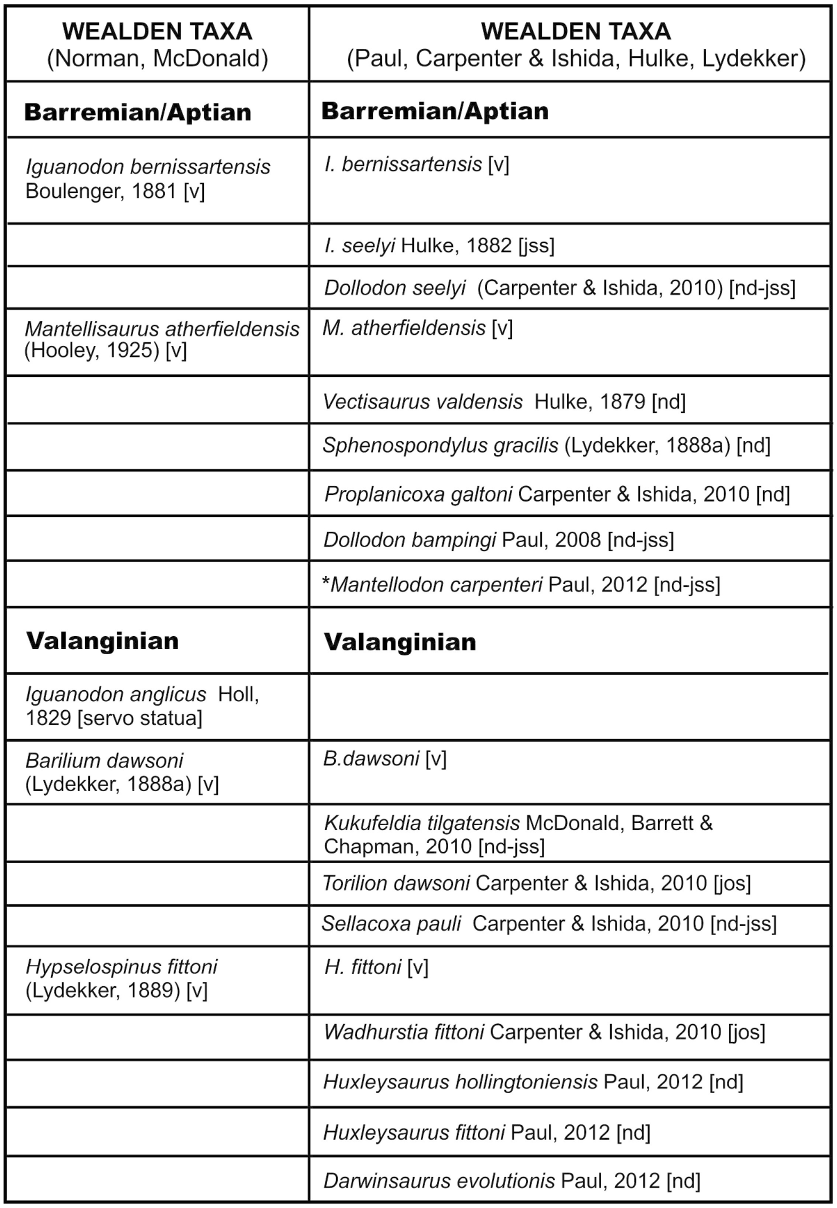


181x235mm (300 x 300 DPI)

Fig 52



271x301mm (300 x 300 DPI)



WEALDEN TAXA (Norman, McDonald)	**WEALDEN TAXA** (Paul, Carpenter & Ishida, Hulke, Lydekker)
Barremian/Aptian	**Barremian/Aptian**
Iguanodon bernissartensis Boulenger, 1881 [v]	*I. bernissartensis* [v]
	I. seelyi Hulke, 1882 [jss]
	Dollodon seelyi (Carpenter & Ishida, 2010) [nd-jss]
Mantellisaurus atherfieldensis (Hooley, 1925) [v]	*M. atherfieldensis* [v]
	Vectisaurus valdensis Hulke, 1879 [nd]
	Sphenospondylus gracilis (Lydekker, 1888a) [nd]
	Proplanicoxa galtoni Carpenter & Ishida, 2010 [nd]
	Dollodon bampingi Paul, 2008 [nd-jss]
	**Mantellodon carpenteri* Paul, 2012 [nd-jss]
Valanginian	**Valanginian**
Iguanodon anglicus Holl, 1829 [servo statua]	
Barilium dawsoni (Lydekker, 1888a) [v]	*B.dawsoni* [v]
	Kukufeldia tilgatensis McDonald, Barrett & Chapman, 2010 [nd-jss]
	Torilion dawsoni Carpenter & Ishida, 2010 [jos]
	Sellacoxa pauli Carpenter & Ishida, 2010 [nd-jss]
Hypselospinus fittoni (Lydekker, 1889) [v]	*H. fittoni* [v]
	Wadhurstia fittoni Carpenter & Ishida, 2010 [jos]
	Huxleysaurus hollingtoniensis Paul, 2012 [nd]
	Huxleysaurus fittoni Paul, 2012 [nd]
	Darwinsaurus evolutionis Paul, 2012 [nd]

190x275mm (300 x 300 DPI)