A revised taxonomy of the iguanodont dinosaur genera and species

Gregory S. Paul

3109 North Calvert Station, Side Apartment, Baltimore, MD 21218-3807, USA

Abstract

Criteria for designating dinosaur genera are inconsistent; some very similar species are highly split at the generic level, other anatomically disparate species are united at the same rank. Since the mid-1800s the classic genus *Iguanodon* has become a taxonomic grab-bag containing species spanning most of the Early Cretaceous of the northern hemisphere. Recently the genus was radically redesignated when the type was shifted from nondiagnostic English Valanginian teeth to a complete skull and skeleton of the heavily built, semi-quadrupedal *I. bernissartensis* from much younger Belgian sediments, even though the latter is very different in form from the gracile skeletal remains described by Mantell. Currently, iguanodont remains from Europe are usually assigned to either robust *I. bernissartensis* or gracile *I. atherfieldensis*, regardless of location or stage. A stratigraphic analysis is combined with a character census that shows the European iguanodonts are markedly more morphologically divergent than other dinosaur genera, and some appear phylogenetically more derived than others. Two new genera and a new species have been or are named for the gracile iguanodonts of the Wealden Supergroup; strongly bipedal *Mantellisaurus atherfieldensis* Paul (2006. Turning the old into the new: a separate genus for the gracile iguanodont from the Wealden of England. In: Carpenter, K. (Ed.), Horns and Beaks: Ceratopsian and Ornithopod Dinosaurs. Indiana University Press, Bloomington, pp. 69–77) (holotype BMNH R5764) which possesses a camptosaur-like ilial shape, and the long snouted, long bodied, small hipped, semi-bipedal *Dollodon bampingi* gen. nov. sp. nov. (holotype IRSNB 1551) which has a shallow ilium. Insufficiently diagnostic *I. hoggii* is removed from the earlier *Camptosaurus*. Poorly described *I. dawsoni*, *I. fittoni* and *I. hollingtoniensis* are removed from the much later and more derived *Iguanodon* and considered Ornithopoda *incertae sedis* pending redescription. The synonymy of *I. fittoni* and *I. hollingtoniensis* has not been confirmed. A set of remains 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. There has recently been a tendency to consider iguanodonts spatially remote from *I. bernissartensis* to be members of or very similar to the type species, but reanalysis finds that *I. orientalis* is not a junior synonym of *I. bernissartensis* and is a *nomen dubium*, and that basal *I. lakotaensis* is not a member of *Iguanodon* and accordingly is assigned the new genus *Dakotadon* gen. nov. (holotype SDSM 8656). *Dakotadon* is probably basal to *Iguanodon* and not an iguanodontoid. The higher taxonomy of iguanodontoids is confused due to phylogenetic problems, and inconsistent definitions of the Iguanodontidae (which as currently defined appears to be limited to *Iguanodon*) and Hadrosauroidea. *Mantellisaurus* and especially *Dollodon*, for instance, are probably more derived than *Iguanodon*: they may be hadrosauroids depending on which phylogenetic definition of the term is preferred.
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1. Introduction

The classic ornithischian ornithopod dinosaur genus *Iguanodon* (Mantell, 1825) was established on the basis of a few teeth from the early Early Cretaceous, and no species was originally designated. The later named type species *I. anglicus* (= *anglicum*, Holl, 1829) was based on these teeth, as was *I. mantelli* (Meyer, 1832) in part, so the latter is a junior synonym of the former (Norman, 1993; Charig and Chapman, 1998). The only significant bones described by Mantell (1834) were part of an incomplete, gracile skeleton lacking the skull from the late Early Cretaceous. This specimen (BMNH 3741) was examined by Norman (1993) who corrected the common assumption that this specimen is the holotype of *I. mantelli*. To date, BMNH 3741 has yet to be fully described.

E-mail address: gsp1954@aol.com

Having been founded on insufficiently diagnostic teeth, and following inadequate taxonomic methodologies, the 1800s concept of *Iguanodon* became an exemplar of the taxonomic grab-bag, in which the inclusion of an increasing number of species from a wide variety of ages and places expanded the anatomical and temporal parameters that were accommodated within the genus. The result was a feed back system which encouraged the reference in the 1900s of yet more fossils to *Iguanodon* that were either not sufficiently diagnostic, or exhibited major morphological variation, and covered a span of time from the Berriasian to the Albian or later, and ranged over the northern hemisphere.

A large number of English iguanodont taxa based on various skeletal parts are non-diagnostic *nomina dubia* or of questionable identification according to Norman and Weishampel (1990); Glut (1997) and Norman (2004). Among the more important is the holotype mandible of *I. hoggii* (Owen, 1874; often misspelled *I. hoggi* as per Norman and Weishampel, 1990; Norman, 1990, 2004; Glut, 1997; Blows, 1998; Naish and Martill, 2001; Weishampel et al., 2004). Dating from nearly the beginning of the Cretaceous, it has been referred to *Camptosaurus* by Norman and Barrett (2002). From slightly younger sediments came the very incomplete but distinctive postcranial remains of *I. dawsoni* (Lydekker, 1888) and *I. fittoni* (Lydekker, 1889), whose sacra and pelves (Fig. 3Ba, b) were reconstructed by Blows (1998). Similar in age is *I. hollingtoniensis* (Lydekker, 1889). The latter was considered a junior synonym of *I. fittoni* by Norman and Weishampel (1990); Blows (1998) and Norman (2004). A set of remains assigned to much later *I. mantelli* by Owen (1842, 1872, 1874), removed from that taxon by Lydekker (1889), and currently catalogued as similar aged *I. hollingtoniensis*, has received little attention despite its apparent combination of a highly specialized mandible and exceptionally massive arm and spike. Neither the synonymization of *I. fittoni* and *I. hollingtoniensis* nor the assignment of the Owen specimen to the second species have been verified or refuted in detail. The inclusion of these species in *Iguanodon* (as per Norman, 1987a, 2004; Norman and Weishampel, 1990) has been questioned by Norman and Barrett (2002). Glut (1997) considered *I. hoggii, I. dawsoni* and *I. fittoni* *nomina dubia*.

By far the best-described iguanodont specimen from England, the holotype BMNH R5764 of the gracile *I. atherfieldensis* Hooley, 1925, consists of a fine, largely complete skull and much of the skeleton from middle Early Cretaceous beds (Figs. 1C, 2G, 3Ac, Bf, Ce). Based on a fragmentary but distinctive holotype and incomplete referred material, Galton (1976) considered *Vectisaurus valdensis* (Hulke, 1879) to be valid, but in a detailed reanalysis Norman (1990) referred the same fossils (Fig. 3Bj) to the somewhat younger *I. atherfieldensis*. A large number of other fragmentary skeletal remains are known from the middle Early Cretaceous, and some have been published; the great majority represent gracile iguanodonts with a few examples of robust forms also present (Fig. 3Bg, h, i, Cd) (Benton and Spencer, 1995; Naish and Martill, 2001). Based on a fairly good specimen (Fig. 3Be), *I. seelyi* (Hulke, 1882) from the middle Early Cretaceous is

therefore notable. Because it is robust, it has been referred to *I. bernissartensis* Boulenger in Beneden, 1881 by Norman and Weishampel (1990) and Norman (2004).

The Bernissart quarry of the middle Early Cretaceous produced a large number of complete articulated skulls and skeletons of robust *I. bernissartensis* (Beneden, 1881; Dollo, 1882, 1883), the lectotype of which is IRSNB 1534 (Figs. 1B, 2F, 3Aa, Bc, Cb) as ruled by the ICZN (2000). In recognition of the grossly inadequate nature of the holotype for the second named dinosaur genus, as well as one of the most famous, the ICZN (2000) designated *I. bernissartensis* the neotype species. Also found at Bernissart was the similarly complete gracile IRSNB 1551 (Figs. 1D, 2H, 3Ad, Bk, Cf; Dollo, 1882, 1884), which was originally assigned to *I. mantelli* (as per Norman, 1980) before the correct holotype of the species was understood (Norman, 1993), and then to *I. atherfieldensis* by Norman (1986) who considered *I. mantelli* a junior synonym of the latter (also Norman and Weishampel, 1990; Norman, 1993, 2004); the reason for this specific synonymy was not detailed. Norman (1987b) and Norman et al. (1987) described abundant gracile and robust iguanodont material from the German Nehden quarry, which is middle Early Cretaceous in age, and referred the elements to either *I. atherfieldensis* or *I. bernissartensis* (Fig. 3Ab, Bd, Cc, g).

Early Cretaceous fossils from France and Spain have been assigned to *Iguandon*, sometimes to *I. bernissartensis* or *I. atherfieldensis* (Weishampel et al., 2004). Maisch (1997) tentatively referred fragmentary remains from the early Early Cretaceous of Spain to *I. fittoni* and Ruiz-Omeñaca et al. (1997) reported the discovery of *I.* sp. teeth from the middle Early Cretaceous of Spain. The holotype of North American *I. ottingeri* (Galton and Jensen, 1975), from the early Early Cretaceous, is so fragmentary that it is a *nomen dubium* (Norman and Weishampel, 1990; Glut, 1997; Norman and Barrett, 2002; Norman, 2004). Weishampel and Bjork (1989) made SDSM 8656 (Fig. 2D), an incomplete, distinctive skull associated with a couple of vertebrae, the holotype of *I. lakotaensis*; it is from North American sediments that are probably from the middle Early Cretaceous. Norman (1998) considered the skull indistinguishable from *I. bernissartensis*, but it is a distinct species in Norman (2004). Bakker (1998) and Brill and Carpenter (2006) concluded that *I. lakotaensis* is significantly more basal than the latter taxon, and more similar to *Theiophytalia* Brill and Carpenter, 2006, which is probably from the late Early Cretaceous. The holotype of Mongolian *I. orientalis* (Rhozhdestvenskii, 1952), PIN 559-1/1 (Fig. 3Ae), exact age uncertain, is a very fragmentary specimen with some distinctive elements. Norman (1996, 2004) considered the species a junior synonym of *I. bernissartensis*. He also removed a complete, Roman-nosed, late Early Cretaceous iguanodont skull from *I. bernissartensis* (=*orientalis*) and made it the holotype of *Altirhinus kurzanovi* Norman, 1998 (Fig. 2I). A number of Early Cretaceous footprints have been assigned to *Iguanodon* (Norman, 1980; Benton and Spencer, 1995; Glut, 1997), but such trace fossils are only assignable to family level taxa at best and can never be used to assess the presence of a skeletal genus, so they do not receive further attention in this study.
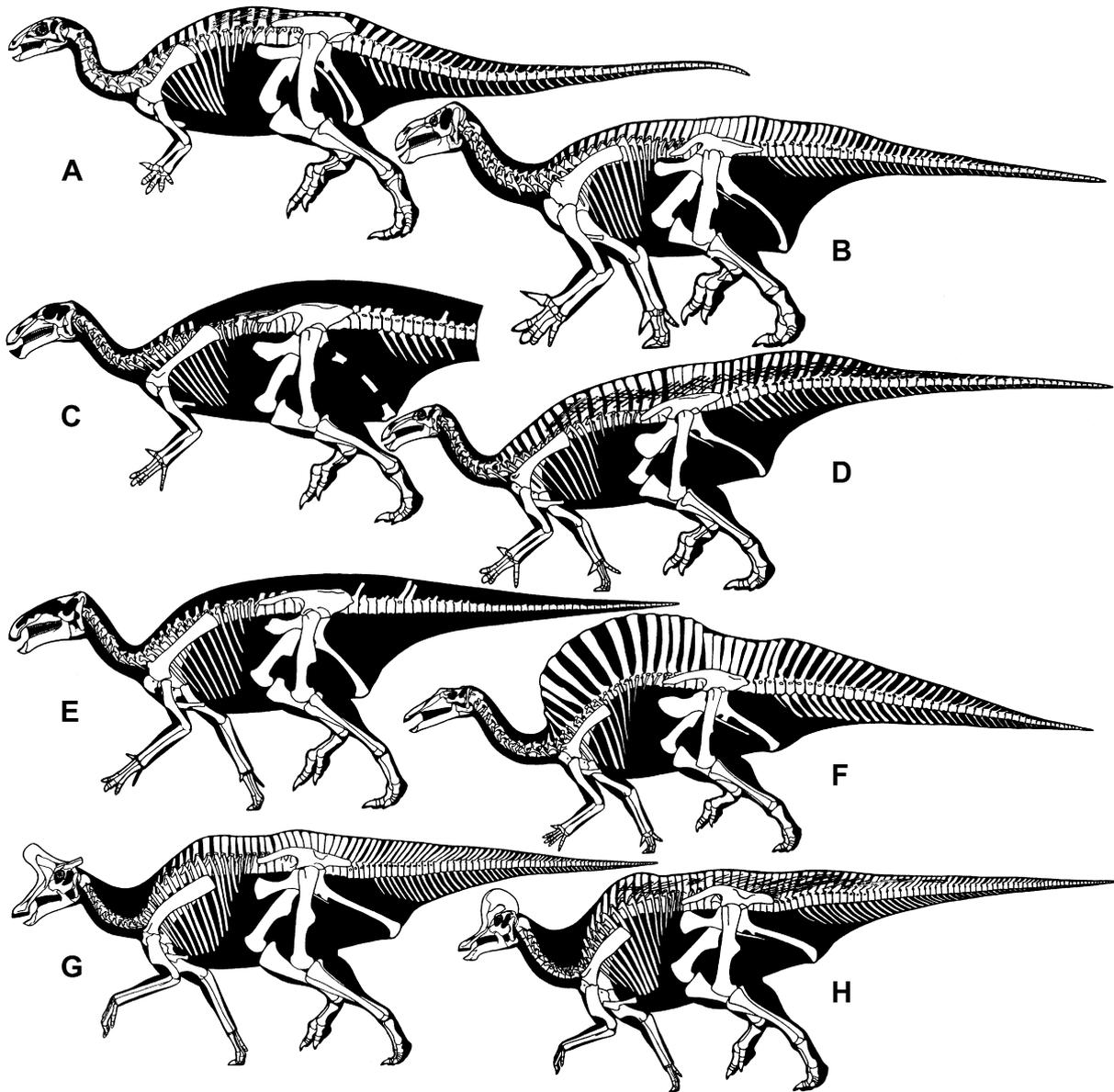
Fig. 1. Ankylopollexian skeletons reproduced to same approximate dorso-sacral column length. A, *Camptosaurus dispar* USNM 5818 etc. (femur length 580 mm, 0.5 t). B—E, iguanodonts. B, *Iguanodon bernissartensis* lectotype (femur length 1025 mm, 3.2 t). C, *Mantellisaurus atherfieldensis* holotype (femur length 678 mm, 0.75 t) largely preserved elements. D, *Dollodon bampingi* gen. nov. sp. nov. holotype (femur length 760 mm, 1.1 t). E, *Probactrosaurus gobiensis* composite (femur length up to 750 mm, 1 t) largely preserved elements. F, *Ouranosaurus nigeriensis* holotype (femur length 945 mm, 2.2 t), proportions approximate. G, H, hadrosaurids showing strong skeletal similarity despite current generic separation. G, *Lambeosaurus* ROM 1218 (femur length 1067 mm, 2.4 t). H, *Corythosaurus* AMNH 5240 (femur length 1080 mm, 2.8 t). Total body masses based on volumetric models.

Following the evolving analysis of Norman and Weishampel (1990), Norman (1987a, 1990, 1996, 1998, 2004), Glut (1997), Norman and Barrett (2002) and ICZN (2000), the species of *Iguanodon* currently considered valid are *I. bernissartensis, I. atherfieldensis,* and *I. lakotaensis,* all based on adequate material, and fragmentary *I. dawsoni* and *I. fittoni*. The latter two species are both considered dubious members of *Iguanodon* but have not been formerly removed. To date a detailed case for retaining the first three species in the one genus *Iguanodon*, including robust *I. bernissartensis* and the much more gracile *I. atherfieldensis*, has not been offered. As a result of this taxonomic imprecision most cladistic analyses that include iguanodonts have assumed that *Iguanodon* is an anatomically consistent genus and have scored it as one taxon (Norman, 1990, 1998; Norman and Weishampel, 1990; Head, 1998, 2001; Sereno, 1999; Kobayashi and Azuma, 2003). Such scoring of different specimens as one genus in a manner that appears to affirm their generic synonymy constitutes circular reasoning, leaving the issue without proper examination. Suzuki et al. (2004) examined *I. bernissartensis* and *I. atherfieldensis* separately, placing them in their own clade. Interestingly, in Norman's (2002) phylogenetic analysis the two species did not group together, while in Norman (2004) they grouped apart in a strict consensus tree, but
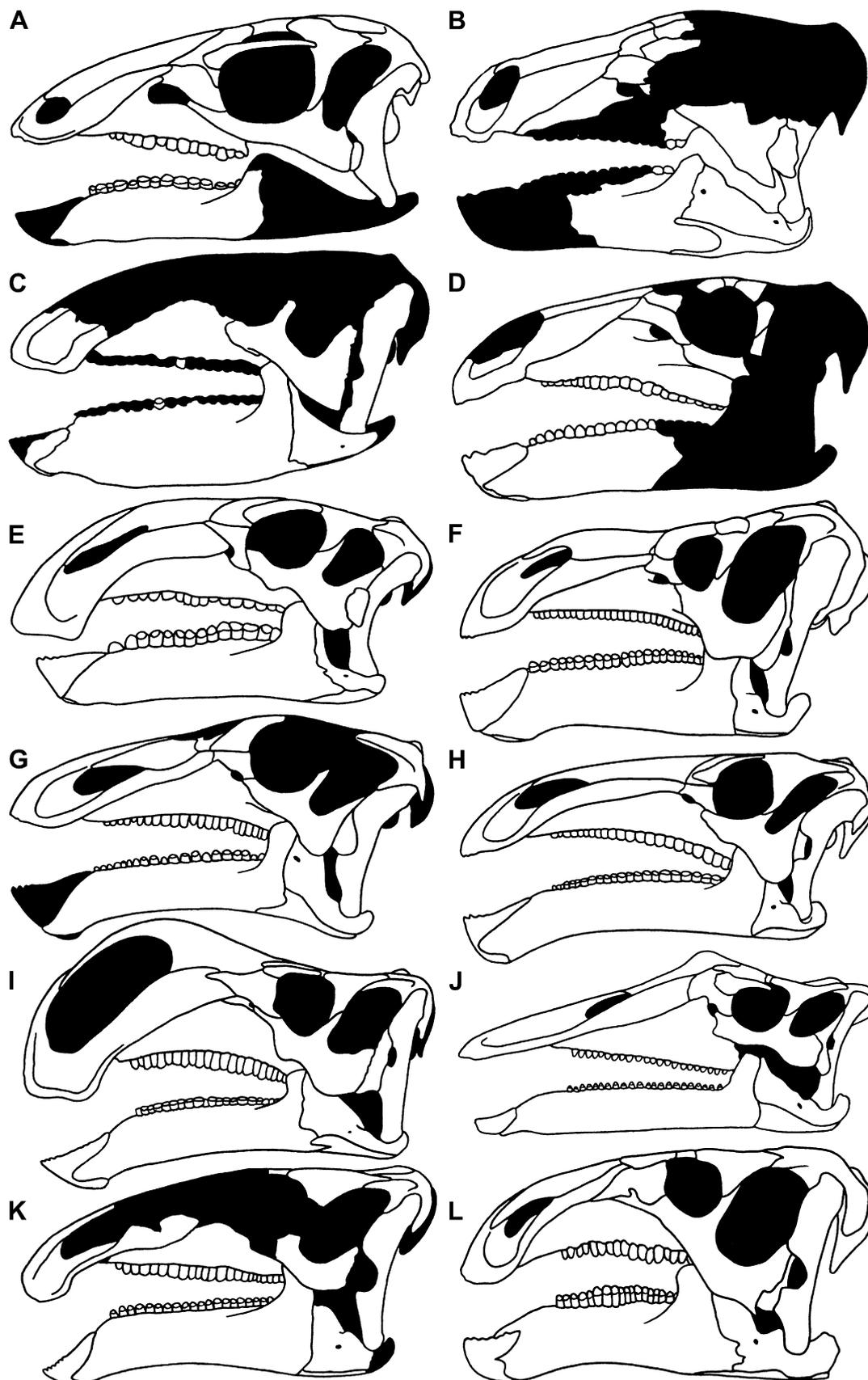
Fig. 2. Non-hadrosaurid ankylopollexian skulls in left (some reversed) lateral views, bones as preserved, each drawn to same total length. A, *Camptosaurus dispar* composite. B, *Theiophytalia kerri* holotype. C, *Fukuisaurus tetoriensis* composite. D–L, iguanodonts. D, *Dakotadon lakotaensis* gen. nov. holotype. E–L, iguanodontoids. E, *Jinzhousaurus yangi* holotype. F, *Iguanodon bernissartensis* lectotype. G, *Mantellisaurus atherfieldensis* holotype. H, *Dollodon bampingi* gen. nov. sp. nov. holotype. I, *Altirhinus kurzanovi* holotype. J, *Ouranosaurus nigeriensis* holotype. K, *Probactrosaurus gobiensis* holotype etc. L, *Equijubus normani* holotype.
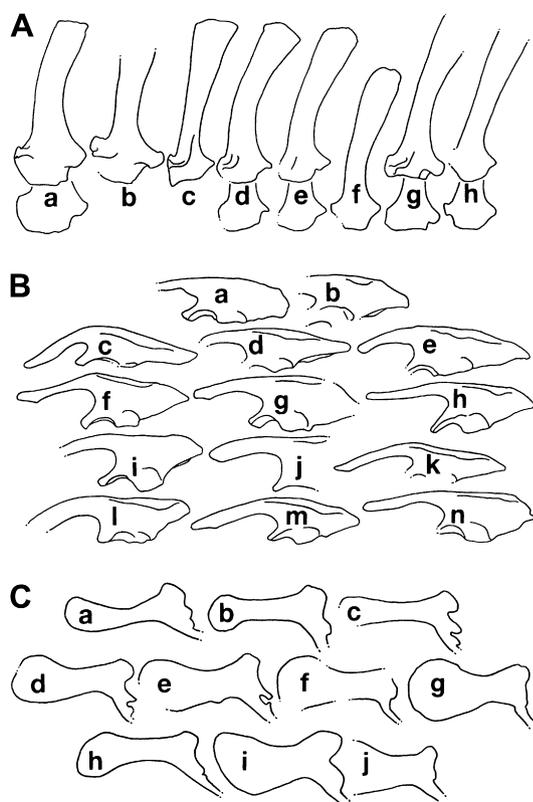
Fig. 3. Non-hadrosaurid styracosternan elements (some reversed) as preserved, each drawn to same total length. A, left scapulae in top row and/or right scapulae in medial view in bottom row; a, *Iguanodon bernissartensis* lectotype; b, *Iguanodon* sp. GPI-D.559 (Nehden quarry); c, *Mantellisaurus atherfieldensis* holotype; d, *Dollodon bampingi* gen. nov. sp. nov. holotype; e, *''I.'' orientalis* holotype; f, *Altirhinus kurzanovi* PIN 3388; g, *Ouranosaurus nigeriensis* holotype; h, *Probactrosaurus gobiensis* holotype and PIN 2232/41-3. B, left ilia in lateral view; a, *''I.'' dawsoni* holotype; b, *''I.'' fittoni* holotype; c, *Iguanodon bernissartensis* lectotype; d, *I.* sp. GPI-E.191; e, *I.* sp. (= *seelyi*) holotype; f, *Mantellisaurus atherfieldensis* holotype; g, *M.* sp. BMNH R9290; h, *M.* sp. BMNH R11521; i, *M.* sp. BMNH R6462; j, *M.* (= *Vectisaurus*) sp. (= *valdensis*) holotype juvenile; k, *Dollodon bampingi* gen. nov. sp. nov. holotype; l, *Altirhinus kurzanovi* PIN juvenile; m, *Ouranosaurus nigeriensis* holotype; n, *Probactrosaurus gobiensis* PIN 2232/19-1. C, left prepubic processes of the pubis in lateral view; a, *Lurdusaurus arenatus* holotype; b, *Iguanodon bernissartensis* lectotype; c, *Iguanodon* sp. GPI-D.203; d, *Mantellisaurus* sp. BMNH R2194; e, *M. atherfieldensis* holotype; f, *Dollodon bampingi* gen. nov. sp. nov. holotype; g, *D.* sp. GPI-D.411; h, *Altirhinus kurzanovi* PIN 3386/8; i, *Ouranosaurus nigeriensis* holotype; j, *Probactrosaurus gobiensis* PIN 2232/23-56.

formed a clade in a most parsimonious tree where some characters were weighted. Because specimens from widely disparate locations are placed within *Iguanodon*, its presence has been taken as evidence for major intercontinental interchanges in the Early Cretaceous (Galton and Jensen, 1975; Weishampel and Bjork, 1989). Sanz (2005) noted that *Iguanodon* is probably paraphyletic, and that its presence outside Europe is consequently questionable.

Paul (2006) agreed that *Iguanodon* is probably paraphyletic, and also observed that its members are in any case too anatomically divergent to be classified within one genus. The holotype of *I. atherfieldensis* was assigned the new genus *Mantellisaurus* Paul, 2006. It was implied that IRSNB 1551

can be referred to *M. atherfieldensis*. Due to confusion in handling the manuscript it dates from 2004 and is out of date in some regards: the present study takes precedence over Paul (2006) whenever differences are present.

Outside of *Iguanodon*, a number of Early Cretaceous potential iguanodonts have been named in the last half-century based on material ranging from excellent to inadequate. They include *Probactrosaurus mazongshanensis* Lu, 1997, little *Nanyangosaurus zhugeii* Xu et al., 2000, *Jinzhousaurus yangi* Wang and Xu, 2001 and colossal bodied and big toothed *Lanzhousaurus magnidens* You et al., 2005 from China (Fig. 2E), Japanese *Fukuisaurus tetoriensis* Kobayashi and Azuma, 2003 (Fig. 2C), and the Nigerian duckbilled *Ouranosaurus nigeriensis* Taquet, 1976 (Figs. 1F, 2J, 3Ag, Bm, Ci), and extraordinarily massive *Lurdusaurus arenatus* Taquet and Russell, 1999 (Fig. 3Ca). The Mongolian, hadrosaur-toothed *Probactrosaurus gobiensis* Rhozhdestvenskii, 1966 (Figs. 1E, 2K, 3Ah, Bn, Cj) and *P. alashanicus* Rhozhdestvenskii, 1966, redescribed by Norman (2002), have usually been considered iguanodontids, but are placed among hadrosauroids by the latter researcher, and by You et al. (2003) who do the same with *Equijubus normani* You et al., 2003 (Fig. 2L) from the Chinese portion of the Gobi desert.

As noted by Sanz (2005), the possibility that Iguanodontidae is paraphyletic and includes basal hadrosauroids is indicated by numerous phylogenetic analyses. For this reason, these large ornithopods are generally and informally referred to as iguanodonts here, rather than as iguanodontids. Although higher-level taxonomic issues are discussed, this study focuses on genera and species, and formally rediagnoses only those taxa that are adequately preserved and described. Basal iguanodontian taxa that lie outside the iguanodonts are examined only if they have long been considered iguanodonts, or have recently been assigned to the assemblage. Therefore *Muttaburrasaurus* and rhabdodonts are not considered herein because they have been correctly placed outside the iguanodonts (Norman and Weishampel, 1990; Norman, 2004. Note that, in the latter, *Muttaburrasaurus* is listed under Iguanodontoidea contrary to both the analysis in the text and the cladogram). Nor are such near-hadrosaurid hadrosauroids as *Eolambia* and *Protohadros* examined. This paper and Paul (2006) only formally name Barremian and later taxa because they are based on reasonably complete and well described specimens. Valanginian taxa are not formally addressed because the specimens are inadequately described, less complete, and because overlapping elements are scarce. These specimens are currently under investigation and will be dealt with in future work.

2. Determining genera and species in ornithischians and other vertebrates: the Goldilocks Principle, and problems with autapomorphy-only diagnoses

The taxonomic status of a given genus is open to challenge because designation of a taxon at that level is arbitrary and methods for doing so are poorly defined (Wood and Collard, 1999; Mayr and Bock, 2002; Paul, 2006). There are, however, some basic requirements. One is that each genus must be

monophyletic. However, just because a group of species is monophyletic does not automatically mean they all form one genus: for example, bovids form a monophyletic group of ungulates, but the anatomical variation within the group is so extensive that the group contains many genera. Similarly, *Triceratops* and *Torosaurus* are in a monophyletic clade at the terminus of the Ceratopsidae, yet are too morphologically divergent to be in the same genus. Therefore, another fundamental requirement for including more than one species within a genus is a reasonably consistent standard of skeletal variation allowed within a given genus. Each vertebrate genus should encompass about the same degree of variation in terms of morphology, function, habits, habitats and so forth. Even if two species are firmly placed together within a distinct clade separate from other relatives, they can be placed in the same genus only if the gradistic difference is within the maximum present in accepted genera. Otherwise the genus has little practical biological meaning or utility, and consists merely of inconsistently delineated accumulations of monophyletic species: in that case the practice of using genera to compare biological diversity over time and place (as per Carroll, 1988; Dingus and Rowe, 1998; Jablonski, 2005) can be more misinformative than informative. So, if the degree of morphological variation between species is beyond that normally included in other tetrapod genera, and/or if the species possess numerous characters that indicate that one or more is markedly closer to another major clade than are others, then the species need to be placed in separate genera.

There is, however, a danger of over splitting at the genus level, as evidenced by some small, monophyletic, multi-genera ornithopod and other ornithischian clades in which anatomical diversity is limited. For example *Hypacrosaurus, Corythosaurus* and *Lambeosaurus* (Fig. 1G, H) are very similar in cranial and postcranial morphology, and are distinct from other hadrosaurid genera. Significant variation is concentrated in the cranial crest and the height of the vertebral neural spines. Such differences are of the type and extent expected among closely related species that use visual cues to distinguish one another: they do not reflect major functional or phylogenetic separators. The same situation is present in *Prosaurolophus* and *Saurolophus*, which are very alike cranially and postcranially except for the form of the crest. A similar situation is also observed in *Centrosaurus, Styracosaurus, Einiosaurus* and *Pachyrhinosaurus*, where the skulls and skeletons show little variation, the differences being concentrated in the horns and cranial crests. The equivalent degree of cranial and postcranial consistency, except for cranial adornments, mark *Chasmosaurus* and *Pentaceratops*. Again, the differences present within these two ceratopsian groups appear to have evolved for purposes of species identification between otherwise similar forms. Whether these ornithischian genera are taxonomically over split or not, they show that the degree of morphological variation that can be accommodated within a dinosaur genus has limits.

The giant herbivore *Deinotherium* is credited as lasting about 20 million years from the Miocene to the Pleistocene (Carroll, 1988). But such longevity is exceptional. Large

herbivores tend to evolve rapidly with genera typically lasting less than ten million years (Carroll, 1988). Synonymizing incomplete material widely separated in time risks artificially increasing the time span a genus existed for. Therefore, generically diagnostic material separated by two or more stages should not be referred to the same genus unless sufficiently complete remains clearly show that their anatomical diversity does not exceed the maximum allowed at that systematic level. But if morphological diversity is so low, then generic synonymy is required regardless of the time separation in order to avoid the circular reasoning that genera do not last for very long time, and to properly recognize that a major taxon is not exhibiting marked morphological change over a long period of time.

Over-lumping at the level of the genus can lead to inappropriate use of species as de-facto genera equivalents that are then used to accommodate large sets of remains from widely separated places and times. Tetrapod species are typically short lived, usually lasting 1—3 million years (Carroll, 1988; Kutschera and Niklas, 2004; *Panthera leo* appeared 3.5 million years ago, Turner and Anton, 1997). Specimens should, therefore, be assigned to the same species only if they are very similar morphologically (including variation that may be due to sexual dimorphism) in all aspects based on examination of a sufficient sample of fairly complete skeletons, or if they are from the same horizon and cannot be adequately distinguished morphologically. It is therefore, at best, rare for dinosaurs from different stages based on high quality material to be assigned to the same species, exceptions being when the sets of remains are from near the boundary common to two stages. When the specimens from a given horizon lack the combination of cranial and postcranial material needed to be certain that they are the same species as are remains (including the type) from another stage, it is preferable to label them 'genus sp.' rather than refer them to the species from the other stage. In accord with these principles it is not automatically assumed in this study that the poorly dated Bernissart quarry specimens are the same species or genera as the better dated English taxa.

The last principle is in accord with the tenet that dinosaur taxa make rather poor stratigraphic age indicators because of the possibility of static evolution, especially in genera and even in species, and because of the difficulty of reliably assessing species via skeletal morphology, especially when incomplete (Itterbeeck et al., 2004).

Currently a number of dinosaur taxa are over-split with multiple genera contained within small monophyletic clades of limited diversity, while a few are over-combined to the point that a single genus contains species that exhibit much greater anatomical variation and may be paraphyletic. This state of inconsistency is not acceptable and hinders scientific assessment of their diversity and evolution, as well as their use in examining palaeogeography. In the tradition of the tale of Goldilocks and her search for porridge of just the right temperature, the taxonomic goal should be to neither over-split, nor over-lump and thereby create grab-bag taxa, but to achieve just the right level of discrimination between differing

genera and species via reasonably consistent application of the degree of anatomical and phylogenetic variation that matches that present in other well established vertebrate taxa. Adoption of the Phylocode system would not necessarily solve this problem. If a binomial system remains in use, decisions will still have to be made as to how much specific diversity and consistency to include in each group of species consolidated within a given first name.

It is currently standard procedure to diagnose genera on the possession of autapomorphies. However, there are problems with this arrangement. In principle it is possible for a family level collection of genera to be so uniform that none of the genera possesses an autapomorphy not found in the other genera. Instead, the unique combination of characters present in each genus defines it as distinct from the others. More realistically, one or a few genera within a family may lack any distinctive autapomorphies, even though their overall configuration is too different to warrant their being synonymized with any other genera. Farke (2007), for example, notes that *Torosaurus* has no unique features relative to other chasmosaurines and can only be diagnosed by its unique combination of characters.

Another problem associated with autapomorphy-only diagnoses occurs when only one autapomorphy is used to define a particular genus. If that character is later found in an otherwise distinct genus in the family then the diagnosis is invalidated. For example Barrett et al. (2005) diagnosed one small ornithopod genus on the basis of a laterally concave postorbital, and another on the basis of a proximally straight humerus. What will happen if another small ornithopod is found with a laterally depressed postorbital, or a proximally straight humerus?

Because autapomorphy-only diagnoses are inherently fragile, and in some cases may not be able to define a genus even when the genus is clearly justified by its unique combination of characters, genera should be defined by a large set of characters that cumulatively establish its exclusive combination of features. The result is a robust diagnosis that cannot be rendered obsolete by the discovery of a few of the characters in other genera. As the knowledge base expands with further discovery and research the diagnosis of a given genus can be emended by adding and subtracting characters as needed.

It will be demonstrated herein that even though iguanodont genus-level taxa are clearly distinct from one another, they are such a uniform group that most share so many features with other family members that autapomorphies are usually scarce. Because all probable valid iguanodont taxa are diagnosed or rediagnosed, the opportunity is taken to compare the extensive character listings, each of which includes only characters not present in all the other taxa. Hence the lack of a diastema, for example, does not distinguish some basal iguanodont genera from one another, but does distinguish them from other genera within the group. Similarly, a deep prepubic process of the pubis helps separate genera once united with *Iguanodon,* even though the same configuration is found in other genera as well. An asterisk precedes unambiguous autapomorphies.

3. Institutional abbreviations

BMNH, The Natural History Museum, London, England; FDPM, Fukui Prefectural Dinosaur Museum, Fukui, Japan; GPI, Geologisch-Palaontologisches Institute, Munster, Germany; GSLTZP Repository Fossil Research and Development Center of the Third Geology and Minerals Resources Exploration Academy of Gansu Province, Lanzhou, China; IRSNB, Institute Royal des Sciences Naturalle de Belgique, Brussells, Belgium; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; MIWG, Museum of Isle of Wight Geology, Sandown, England; MNHN, Museum National d'Histoire Naturelle, Paris, France; SDSM, South Dakota School of Mines and Technology, Rapid City, USA.

4. Systematic palaeontology

Ornithischia Seeley, 1888
Ornithopoda Marsh, 1881
Iguanodontia Dollo, 1888
Ankylopollexia Sereno, 1986
Styracosterna Sereno, 1986

Iguanodonts

Provisional diagnosis. Medium-sized to gigantic ornithopods. Skull narrow, long, low, usually subrectangular in lateral view, rostrum at least somewhat elongated, mandible at least fairly shallow. Beak usually large, usually narrow. External nares further enlarged, posterior margin is posterior to anterior tip of maxilla. Maxilla long and low. Antorbital fossa and fenestra small if present. Peg-in-socket articulation between maxilla and jugal. Most or all of palpebral appressed to orbital rim. Braincase subrectangular in lateral view. Occipital condyle usually directed ventro-posteriorly. Primary palate well developed. Coronoid process tall. Maxillary and dentary teeth form dense continuous battery. Cervicals strongly opithocoelus, 10—14 cervicals, 16—17 dorsals, 6—8 fused sacrals, most of tail deep, transversely flattened. Bipedal to semi-quadrupedal with forelimb markedly more slender than, and 50—70% length of, hindlimb. Scapula blade long, acromion process is a well-developed ridge. Coracoid usually small. Sternals hatchet-shaped. Olecranon process usually moderate in size. Carpals usually ossified into massive blocks, metacarpal I very short and incorporated into wrist, phalanx 1 of digit I very reduced or absent, pollex is a spike. Dorsal margin of ilium has simple dorsally convex curve, suprailiac crest ("antitrochantor") antero-posteriorly elongated, weakly developed, posterior ilium subtriangular. Postpubic process of pubis abbreviated. Femur longer than tibia. Femoral shaft curvature modest to absent, apex of 4th trochantor directed distally, ends in spike in cases. Metatarsals stout, I reduced or absent, digit I absent, other digits usually strongly abbreviated.

Dakotadon gen. nov.

Etymology. For the state of the holotype's origin.
Diagnosis. As for the type and only known species.

Dakotadon lakotaensis (Weishampel and Bjork, 1989)

Holotype. SDSM 8656.

Type horizon, locality, age. Lakota Formation, South Dakota, possibly Barremian.

Emended diagnosis. *Ventral margin of premaxilla not below maxilla, maxillary process of premaxilla deep. *Dorsal midline trough in nasals. *Dorsal apex of maxilla near middle of element. Antorbital fossa and fenestra *large. Lacrimal long, does not contact maxilla posterior to antorbital fossa. Dentary moderately deep, diastema absent. Tooth positions *19 in maxilla.

Lurdusaurus Taquet and Russell, 1999

Diagnosis. As for the type and only known species.

Lurdusaurus arenatus Taquet and Russell, 1999
Holotype. MNHN GDF 1700.

Holotype horizon, locality, age. Upper Elrhaz Formation, Niger, Aptian.

Emended diagnosis. Adults large. Overall *extremely massively constructed. Occipital condyle *directed posteriorly. Quadrate *very short, shaft straight, transversely broad, dorso-posterior buttress large. Cervical series *elongated, *well developed hypapophyses on posterior cervical centra. Dorsal neural spines short, ossified vertebral ligaments *probably absent. Ribcage *rotund. Forelimb ~60% length of hindlimb. Coracoid large. Olecranon process large. Manus short and broad, pollex spike very large. Anterior ilia *diverge widely. Prepubic process of pubis shallow, postpubic process very short.

Lanzhousaurus You et al., 2005

Diagnosis. As for the type and only known species.

Lanzhousaurus magnidens You et al., 2005
Holotype. GSLTZP01-001

Holotype horizon, locality, age. Hekou Group, Gansu, China, Early Cretaceous.

Emended diagnosis. *Adults gigantic. Overall massively constructed. Dentary pre-coronoid process length/minimum depth ratio under 5, diastema absent. Teeth *extremely large, maximum tooth positions *14 in dentary, one tooth in each position. Dorsal neural spines moderately tall, *modest withers present. Prepubic process of pubis deep.

Iguanodontoidea Sereno, 1986

Emended diagnosis. Ventral margin of premaxilla below ventral edge of maxilla. Dorsal apex of maxilla sited posteriorly on the element. Antorbital fossa and fenestra further reduced. Lacrimal usually has a contact with maxilla posterior to antorbital fossa, does not wedge between premaxilla and maxilla, ventral portion is ventral to dorsal tip of maxilla. Maxillary tooth positions 19–29, dentary tooth positions 21–25, maxillary teeth narrow, teeth usually 2 in each position, asymmetrically lozenge-shaped in labial view with prominent primary ridge which is displaced distally, dentary teeth broad and asymmetrically diamond shaped in lingual view with primary and secondary ridges separated by a median groove, and distal denticulate margins rolled lingually to produce a slight cingulum. Rhombic lattice of ossified ligaments astride mid-dorsal to mid-caudal neural spines. Manus usually narrow and compact, digits abbreviated.

Iguanodon Mantell, 1825

Horizon, locations, ages. Upper Wealden Supergroup (= Hainaut Group), Belgium, probably England and Germany, probably Barremian, possibly earliest Aptian.

Diagnosis. As for the type and only determinate species.

Iguanodon bernissartensis Boulenger in Beneden, 1881

Lectotype. IRSNB 1534.

Lectotype horizon, locality, age. Upper Hainaut Group, SW Belgium, probably late Barremian, or mid Barremian or earliest Aptian.

Referred specimens. All robust material from lectotype quarry.

Emended diagnosis. Adults large at 8+ m and 3+ tonnes. Overall massively constructed. Premaxillary tip to anterior orbital rim/latter to paraoccipital process tip length ratio ~1.1; dentary pre-coronoid process length/minimum depth ratio under 4. Maxillary process of premaxilla shallow. Dorsal apex of maxilla set posteriorly. Antorbital fossa and fenestra *moderate in size. Lacrimal short, does not contact nasal. Accessory palpebral *present. Posterior border of occiput deeply indented. Lateral temporal fenestra large. Posterior portion of jugal short. Quadratojugal tall. Quadrate tall, transversely broad, shaft straight, lateral foramen set low, dorso-posterior buttress *very large. Diastema absent. Maximum tooth positions *29 in maxilla, *25 in dentary. Dorso-sacral/hindlimb length ratio ~1. Posterior dorsal centra antero-posteriorly compressed. Neural spines of dorsals, sacrals and caudals short. *8 fused sacrals. Scapula blade *consistently broad, *base very broad, *acromion process placed dorsally and directed anteriorly. Coracoid large. Forelimb *~70% length of hindlimb. Deltopectoral crest of humerus *proximally located and modest in size. Olecranon process large. Manus *massive, phalanx 1 of digit I *present, pollex spike and other unguals large. Anterior process of ilium *much shorter than main body, main body shallow, posterior acetabular body *long. Prepubic process of pubis shallow. Femoral shaft straight. Metatarsal I present, II long.

Jinzhousaurus Wang and Xu, 2001

Diagnosis. As for the type and only known species.

Jinzhousaurus yangi Wang and Xu, 2001

Holotype. IVPP V126991.

Holotype horizon, location, age. Yixian Formation, Liaoning, China, late Barremian or earliest Aptian.

Emended diagnosis. Premaxillary tip to anterior orbital rim/latter to paraoccipital process tip length ratio ∼1.25; dentary pre-coronoid process length/minimum depth ratio under 5. Rostrum subtriangular in lateral view. Premaxilla projects well below level of tooth rows, maxillary process is moderately deep. Dorsal apex of maxilla set posteriorly. Antorbital fossa and fenestra reduced. Lacrimal short, contacts nasal. Frontals *do not participate in orbital rim. Lateral temporal fenestra small. Posterior portion of jugal short. Quadratojugal short. Quadrate moderately tall, shaft curved, dorso-posterior buttress small. Squamosals *contact one another. Diastema absent. Tooth position numbers low.

Mantellisaurus Paul, 2006

Emended etymology. For Mary and Gideon Mantell, who discovered and described the first Wealden iguanodonts.

Horizons, locations, age. Lower Lower Greensand and probably Upper Wealden Supergroup, England, possibly northern Europe, early Aptian, possibly Barremian.

Diagnosis. As for the type and only determinate species.

Mantellisaurus atherfieldensis (Hooley, 1925)

Holotype. BMNH R5764.

Holotype horizon, locality, age. Upper Vectis Formation, Isle of Wight, earliest Aptian.

Referred specimen. BMNH 3741.

Horizon, locality, age. Lower Lower Greensand Formation, England, early Aptian.

Emended diagnosis. Probably modest sized as adults. Overall lightly constructed. Premaxillary tip to anterior orbital rim/latter to paraoccipital process tip length ratio ∼1.25; dentary pre-coronoid process length/minimum depth ratio under 5. Rostrum subtriangular in lateral view. Maxillary process of premaxilla shallow. Dorsal apex of maxilla set posteriorly. Antorbital fossa and fenestra reduced. Lacrimal short, does not contact nasal. Lateral temporal fenestra moderate in size. Posterior portion of jugal short. Quadratojugal short. Quadrate tall, transversely narrow, shaft curved, lateral foramen set high, dorso-posterior buttress small. Diastema absent. Tooth positions 23 in maxilla, 22 in dentary. Dorso-sacral/hindlimb length ratio ∼1. Posterior dorsal centra not compressed antero-posteriorly. 7 fused sacrals. Scapula blade narrow and constricted at middle of blade, base rather narrow, acromion process placed rather dorsally and directed anteriorly. Forelimb ∼50% of hindlimb length. Deltopectoral crest of humerus distally placed, fairly large and incipiently hatchet shaped. Manual phalanx 1 of digit I absent, pollex spike and other unguals moderate in size. Pelvis *relatively large. Main body of ilium deep. Prepubic process of pubis deep. Femoral shaft curved. Metatarsal I present, II short. Distal phalanges of toes *not strongly abbreviated.

Dollodon gen. nov.

Horizon, locations, age. Upper Wealden Supergroup (= Hainaut Group), Belgium, possibly Germany, England, probably Barremian, possibly earliest Aptian.

Etymology. For Louis Dollo, who first described this and other Bernissart iguanodonts.

Diagnosis. *Tooth positions over 25? in dentary. Otherwise as for the type and only determinate species.

Dollodon bampingi sp. nov.

Holotype. IRSNB 1551.

Holotype locality, horizon, age. Upper Hainaut Group, Belgium, probably late Barremian, or mid Barremian or earliest Aptian.

Etymology. Named in honour of Mr D. Bamping for his support of this research.

Diagnosis. Probably modest sized as adults at 6+ m and 1+ tonnes. Overall lightly constructed. Premaxillary tip to anterior orbital rim/latter to paraoccipital process tip length ratio ∼1.6 via elongation of posterior nasal, maxillary process of premaxilla and maxilla; dentary pre-coronoid process length/minimum depth ratio over 5. Maxillary process of premaxilla shallow. Dorsal apex of maxilla set posteriorly. Antorbital fossa and fenestra reduced. Lacrimal short, does not contact nasal. Accessory palpebral absent. Posterior border of occiput straight. Lateral temporal fenestra small. Posterior portion of jugal short. Quadratojugal short. Quadrate short, transversely narrow, shaft curved, lateral foramen set high, dorso-posterior buttress small. Diastema short. Dorso-sacral/hindlimb length ratio ∼1.2. Posterior dorsal centra not compressed antero-posteriorly. Neural spines of dorsals, sacrals and caudals form moderately tall sail. 7 fused sacrals. Scapula blade narrow and constricted at middle of blade, base rather narrow, acromion process placed ventrally and directed distally. Forelimb ∼55% of hindlimb length. Deltopectoral crest of humerus distally placed, fairly large and incipiently hatchet shaped. Manus narrow. Manual phalanx 1 of digit I present, pollex spike and other unguals moderate in size. Main body of ilium shallow. Prepubic process of pubis deep. Femoral shaft moderately curved. Metatarsal I present, II long.

Altirhinus Norman, 1998

Location, age. Mongolia, late Aptian or early Albian.
Diagnosis. As for the type and only known species.
Altirhinus kurzanovi Norman, 1998

Holotype. PIN 3386/8.
Emended diagnosis. Adults large. Overall lightly constructed. Premaxillary tip to anterior orbital rim/latter to paraoccipital process tip length ratio ∼1.6 via elongation of posterior nasal, maxillary process of premaxilla and maxilla; dentary pre-coronoid process length/minimum depth ratio under 5. Premaxilla and nasal *form large crest. Premaxilla projects well below level of tooth rows, maxillary process is moderately deep. Dorsal apex of maxilla set posteriorly. Antorbital fossa small. Lacrimal long, contacts nasal. Accessory palpebral absent. Lateral temporal fenestra moderate in size.

Posterior portion of jugal long. Quadratojugal tall. Quadrate short, transversely narrow, shaft straight, lateral foramen set high, dorso-posterior buttress absent. Diastema short. Tooth positions *26 in maxilla, *24 in dentary, incipient 3rd row in many positions. Scapula blade narrow and constricted at middle of blade, base rather narrow, acromion process placed rather dorsally. Deltopectoral crest of humerus distally placed, modest in size. Manus narrow, pollex spike and other unguals moderate in size. Anterior prong of ilium *robust, *strongly arced ventrally, main body deep. Prepubic process of pubis moderate in depth.

Ouranosaurus Taquet, 1976

Horizon, location, age. Upper Elrhaz Formation, Niger, late Aptian.

Diagnosis. As for the type and only known species.
Ouranosaurus nigeriensis Taquet, 1976

Holotype. MNHN GDF 300.
Emended diagnosis. Adults large at 8+ m and 2+ tonnes. Overall lightly constructed. Premaxillary tip to anterior orbital rim/latter to paraoccipital process tip length ratio * ∼ 1.9; dentary pre-coronoid process length/minimum depth ratio over 5. Rostrum and beak flattened, strongly subtriangular in lateral view. External nares *retracted posteriorly. Maxillary process of premaxilla moderately deep. Antorbital fossa and fenestra reduced. Dorsal apex of maxilla sited very posteriorly. Lacrimal long, contacts nasal. Accessory palpebral absent. Posterior border of occiput deeply indented. Lateral temporal fenestra small. Posterior portion of jugal long. Quadratojugal tall. Quadrate short, transversely broad, shaft curved, lateral foramen set high, dorso-posterior buttress absent. Diastema long. Tooth positions *22 in maxilla and dentary. Dorso-sacral/hindlimb length ratio ∼ 1.2. Posterior dorsal centra not compressed antero-posteriorly. Neural spines of dorsals, sacrals and caudals *very tall forming prominent sail. 6 fused sacrals. Scapula blade narrow and constricted at middle of blade, base rather narrow, acromion process placed ventrally and directed distally. Forelimb ∼ 55% of hindlimb length. Deltopectoral crest of humerus distally placed, modest in size. Manus short and broad, phalanx 1 of digit I absent, pollex spike and other unguals small. Main body of ilium deep. Prepubic process of pubis *very deep. Femoral shaft straight. Metatarsal I absent, II long.

Probactrosaurus Rhozhdestvenskii, 1966

Diagnosis. As for the type and only determinate species.

Probactrosaurus gobiensis Rhozhdestvenskii, 1966 (= *P. alashanicus* Rhozhdestvenskii, 1966)

Holotype. PIN 2232/1.
Horizon, location, age. Dashuiguo Formation, Mongolia, Albian.
Emended diagnosis. Probably modest sized as adults. Overall lightly constructed. Premaxillary tip to anterior orbital rim/latter to paraccipital process tip length ratio ∼ 1.1; dentary

pre-coronoid process length/minimum depth ratio under 5. Premaxilla projects well below level of tooth rows, maxillary process is anteriorly shallow and posteriorly deep. Lateral temporal fenestra moderate in size. Posterior portion of jugal long. Quadrate tall, transversely narrow, shaft moderately curved, lateral foramen set high, dorso-posterior buttress small. Diastema short. Tooth positions 23 in dentary, incipient 3rd row in many positions, battery tightly packed. Posterior dorsal centra compressed antero-posteriorly. 6 fused sacrals. Scapula blade narrow, not strongly constricted at middle of blade, base rather narrow, acromion process placed rather dorsally and directed anteriorly. Deltopectoral crest of humerus distally placed, fairly large and incipiently hatchet shaped. *Forelimb very slender. Olecranon process moderate in size. Manus very narrow, *digits further abbreviated, *pollex spike and other unguals small. Main body of ilium deep. Prepubic process of pubis deep, postpubic process very short. Femoral shaft moderately curved. Metatarsal II shortened.

Equijubus You et al., 2003

Diagnosis. As for the type and only known species.

Equijubus normani You et al., 2003

Holotype. IVPP 12534.
Horizon, location, age. Xinminbao Group, Gansu China, Barremian-Albian.
Emended diagnosis. Premaxillary tip to anterior orbital rim/latter to paraoccipital process tip length ratio ∼ 1.0; dentary pre-coronoid process length/minimum depth ratio under 4. Premaxilla projects well below level of tooth rows, maxillary process is shallow. Dorsal apex of maxilla sited anteriorly. Antorbital fossa small. Lacrimal long, does not contact nasal, *anterior process wedges between premaxilla and maxilla, *ventral edge at level of dorsal edge of maxilla. *Primary palpebral absent. Lateral temporal fenestra large. Anterior prong of jugal long and slender, *dorsal finger projects in lacrimal, posterior portion long. Quadratojugal tall. Quadrate tall, shaft nearly straight, lateral foramen set moderately low, dorso-posterior buttress small. Diastema long. Tooth positions 23 in maxilla, incipient 3rd row in many positions, battery tightly packed. Posterior dorsal centra compressed antero-posteriorly. 6 fused sacrals. Main body of ilium deep.

Iguanodontia or Iguanodontidae *nomina dubia* and/or *incertae sedis*

Camptosaurus (= *Iguanodon*) *hoggii* (Owen, 1874)
Iguanodon anglicus Holl, 1829 (= *I. mantelli* Meyer, 1832)
I. ottingeri Galton and Jensen, 1975
Vectisaurus valdensis Hulke, 1879
I. orientalis Rhozhdestvenskii, 1952
Probactrosaurus mazongshanensis Lu, 1997

Iguanodontia or Iguanodontidae status not fully resolved by this study

I. dawsoni Lydekker, 1888
I. fittoni Lydekker, 1889
I. hollingtonensis Lydekker, 1889
I. seelyi Hulke, 1882
Nanyangosaurus zhugeii Xu et al., 2000

5. Character descriptions and comparisons

A list of osteological characters pertinent to the taxonomy of iguanodonts is presented in Table 1. Although it has phylogenetic implications the tabulation is not a comprehensive character list, the formulation of such being beyond the scope of this study. As detailed in the list, and in the following discussion, emphasis is placed on assessing and comparing the characters present in holotypes, with data from referred specimens discussed separately except in cases where assignment is sufficiently reliable.

It has long been recognized that *Iguanodon bernissartensis* differs greatly in skeletal proportions from the holotypes of *Mantellisaurus atherfieldensis* and *Dollodon bampingi* (Fig. 1B−D; Dollo, 1882, 1883, 1884; Hooley, 1925; Norman, 1980, 1986, 2004), being much more robustly constructed, longer armed, and overall larger. It has often been assumed that the gracile forms were similar to one another (Norman, 1986, 1987b, 2004; Norman et al., 1987; Norman and Weishampel, 1990; Naish and Martill, 2001; Suzuki et al., 2004; Paul, 2006). However, the first technical skeletal restoration of the holotype of *M. atherfieldensis* shows that it and the *D. bampingi* holotype also differ markedly from one another (Fig. 1C, D; the divergence is also apparent in careful examination of the lateral view photographs of the specimens in Dollo, 1884; Norman, 1986; Glut, 1997). The results emphasize the importance of high fidelity skeletal restorations in palaeosystematic work: technical skeletal restorations of sufficiently complete holotype specimens should be a required part of a description. Proportionally, the holotype *M. atherfieldensis* is much shorter trunked and larger hipped than *I. bernissartensis* and *D. bampingi*, to the point that the ilia are nearly equal in absolute length in *D. bampingi* and *M. atherfieldensis*, despite the latter being a smaller individual. The arms of the *M. atherfieldensis* holotype are so short that, combined with the short trunk, the skeleton cannot be realistically posed quadrupedally, indicating it went onto all fours only when standing or moving very slowly. With longer trunks and/or arms the holotype of *D. bampingi* and especially *I. bernissartensis* can be easily posed quadrupedally. The holotype of *M. atherfieldensis* is only 10% smaller than that of *D. bampingi* so the differences are not readily attributable to size or ontogeny. Among the three iguanodonts, *I. bernissartensis* has the proportionally largest and most robust skull, the *D. bampingi* holotype the smallest and most gracile, and the *I. atherfieldensis* holotype is intermediate in these regards. The proportional differences alone are not sufficient to warrant generic separation, but the robust and the gracile iguanodonts differ strongly from one another in many details of their skeletal morphology (Figs. 2F−H, 3Aa−d, Bc−k, Cb−g).

The skulls of the *M. atherfieldensis* holotype and *I. bernissartensis* lectotype (new restoration) are relatively short snouted (Figs. 2F, G, 4). Although the posterior skulls of the holotypes of *M. atherfieldensis* and *D. bampingi* (new restoration, Fig. 2H) are nearly identical in absolute height and length (Fig. 4), the rostrum of the latter is much longer both absolutely and relative to the posterior section of the skull through elongation of the nasal, maxillary process of the premaxilla, maxilla, anterior palate and dentary. In comparison to the highly extended dentary of *D. bampingi*, the element is shallow but not as elongated in the *M. atherfieldensis* holotype, and is short and deep in *I. bernissartensis*. The posterior skull of *I. bernissartensis* is expanded vertically and has a large lateral temporal fenestra to accommodate a powerful musculature for the proportionally short jaws. The holotype of *D. bampingi* presents the opposite condition with regard to these features, and the *M. atherfieldensis* holotype is intermediate. The quadratojugal of *I. bernissartensis* is relatively much taller than those of the two gracile iguanodonts. The quadrate is more antero-posteriorly curved, is transversely narrower, the dorso-posterior buttress is shorter and the quadrate foramen is more dorsally located in the holotypes of *M. atherfieldensis* and *D. bampingi* than in the robust iguanodont. In dorsal view the posterior border of the occiput is strongly indented in *I. bernissartensis* (Dollo, 1883; Norman, 1980), but appears to be nearly straight in the holotype of *D. bampingi* (Dollo, 1884; Norman, 1986).

IRSNB 1551 possesses a short diastema not present in either BMNH R5764 or *I. bernissartensis*. The latter has many more tooth positions along its maxilla and dentary than the *M. atherfieldensis* holotype (I follow Norman (1980, 1986) in considering these numerical differences taxonomically significant and not merely reflective of size or ontogeny). The number of tooth sockets in *Mantellisaurus* and especially *Dollodon* is obscure. According to Hooley (1925) the holotype of *M. atherfieldensis* has 23 maxillary and 22 tooth positions (of which 20 are visible anterior to the coronoid process in lateral view), and this appears to be verified by the figures of these elements. Norman (1986) scores the upper and lower tooth positions of *I. atherfieldensis* (= *D. bampingi*) as 23 and 21, but it is not clear whether this count is based on BMNH R5764, IRSNB 1551, or both. In Norman (1986; figs. 3, 6, 19) the composite restorations of the skull and dentary of *I. atherfieldensis* show 18 dentary teeth visible in lateral view, and the figure of the IRSNB 1551 skull shows 18 maxillary and 20 dentary teeth observable on the right side, and 19 maxillary and dentary positions on the left. In Dollo (1884, fig. 3) 23 left maxillary and dentary tooth positions can be seen anterior to the coronoid process. The dentary tooth count for remains that may be assignable to *D.* sp. (MIWG 6344, see below) is 27−28 (Naish, pers. comm. 2006), exceeding even *I. bernissartensis*; it is not surprising that an ornithopod with such elongated jaws and tooth rows had so many teeth.

The differences between *Iguanodon*, *Mantellisaurus* and *Dollodon* are even more extensive in the postcrania.

The holotype of *M. atherfieldensis* and *D. bampingi* have relatively longer posterior dorsal centra and fewer functional

Table 1
Iguanodont characters

	I. d.	I. f.	D. l.	I. b.	M. a.	D. b.	I. o.	A. k.	O. n.	P. g.	E. n.	had
Rostrum			short	short	short	long		long	long	short	short	variable
Beak/rostrum depth			deep	deep	deep	deep		deep	flat	deep	deep	flat
Premaxilla set below maxilla			no	yes	yes	yes		yes	yes	yes	yes	yes
Premaxilla maxillary process			deep	shallow	shallow	shallow		shallow	medium	medium	shallow	shallow
Apex of maxilla sited			near middle	aft	aft	aft	aft	aft	well aft	aft	at middle	variable
Accessory palpebral				present		absent		absent	absent		absent	absent
Palpebral				present	present	present		present	present		absent	absent
Antorbital fossa/fenestra			large	modest	smaller	smaller		small	smaller		small	small
Lacrimal			long	short	medium	short		long	medium		long	variable
contacts nasal				no	no	no		yes	yes		yes	variable
Posterior jugal				short	short	short		long	long	long	long	long
Quadratojugal				tall	short	short		tall	tall		tall	short
Quadrate shaft				straight	curved	curved		straight	curved	curved	straight	variable
height				tall	tall	short		short	short	tall	tall	variable
transversely				broad	narrow	narrow		narrow	broad	broad		
lateral foramen set				low	high	high		high	high	high	low	variable
dorso-post. buttress				large	small	medium		medium	absent	small	medium	absent
Dorsal occiput rim				indented		straight			idented	variable		straight
Dentary			medium	deep	medium	shallow		medium	shallow	medium	deep	variable
diastema			absent	absent	absent	short		short	short	long	long	long
Tooth positions upper/lower			19/	29/25	23/22		26/24	22/22	27+/	/23	23/	20–60/25–50
number/position			2	2	2	2	3	2	72	3	3	3–5
battery			dense	dense	dense	dense	dense	denser	dense	denser	denser	very dense
Skeletal build				robust	gracile	gracile	gracile?	gracile	gracile	gracile		gracile
Neural spines	tall	tall		short		tall			tall			variable
Dorsal centra	short	short		short	long	long			long		short	short
Trunk length				medium	short	medium			medium			
Fused sacrals				8	7	7			6	6	6	7–12
Scapula blade				broad	narrow	narrow	medium	narrow	narrow	narrow		narrow
blade edges				parallel	taper	taper	taper	taper	taper	taper		taper
base				robust	narrow	narrow	narrow	narrow	narrow	narrow		narrow
Acromion process position				dorsal	medium	ventral	ventral	medium	ventral	medium		ventral
orientation				anterior	anterior	distal	distal		distal	anterior		distal
Coracoid				large	small	small		small	small	small		small
Forelimb length				long	short	medium			medium			medium
proportions				robust	slender	slender		slender	slender	slenderer		slenderer
Pectoral crest position				proximal	distal	distal		distal	distal	distal		distal
size				small	medium	medium		medium	small	medium		large
Olecranon process				large	medium			medium	medium	medium		medium
Carpal blocks				present	present	present		absent	present			absent
Manus				massive	narrow	narrow		narrow	small	narrower		narrower
phalanx 1, digit I				present	absent	absent			absent			absent
unguals				large	medium	medium		medium	small	small		small
Ilium main body	deep	deep		shallow	deep	shallow		deep	deep	deep	deep	shallow
anterior process				short	long	long		long	long	long		long
posterior process	very short	short		long	short	short		short	short	short		variable
Prepubic process depth		medium		shallow	deep	deep		medium	deep	deep		deep

Femoral shaft	straight	curved	medium	straight	medium	straight
Metatarsal I	present	present	present	absent		absent
Metatarsal II	long	short	long	long	short	
Distal pedal phalanges	short	medium	short	short	short	short

I. d. = "I." *dawsoni* holotype, tentatively includes material referred by Blows (1998).
I. f. = "I." *fittoni* holotype, tentatively includes material referred by Blows (1998).
D. l. = *Dakotadon lakotaensis* holotype.
I. b. = *Iguanodon bernissartensis* lectotype and referred Bernissart quarry material.
M. a. = *Mantellisaurus atherfieldensis* holotype.
D. b. = *Dollodon bampingi* holotype.
A. k. = *Altirhinus kurzanovi* holotype and material referred by Norman (1996).
I. o. = "I." *orientalis* holotype.
O. n. = *Ouranosaurus nigeriensis* holotype and material referred by Taquet (1976).
P. g. = *Probactrosaurus gobiensis* holotype and material referred by Rhozhdestvenskii (1966), Norman (2002).
E. n. = *Equijubus normani* holotype.
had = hadrosaurids general.
Underlining indicates characters that approach or match the hadrosaurid condition, when gradistic differences are present the longer the underlining the closer the approach.
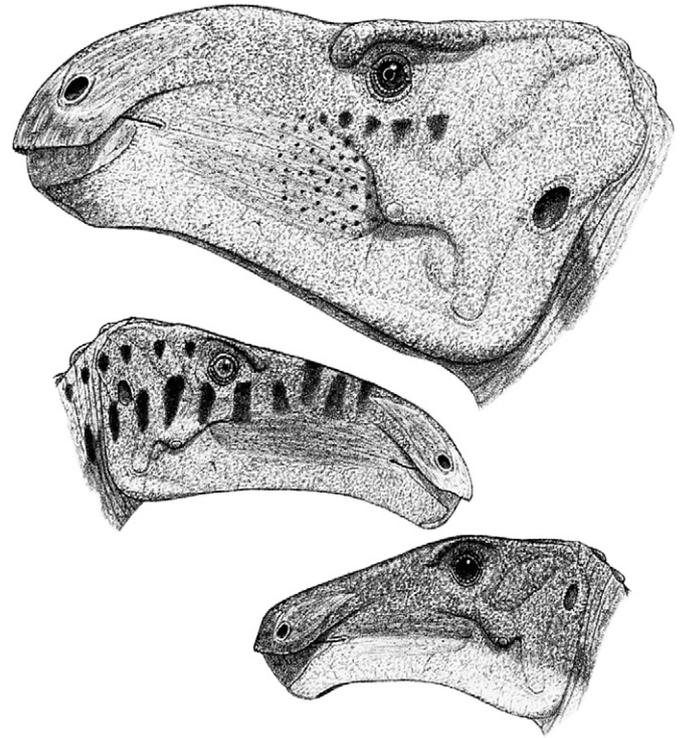

Fig. 4. Same scale life restorations of heads of, from top to bottom, *Iguanodon bernissartensis*, *Dollodon bampingi* and *Mantellisaurus atherfieldensis*, all based on type skulls.

sacrals than does *I. bernissartensis*. There is strong divergence in the height of the neural spines, the taller structures of the holotype of *D. bampingi* forming a shallow sail not present in *I. bernissartensis* (Fig. 1B, D).

The scapulae of the *D. bampingi* and *M. atherfieldensis* holotypes and material commonly referred to the latter, including BMNH 3741, are more slender over all, and narrower at mid-blade, than that of *I. bernissartensis* which is far broader at the base (Fig. 3Aa–d). A massive Nehden scapula referred to *I. bernissartensis* emphasizes the radical difference between robust and gracile iguanodonts concerning the dimensions of the scapula base (Fig. 3Ab). The acromion process of *I. bernissartensis* is dorsally placed and is directed strongly anteriorly; that of the holotype of *D. bampingi* appears to be more ventrally placed and oriented, while the process is intermediate in the holotype of *M. atherfieldensis*. In the latter two specimens (and in commonly referred material) the coracoid is proportionally much smaller than in *I. bernissartensis*. Even though the humeri of the *D. bampingi* and *M. atherfieldensis* holotypes (and specimens commonly referred to the latter) are more slender than that of *I. bernissartensis* (and commonly referred specimens), the former's deltopectoral crests are larger, extend further distally, and are more hatchet shaped. The olecranon process is relatively larger in *I. bernissartensis* than in the other taxa. In the manus, the unguals, including the thumb spike, are proportionally markedly shorter in the holotypes of *M. atherfieldensis* and *D. bampingi* than in *I. bernissartensis*.

The ilia of the *M. atherfieldensis* holotype (and commonly referred material, including BMNH 3741) resemble those of camptosaurs in profile, including deep main bodies (Fig. 3Bf–j). The holotype skeleton of *D. bampingi* was preserved on its side, and both ilia figured by Norman (1986) appear to be markedly shallower than both ilia of the *M. atherfieldensis* holotype (Fig. 3Bf, k), which argues against their being distorted in the manner of the right ilium of BMNH R8649 (compare to the specimen's deeper left ilium in Galton, 1976 and Norman, 1990). This marked difference in ilial morphology initiated the author's concern that *M. atherfieldensis* was not a single taxon, leading to the skeletal restoration of BMNH R5764. As illustrated by Norman (1980) the ilium of Belgian *I. bernissartensis* is shallow, as are those of the Nehden quarry specimens referred to the species and the *I. seelyi* holotype (Fig. 3Bc–e). The postacetabular bodies of *I. bernissartensis*, the referred Nehden ilia and the *I. seelyi* holotype are longer, while the anterior iliac processes are shorter, than those of the *M. atherfieldensis* and *D. bampingi* holotypes (Fig. 3Bc–f, k). Contrary to the overall greater robustness of its skeleton, the prepubic process of the pubis of the Belgian *I. bernissartensis* is much shallower than those of the *D. bampingi* and *M. atherfieldensis* holotypes (and elements commonly referred to the latter: Fig. 3Cb,d–g). The difference is particularly dramatic when the robust and gracile prepubic processes from the Nehden quarry are compared (Fig. 2Bc, g, see also fig. 13 in Norman, 1990), and exceeds that of any other ornithischian genus. The 2nd metatarsal of the *M. atherfieldensis* holotype is, proportionally, significantly smaller than in the holotype of *D. bampingi* or *I. bernissartensis*. The distal pedal phalanges of the *M. atherfieldensis* holotype (fig. 8 in Hooley, 1925) are not abbreviated in the manner seen in the holotype of *D. bampingi*, or *I. bernissartensis.*

The iguanodont remains described by Owen (1842, 1872, 1874) are labelled specimen B and appear to represent a single individual (cataloged as BMNH R1831–1833). The dentary BMNH R1831 is very elongate, matching or exceeding that of the *D. 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. In other iguanodonts the diastema ranges from essentially absent to a third the length of the tooth row; in BMNH R1831 it is half as long as the dental battery. Although as just noted the anterior dentary teeth appear to be unusually small, the rest of the teeth are large, but not extremely so compared to other iguanodonts. The wrist and spike BMNH R1832 are, if anything, more robust and ankylosed than those of published *I. bernissartensis* specimens. According to Blows (1998) the prepubic process of the pubis of BMNH R1833 is deeper than in camptosaurs or *I. bernissartensis*, and approaches the depth seen in later, gracile iguanodonts, although it appears to differ in profile. The ilia of the holotypes of *I. dawsoni* and *I. fittoni* are similar to those of camptosaurs, including having deep main bodies (Fig. 3a, b). The first is further camptosaur-like in lacking the suprailiac

crest (often incorrectly labeled the antitrochantor) characteristic of iguanodonts. Between *I. dawsoni* and *I. fittoni* the ilium of the latter is more like that of various iguanodonts in having a sharply triangular posterior blade. An ischium referred to *I. dawsoni* (Blows, 1998) has a robust shaft more like that of earlier camptosaurs than those of later iguanodonts. The tall dorso-sacral neural spines of *I. fittoni* are similar to those found in some iguanodontoids.

Norman (1986) noted that the scapulae of the holotype *I. orientalis* differ from those of Belgian *I. bernissartensis*, that of the former being much more slender overall, and apparently having a more distally directed acromion process (Fig. 3Aa, e). Instead, the scapula of *I. orientalis* resembles those of the holotypes of *M. atherfieldensis* and especially *D. bampingi* (Fig. 3Ac–e).

The holotype skull of *Dakotadon lakotaensis* (new restoration, Fig. 2D) differs markedly from *I. bernissartensis*, *M. atherfieldensis* and *D. bampingi* in having a deeper maxillary process of the premaxilla, a proportionally larger and antero-posteriorly longer lacrimal, and a relatively larger antorbital fossa. In these details *D. lakotaensis* is more similar to *Theiophytalia* (new restoration, Fig. 2B), although a number of iguanodont characters are present in the former that are lacking in the latter (Weishampel and Bjork, 1989; Bakker, 1998; Brill and Carpenter, 2006). Weishampel and Bjork (1989) and Brill and Carpenter (2006) disagree on whether the lacrimal contacts the nasal in *D. lakotaensis*. The premaxilla-prefrontal contact illustrated by Weishampel and Bjork (1989) is too extensive, but whether the lacrimal and nasal contact one another is difficult to determine; the four elements seem to meet at a point. A new restoration (Fig. 2I) of the skull of *Altirhinus* confirms that the nasal is strongly arched (more so than restored in Norman, 1998). Norman (2002) provided new information on *Probactrosaurus*, and a new restoration of the skull (Fig. 2K) largely supports his effort.

6. Biostratigraphy

The horizons and stages of all significant iguanodont specimens have yet to be tabulated in one study. While this area is plagued by uncertainty and confusion, new work has clarified some long standing problems.

The age of English iguanodont-bearing beds is largely well determined (Fig. 5; Norman, 1987a, 1993; Kerth and Haildwood, 1988; Allen and Wimbledon, 1991; Benton and Spencer, 1995; Cook, 1997; Blows, 1998; Charig and Chapman, 1998; Naish and Martill, 2001; Norman and Barrett, 2002; Radley, 2004, 2006; Robinson and Hesselbo, 2004; Weishampel et al., 2004). The holotype of *I. hoggii* was found in the middle Berriasian Lulworth Formation. The middle Valanginian Wadhurst Clay produced the holotypes of *I. dawsoni*, *I. fittoni*, and *I. hollingtoniensis*. Also from lower Hasting Beds of similar age is BMNH R1831–1833. The *I. anglicus* holotype has been attributed to the latest Valanginian Upper Tunbridge Wells Sands by Norman (1987a), and to the Tilgate Forest Beds (Tilgate Grit) by Charig and Chapman (1998), which they placed in the Hauterivian. The teeth actually derive
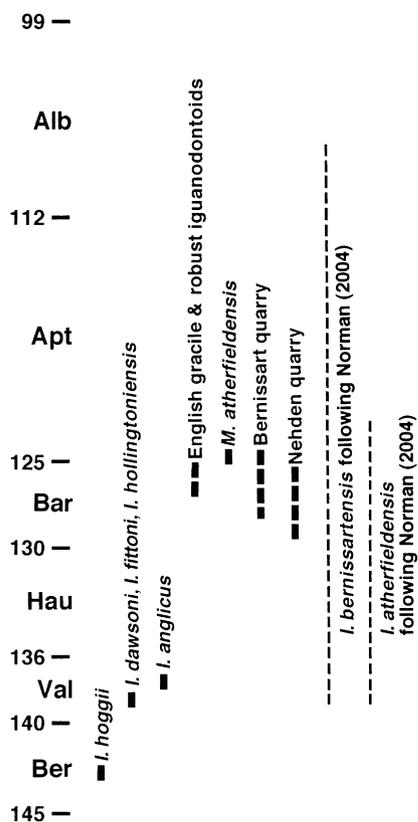
Fig. 5. Actual and estimated temporal placement of English, Belgian and German iguanodont type specimens, genera and species, except that *I. bernissartensis* (Norman, 2004) includes Asian *I. orientalis*. Many ages represent broad range estimates, stage boundary ages after Gradstein et al. (2004).

from the Grinstead Clay Formation, which includes the Tilgate stone of Mantell, and dates from the later portion of the middle Valanginian (Topley, 1875; Blows, 1998; Radley, 2004, 2006; Naish pers. comm. 2006). The *Vectisaurus valdensis* holotype and the referred specimen BMNH 8649, as well as a large number of partial remains assigned to *M. atherfieldensis* and *I. bernissartensis* (including *I. seelyi*), are from the late Barremian portion of the upper Wessex Formation (Kerth and Haildwood, 1988; Allen and Wimbledon, 1991; Radley, 2004, 2006). The *M. atherfieldensis* holotype originated in the Vectis Formation near its top, which is earliest Aptian (Robinson and Hesselbo, 2004) rather than latest Barremian as previously thought. Similar in age is BMNH 3741 from the early Aptian Kentish Rag of the lower Lower Greensand.

Outside of England, some ages have been firmed up (Fig. 5). Most importantly, the temporal placement of the Bernissart quarry has been resolved; previously the site has bounced around the entire Early Cretaceous (Norman, 1980, 1990, 2004; Charig and Chapman, 1998; Weishampel et al., 2004; Yans et al., 2005), with Taquet (1975) favouring the Barremian judging from the evolutionary grade of the site's iguanodonts, while early palynological work based on imprecise gymnosperms suggesting the Hauterivian (Allen and Wimbledon, 1991). Subsequent angiosperm data places the iguanodont remains as mid-Barremian to earliest Aptian (Yans et al., 2004, 2005, 2006). The Nehden quarry is Aptian

according to Norman (1987b, 2004), Norman et al. (1987), Norman and Weishampel (1990) and Weishampel et al. (2004), but Norman et al. (1987) also considered Nehden similar in age to the English Weald Clay even though the latter is not younger than Barremian (Benton and Spencer, 1995). This study follows Schudack (1987) and Wilde and Hemsley (2000) in dating the Nehden quarry to the Barremian. Spanish teeth referred to *I*. sp. (Ruiz-Omeñaca et al., 2001) are from the lower Barremian. Maisch (1997) listed Spanish Tera Group bones referred to *I. fittoni* as Early Cretaceous; Ruiz-Omeñaca et al. (1998) dated the beds as Berriasian-Valanginian. Other Spanish and French remains assigned to *I*. sp., *I. bernissartensis* or *M. atherfieldensis* have been dated from the Berriasian to the Aptian (Weishampel et al., 2004).

Outside Europe, the Lakota Formation, the unit in which the holotype of *D. lakotaensis* was discovered, is tentatively listed as Barremian by Weishampel and Bjork (1989), Norman and Weishampel (1990), Norman (2004) and Weishampel et al. (2004). Long thought to be from the camptosaur-rich latest Jurassic Morrison (Gilmore, 1909), the *Theiophytalia* holotype is more likely from the Aptian-Albian Purgatoire Formation (Brill and Carpenter, 2006). The estimated age of the Huhteeg Svita beds that contain *I. orientalis* has ranged from Barremian to Maastrichtian (Norman and Weishampel, 1990; Norman, 1996), with Norman (1996) favouring a Barremian/Aptian age based largely on its supposed conspecific status vis-à-vis *I. bernissartensis*; Weishampel et al. (2004) favoured the Aptian-Albian. Part of an unnamed complex of beds, the quarry that yielded the holotype of *Altirhinus* is late Aptian or early Albian according to Norman (1998). The Kitadani Formation that produced *Fukuisaurus* is late Hauterivian to Barremian according to Kobayashi and Azuma (2003), but is listed as Aptian-Albian in Weishampel et al. (2004). The Yixian Formation that *Jinzhousaurus* comes from is late Barremian to perhaps earliest Aptian (Swisher et al., 1999; Weishampel et al., 2004). Listed simply as Early Cretaceous by Xu et al. (2000), the Sangping Formation that produced *Nanyangosaurus* was tentatively placed in the Albian by Norman (2004) and Weishampel et al. (2004). *Lanzhousaurus* is also listed as simply from the Early Cretaceous by You et al. (2005, 2006). The Dashuiguo Formation that produced *Probactrosaurus* has been considered Barremian to late Albian in part based on the dinosaurs, but micropalaeontological data places it in the Barremian (Itterbeeck et al., 2004). *Equijubus* is listed as late Early Cretaceous by You et al. (2003); according to Norman (2004) and Weishampel et al. (2004) the Xinminbo Group it is Barremian-Albian. *Ouranosaurus* and *Lurdusaurus* are from the late Aptian upper Elrhaz Formation (Taquet and Russell, 1999).

If *I. dawsoni*, *I. fittoni*, *I. hollingtoniensis* and BMNH R1831—1833 continue to be referred to *Iguanodon*, then English examples of the genus span most of the Wealden and continue beyond it, and globally the genus lasted some 20 million years from the Valanginian to the Aptian (perhaps much longer depending on the uncertain dating of *I. orientalis*). An entire stage, the Hauterivian, and large portions of the Valanginian and the Barremian, separate *I. anglicus* from

the neotype species of *Iguanodon* (Fig. 5). Norman and Weishampel (1990) and Norman (2004) cited *I. bernissartensis*, a single species, as spanning the Valanginian to the Albian (Fig. 5), about 30 million years (perhaps more depending on the temporal placement of *I. orientalis*). In Norman and Weishampel (1990) and Norman (2004), *M. atherfieldensis* spans over 10 million years from the Valanginian to the Aptian (Fig. 5). It is problematic that genera lasted so long; it is practically impossible for species to have survived for tens of millions of years.

7. Analysis

The ruling of the ICZN (2000) designating *I. bernissartensis* the type species of *Iguanodon* is problematic in a number of respects (Sues, 1998), although it is not clear that a better solution to the *Iguanodon* conundrum is available. In an earlier ruling (ICZN, 1996), the Ghost Ranch theropod specimen that was made the lectotype of *Coelophysis bauri* came from the same level and just a few kilometers from the holotype, and may have belonged to the same species. In the case of *Iguanodon* the holotype and lectotype are separated by 250 km. More significantly, the *I. anglicus* teeth are from the middle Valanginian, while the type *I. bernissartensis* material is from the mid-Barremian at the earliest, so the time difference is 10 million years or more. On a temporal basis alone there is no reason to doubt that the two sets of remains derive from different species, and very probably from different genera. Charig and Chapman (1998) incorrectly stated that Barremian-Aptian *I. bernissartensis* is only "a little younger" than the supposedly Hauterivian *I. anglicus*, and noted that there may be a larger time gap between the latter and the holotype of *M. atherfieldensis*. Otherwise the disparities in time, species and genera were not a matter of significant discussion in the ICZN process. Anatomically, although it is not possible to assess the morphology of the original type of *Iguanodon*, it was much more likely to be similar to the earlier Valanginian *I. dawsoni*, *I. fittoni, I. hollingtoniensis* or BMNH R1831−1833, all of which are quite distinct from *I. bernissartensis*. None of the diagnostic postcrania described by Mantell (1834, 1841; Norman, 1993) are robust examples with shallow prepubic processes and ilia, stout scapulae, massive thumb spikes and so forth, similar to those of *I. bernissartensis*, and the one major skeletal specimen, the gracile, Aptian BMNH 3741, is much younger than *I. anglicus* and may or may not be significantly younger than the neotype of *Iguanodon*. The great majority of English specimens including the best, the holotype of *M. atherfieldensis*, are gracile forms. Although a small number of robust English remains from the Barremian-Aptian are morphologically similar to *I. bernissartensis*, at this time no specimen from the nation where the legendary name originated can be assigned to the genus with certainty. It might have been better to make the lectotype of *Iguanodon* the one described English specimen that includes a good skull and skeleton and that is gracile, as well as accurately dated: the *M. atherfieldensis* holotype, but it is as young or younger relative to the original holotype than is *I. bernissartensis*. Most suitable

in terms of time, place and probably in anatomical grade were *I. dawsoni*, *I. fittoni, I. hollingtoniensis* or BMNH R1831−1833, any one of which may actually be the same taxon as *I. anglicus*. *I. dawsoni* may be too basal to be the basis of an iguanodontid taxon; the rest appear more suitable in this particular. *I. dawsoni*, *I. fittoni* and *I. hollingtoniensis* consist of minimally diagnostic sacral/pelvic material, but none of these sets of skeletal remains is complete to the desired degree. BMNH R1831−1833 includes a complete dentary with almost all its teeth, and it may not be referable to a previous taxon that would have complicated its being a neotype for *Iguanodon*, perhaps even *I. anglicus* if they are sufficiently close in time. However, this specimen has been scientifically overlooked since its description and is not familiar to the public. Of course the choice of one of these specimens and taxa over the other would have been arbitrary, but the final decision was itself entirely subjective. If *Iguanodon* had been defined so that it is applicable to one of the iguanodonts from in or close to the Valanginian stage the type teeth come from, then all the iguanodonts from the Barremian and Aptian would need new generic titles, including *I. bernissartensis*. Instead, *Iguanodon* as now designated and diagnosed is a radically revised ornithopod taxon that is much later than, and probably very different from, the iguanodont the name was originally attached to − to the point that the highly specialized neotype species may well be in a different family than the probably more basal type species − but it does match the long-standing popular and palaeontological image of the genus formed by Dollo's work on the large, robust Belgian dinosaur, and technically is anchored on the first named species based on good material, *I. bernissartensis* (Barrett, 1998). This major change makes all the more urgent the need to limit species included in the redefined genus to only those that properly meet the new anatomical and phylogenetic criteria.

The following analysis of ankylopollexian taxa generally progresses from basal to derived and from early to later examples, with some exceptions.

Camptosaurus has long been restored with a long, low, rather iguanodont-like skull (Gilmore, 1909), but this is incorrect due to both misidentification of the primary specimen used in the classic restoration (which actually dates from the Early Cretaceous, Brill and Carpenter, 2006), and to an inaccurate restoration of the same partial skull. *Camptosaurus* actually had a deeper, more triangular, broader, hypsilophodont-style skull (Fig. 2A; Brill and Carpenter, 2006).

Although it is not *Iguanodon* as currently defined (Norman and Barrett, 2002), and probably not an iguanodont or even a styracosternan, Berriasian *I. hoggii* is much too fragmentary to be referred to the Tithonian genus *Camptosaurus* (contra Norman and Barrett, 2002). The latter genus should be considered limited to the late Late Jurassic unless sufficiently complete and unambiguous Cretaceous remains are found. While it is possible that the specimen is a camptosaur, this study agrees with Glut (1997) that it should be considered a *nomen dubium*, and Ornithopoda or Camptosauridae *incertae sedis*.

The incompleteness of *I. dawsoni, I. fittoni* and *I. hollingtoniensis* and BMNH R1831−1833, the sparsity of overlapping

elements, and the lack of better description hinder comparisons and assessment, so these taxa are only briefly considered here. *I. dawsoni* on the one hand, and *I. fittoni*, *I. hollingtoniensis* and BMNH R1831–1833 on the other, are very distinct from one another, probably at the genus and even the family level. Whether or not *I. fittoni* and *I. hollingtoniensis* are actually conspecific or even congeneric (as per Norman and Weishampel, 1990; Blows, 1998; Norman, 2004) has not been properly documented, so although the synonymy is possible it is not accepted at this time. Lydekker (1889) was correct to remove BMNH R1831–1833 from *I. mantelli*, and to not assign it to another taxon without substantiation. The deep, camptosaur-style ilia of the various Valanginian iguanodonts are very different from the shallow ilium of Barremian *Iguanodon*, as well as that of *Dollodon*. Lacking a suprailiac crest or strongly triangular posterior ilium, and in having a robust ischium, *I. dawsoni* may be a camptosaurid, or it may represent a new family, and it may not be an iguanodont. *I. fittoni*, *I. hollingtoniensis* and BMNH R1831–1833 appear to be iguanodont in grade, and may even be iguanodontoid. Although the elongation of the dentary of BMNH R1831 is similar to that of the *Dollodon* holotype and MIWG.6344 discussed below, the ventral diastema is so long, and the tooth row so short, that it is reminiscent of the long-snouted hadrosaurid *Edmontosaurus* (*Anatotitan*) *annectens*. Even long-nosed *Ouranosaurus* does not have as great a gap between beak and teeth. Meanwhile the robustness of the arm of apparently associated BMNH R1832, especially the wrist and spike, are exceeded only in *Lurdusaurus*. The cranial specializations and arm proportions of BMNH R1831–1833 are not due to great size because the modest dimensions of the specimen are similar to those of the *Mantellisaurus* and *Dollodon* holotypes. On one hand the jaw adaptations and long, laterally compressed metacarpals suggest that this specialized ornithopod is an iguanodontoid, and relatively close to hadrosaurs. On the other hand the heavily constructed, *Lurdusaurus*/*Iguanodon*-like arm implies that it is not a highly derived iguanodontoid. It is apparent that BMNH R1831–1833 cannot be assigned to any current valid iguanodont genus. On temporal, anatomical and phylogenetic grounds, it is agreed with Norman and Barrett (2002) that the other Valanginian styracosternans likewise almost certainly do not belong to the same genus as *I. bernissartensis*, or to *Mantellisaurus* or *Dollodon*. The same principle applies to the very incomplete Spanish remains provisionally assigned to *I. fittoni* by Maisch (1997), and to other assorted specimens attributed to *I.* sp., *I. bernissartensis* and *M. atherfieldensis* from the Berriasian to Hauterivian of Spain and France (Weishampel, 2004). Sorting out the relationships and taxonomy of these diverse early Early Cretaceous large ornithopods will require a detailed appraisal of both their morphological characters, and their placement in time, relative to one another.

The skull of *Theiophytalia* is more phylogenetically primitive than *Fukuisaurus* and *Dakotadon* in a number of features. The basal features include the apparently high depth/length ratio of the skull due to a short rostrum, a high breadth/length ratio, small, anteriorly placed external nares, a palpebral bar

that is not merged with the orbital rim, and a low coronoid process. The position of the apex of the maxilla is not entirely certain, but it appears to be more anterior than typical for iguanodonts. Therefore *Theiophytalia* does not qualify as an iguanodont, nor is it a camptosaur; instead it appears to be intermediate to the two groups (Brill and Carpenter, 2006). This matter can only be resolved with more fossils.

The conclusion of Kobayashi and Azuma (2003) that *Fukuisaurus* was more derived than *Iguanodon* is undermined by their mixing basal *I. bernissartensis* with more derived *M. atherfieldensis* and *D. bampingi* (see below), and by the limited set of characters that they examined. Instead the skull is phylogentically primitive in many regards, to the degree that the iguanodont status of *Fukuisaurus* is sufficiently questionable that it is not rediagnosed here. The rostrum, mandible and the skull overall appear to be short and deep, the premaxillary and predentary beaks are small, the primary palate is poorly developed, the apex of the maxilla is set further anteriorly than in iguanodonts, there is no diastema, and the number of teeth is low. The posteriorly positioned external nares, ventrally off set premaxilla, and tall coronoid are iguanodont features not present in *Theiophytalia*; the one derived feature is a long posterior part of the jugal. At this time *Fukuisaurus* cannot be assigned to the iguanodontoids (contra Norman, 2004); the systematic position of the best-preserved Japanese iguanodontian will remain provisional pending discovery of the top half of the skull and the bulk of the skeleton.

The *Dakotadon* skull has the classic iguanodont proportions, being long, low, and narrow due to an elongated rostrum and dentary, and the external nares are large and posteriorly expanded. But contrary to Weishampel and Bjork (1989) and to Norman (1998), *D. lakotaensis* is very different from *I. bernissartensis*. Lacking a ventrally off set ventral margin of the maxilla, and exhibiting a deep maxillary process of the premaxilla, a maxilla with a dorsal apex set more anteriorly than in other iguanodonts, an elongated lacrimal, and a relatively large antorbital fenestra, the *D. lakotaensis* skull appears to be considerably more basal than that of any other iguanodont, enough so that its status as an iguanodont is provisional. The skull is sufficiently diagnostic, and – in contradiction to the title of the original descriptive paper – this study agrees with Bakker (1998) and with Brill and Carpenter (2006) that *D. lakotaensis* warrants its own genus. Because *Dakotadon* appears to be a very basal iguanodont, one basal to *Iguanodon*, it is probably neither an iguanodontoid (contra Norman, 2004) nor an iguanodontid (contra Weishampel and Bjork, 1989); its exact status also awaits the finding of the rest of the skull and the skeleton.

The shallow, *I. bernissartensis*-like prepubic process of the pubis of *Lurdusaurus* suggests it is not a derived iguanodont, nor does the massive pollex spike and the lack of the ossified rhombic tendon complex. *Lurdusaurus* is considered an iguanodontid in Taquet and Russell (1999). Although it does have opithocoelous cervicals, the short, broad hand suggests that it is basal to both *Iguanodon* and the iguanodontoids as diagnosed here (Norman, 2002; in Norman, 2004) *Lurdusaurus* is listed under Iguanodontoidea contrary to the analysis

in the text and the cladogram), and perhaps the iguanodonts as well. On the other hand, as it were, the derived iguanodontoid *Ouranosaurus* from the same habitat also has a laterally splayed, abbreviated manus, so it apparently experienced a reversal to the basal manual condition. If so then *Lurdusaurus* may be an iguanodontoid too, albeit probably a basal example, with a reversed grade manus; again, additional material including the skull is needed for a more accurate assignment.

You et al. (2005, 2006) concluded that the gigantic and heavily constructed *Lanzhousaurus* is a close relative of robust *Lurdusaurus*, that the former is less derived than the latter, and that neither of these taxa are iguanodontoids. The low tooth count and lack of prominent ridges on the tooth crowns suggests exclusion from the iguanodontoids. However, the much deeper prepubic process of the pubis of *Lanzhousaurus* suggests that these two are not intimately related, that *Lanzhousaurus* is more derived, and that it may be an iguanodontoid. Because key elements are missing, these contrasting conclusions cannot yet be verified or denied via the form of the manus and so forth. If *Lanzhousaurus* is an iguanodontoid, it is probably a basal member, and its limited number of tooth positions both parallels and exceeds that seen in BMNH R1831. The selective factors in the two cases differ dramatically. In *Lanzhousaurus*, which lacks a diastema, hyper-enlargement of the individual teeth required a low tooth count. In BMNH R1831 it was the shortening of the dental battery in favor of the diastema that resulted in a low number of tooth positions. The moderate height of the dorsal neural spines is replicated in some other iguanodonts, but the presence of what appears to be shoulder withers formed by the sudden elevation of the anterior spines just posterior to the neck is very unusual for an ornithopod.

Taxa assigned to *Iguanodon* vary considerably in size (Fig. 4), but this is not relevant to the issue of their being congeneric or not, since mass can vary by well over an order of magnitude within a genus (as per *Varanus*, Pianka, 1995; *Felis*, Turner and Anton, 1997).

That *Iguanodon* has been a wastebasket has caused the species *I. bernissartensis* and ''*I.*'' *atherfieldensis* to recently be used as de-facto stand-ins for what are actually multiple genera and species. This process was inadvertently enhanced by Norman's (1986) defining *M. atherfieldensis* by melding the type of the latter with IRSNB 1551. As a consequence the two species have become mini-taxonomic grab-bags into which have been placed robust versus gracile iguanodonts from markedly different times: Norman (2004) listed both *I. bernissartensis* and ''*I.*'' *atherfieldensis* as species lasting over most of the Early Cretaceous, and in the case of *Iguanodon* across all continents of the Northern Hemisphere. Scoring *Iguanodon* as including hadrosaur characters actually limited to *M. atherfieldensis* and *D. bampingi* has the unintended effect of obscuring the more derived nature of the latter two taxa relative to *I. bernissartensis*.

Suzuki et al. (2004) cladistically assessed *I. bernissartensis* (it is not clear whether or not this was limited to the Belgian remains) versus *M. atherfieldensis* (presumably including IRSNB 1551), and listed the two species as identical in all observed characters except for the posterior indentation of the skull. Many of the characters compared by Suzuki et al. (2004) were assessed with criteria that unintentionally failed to catch the differences between the two species. For example, they listed the dorso-posterior buttress of the quadrate as simply either absent or present, thereby failing to observe the contrasting size of the structure in the taxa. Likewise, the tooth position count boundary of 30/29 chosen by Suzuki et al. (2004) is too high to phylogenetically distinguish the European iguanodonts from one another. These problems reveal the limitations of cladistics when complex character states are scored as a simple yes or no, because the method does not utilize an anatomical resolution fine enough to capture and compare key details. Such simplifications and other failures to fully describe differences apply to their investigation of sacral numbers, neural spine heights, scapula and coracoid dimensions, acromion processes, deltopectoral crest shapes, and thumb spike size. A number of characters, such as the accessory palpebral, dimensions of the dorsal centra, and the very different shapes of the prepubic process of the pubis, were not examined by Suzuki et al. (2004). Because the cladistic analysis of Suzuki et al. (2004) failed to encapsulate the many differences between *I. bernissartensis* and *M. atherfieldensis*, much less those between the latter and *D. bampingi*, their conclusion that these taxa form a clade is not supported.

The cladistic analysis in Norman (2002) failed to group *I. bernissartensis* and *M. atherfieldensis* (presumably including IRSNB 1551) as each other's closest relatives, with the latter closer to hadrosaurs, even though many of the characters that separate the taxa were not considered. Norman (2004) found the two species to either form a clade or to group apart depending on details of the cladistic procedure.

This study finds that the holotypes of *M. atherfieldensis* and especially *D. bampingi* possess many more derived iguanodontoid characters, and more closely approach the hadrosaur condition, than *I. bernissartensis*, which retains a more plesiomorphic iguanodont grade in most, albeit not all, regards (Table 1). Although *I. bernissartensis* is more hadrosaur-like concerning its higher tooth position count and sacral count, as well as its deeper posterior dorsal centra, some of these characters may be size related. Also, hadrosaurs often have shallower centra, and so does the derived iguanodontoid *Ouranosaurus* which also shares a low sacral count and low tooth count with *M. atherfieldensis* and *D. bampingi*. Basal hadrosaurs, such as *Bactrosaurus*, have low tooth and sacral counts as well (Table 1). The possession of derived characters is inconsistent between *M. atherfieldensis* and *D. bampingi*; in particular the former's deeper ilium is morphologically more basal than the shallow, hadrosaur-like ilia of both the latter and *I. bernissartensis*. It is also interesting that the holotype of *M. atherfieldensis* has long toes, rather than the abbreviated digits present in other iguanodonts and hadrosaurs. Therefore, mosaic evolution was present in the family. The holotypes of *M. atherfieldensis* and *D. bampingi* are in most regards more similar to each other in gross proportions and detailed morphology than either is to stout *I. bernissartensis*. An exception is the shallowness of the ilia shared by the latter and *D.*

bampingi. Overall the data indicates that the gracile taxa are closer to the *Ouranosaurus*-hadrosaur clade than *I. bernissartensis,* with the latter paralleling hadrosaurs in a few regards. *D. bampingi* has the edge over *M. atherfieldensis* in being hadrosaur-like, so the first may form a clade with more derived iguanodonts and hadrosaurs, or it and *M. atherfieldensis* may form a distinct clade with the former paralleling derived iguanodonts and hadrosaurs in some respects. If so then the genus *Iguanodon* as it has been commonly designated is paraphyletic, with some members markedly closer to hadrosaurs than others.

Concerning morphological variation, even a cursory examination of numerous elements that have routinely been assigned to *Iguanodon* reveals that they cannot be collected into one genus (Fig. 3Aa–e, Bc–k, Cb–g). The degree of divergence present in *Iguanodon* as previously defined is so acute that it exceeds that readily attributable to individual variation, sex, size or growth. The gracile and robust forms, for instance, are distinct among juveniles as well as adults from the Nehden quarry (Norman, 1987b; Norman et al., 1987), and the holotype *of M. atherfieldensis* is not much smaller than that of *D. bampingi*. Possible sexual morphs among dinosaurs, such as those of *Coelophysis bauri, C. rhodesiensis, Tyrannosaurus rex* and *Protoceratops andrewsi*, center on subtle proportional differences that require statistical analysis to verify that they are bimodal (Sampson and Ryan, 1997), or in the case of *Triceratops horridus* differences in rostrum depth and horn configuration. In no other dinosaurs are possible sexual morphs characterized by differences in basic anatomical details as great as those that distinguish the iguanodonts of concern here. Such extreme sexual dimorphism would be unusual if not unique among amniotes. The separate taxa hypothesis is so superior to the sexual dimorphism and other alternatives that the burden of proof is on the latter. Even if it were demonstrated that the Nehden and Bernissart gracile/robust specimens represented sexes rather than taxa, it would still be necessary to separate *Mantellisaurus* from *Iguanodon*. The great disparity in numbers between the robust and gracile iguanodonts at Bernissart, Nehden and English deposits in general, and the fact that the robust morph is common at Bernissart and rare at Nehden and in England (Norman, 1987b; Norman et al., 1987; Naish and Martill, 2001), make it all the more improbable that it can be demonstrated that lithe *Dollodon* was a female, much less a male *Iguanodon*.

The differences in *Iguanodon, Mantellisaurus* and *Dollodon* are not only far more extensive than that present in the hadrosaurid and ceratopsid genera discussed earlier, it is well beyond the variation which would remain even if the genera of each of the three groups discussed above were synonymized; for example *Hypacrosaurus* (= *Corythosaurus, Lambeosaurus*), or *Saurolophus* (= *Prosaurolophus*). The differences between *I. bernissartensis, M. atherfieldensis* and *D. bampingi* markedly exceed those between *Kritosaurus* and *Gryposaurus*, which are distinct in a number of cranial and postcranial features, but are very close relatives that clearly form their own clade. The divergence between the iguanodont's postcrania even exceeds that between *Parasaurolophus* versus the significantly distinctive *Hypacrosaurus*

complex. The differences between the iguanodonts in question markedly exceed those that are preserved in *Probactrosaurus* and *Equijubus* (see below). The difference between the prepubic processes of the robust and gracile European iguanodonts is of the extent normally seen between families. The high degree of anatomical inconsistency among dinosaur genera that ensues if *I. bernissartensis, M. atherfieldensis* and *D. bampingi* remain congeneric is not acceptable. Both the anatomical variation alone and the phylogenetic issue alone force separation.

So, although it is not necessary to split dinosaur taxa to the same degree as outlined above, the degree of both anatomical variation and phylogenetic separation currently present in *Iguanodon* is too great to be united within one genus. Even if *I. bernissartensis, M. atherfieldensis* and *D. bampingi* turn out to form a monophyletic clade, they — like the *Triceratops-Torosaurus* clade — are too morphologically divergent to be accommodated in a single genus. Specifically, gracile Barremian-Aptian iguanodont material cannot be referred to *Iguanodon* whether it be the neotype species or the earlier original. Nor can even *M. atherfieldensis* and *D. bampingi* — more divergent from one another than previously realized as well as possibly somewhat distinct in time — be comfortably placed in a single new genus, much less the same species. This study concurs with previous work (Norman, 1990; Norman and Weishampel, 1990; Glut, 1997) that no other iguanodont genus that has been named to date, and that is potentially assignable to the same taxa as *M. atherfieldensis* or *D. bampingi* in terms of morphology, time and location, is based on sufficiently diagnostic material. Therefore, *M. atherfieldensis* or *D. bampingi* are not assignable to a previously named genus. Consequently two new European genera are coined here and in Paul (2006). So is a new species for IRSNB 1551 herein. In this scheme, *Iguanodon*, although specialized in some regards, is a basal iguanodont (exceeded in this regard only by *Dakotadon*) while *Mantellisaurus* and especially *Dollodon* are moderately derived members of the family.

BMNH 3741 is close to *M. atherfieldensis* in age, and appears similar in morphology including the deep ilium, so, unless the detailed description of the specimen needs shows otherwise, it is referable to the species.

Because the bulk of the English material assigned to *M. atherfieldensis* (Fig. 3Bg–j, Cd) is Barremian, it is not likely to be the same species as the Aptian taxon, especially the material from the early and middle sections of the Barremian. But much of it is probably in the same genus in view of the consistently deep ilia. Until skulls and skeletons sufficiently complete to definitively place them in, or outside, *Mantellisaurus* generally and *M. atherfieldensis* specifically become available, most such gracile pre-Aptian remains are conservatively designated *M.* sp. This includes the *Vectisaurus valdensis* holotype (Fig. 3Bj). Apparently a juvenile, it is also very incomplete, consisting of only part of the ilium and some incomplete vertebrae, so the specimen does not form an adequate basis for a taxon, and the same is true of the much better but still largely incomplete BMNH 8649. Nor can the holotype of *M. atherfieldensis* serve as a diagnostic paratype for *V. valdensis* because the first specimen is younger than the latter

taxon. The prepubic process of the pubis BMNH R2194 (Fig. 3Cd) referred to *M. atherfieldensis* by Naish and Martill (2001) is nearly identical to that of the holotype. A right prepubic process of the pubis referred to *M. atherfieldensis* in Naish and Martill (2001) where it is labeled BMNH R111, but is actually BMNH R109, Naish pers. comm. 2007), is exceptionally deep, but the specimen's left element is normal for *Mantellisaurus* (Naish, pers. comm. 2007). An interesting set of remains are the elongated maxilla and dentary of MIWG.6344 assigned to *M. atherfieldensis* in Naish and Martill (2001, fig. 1—3). The dentary pre-coronoid process length/minimum depth ratio exceeds 5 like that of the *D. bampingi* holotype, and the dentary tooth position count of at least 27 is exceptionally high; both features hint at the presence of the genus in the English Barremian. Most English robust iguanodont remains are too fragmentary to firmly establish that they belong to the same genus and species as *I. bernissartensis*, and that the latter may be Barremian or Aptian in age (but see next paragraph) complicates determining the presence of the particular species in temporal terms. This applies even to the holotype of *I. seelyi*, which has a deeper ilium than at least some of the Bernissart remains (Fig. 3B). Until better evidence is on hand, robust English and other European material that is not younger than Barremian may be tentatively referred to *I.* sp if their detailed morphology warrants the placement. Earlier robust European iguanodont remains probably are not *Iguanodon*, as demonstrated by Valanginian BMNH R1832.

If the robust *Iguanodon* specimens from England and Germany are Barremian, and perhaps late Barremian, then this favours but does not firmly verify a similar rather than early Aptian temporal placement for the Bernissart quarry. If this is correct then robust iguanodonts are not yet known from Europe after the Barremian.

The taxonomy of the Nehden iguanodonts is ambiguous because of issues of time and morphology. It is not clear whether the ilia assigned by Norman (1987b) and Norman et al. (1987) to the gracile taxon are deep or shallow because they are not figured. A deep prepubic process of the pubis from the Nehden quarry is more similar to the *D. bampingi* holotype than to that of *M. atherfieldensis* (Fig. 3Cg). At least some of the gracile Nehden remains may therefore belong to *Dollodon*, but referring the former to the latter may be premature. If gracile material is referred to *Dollodon* it should be to *D.* sp, but it is possible that some or all of the gracile German material may belong to *M.* sp. Likewise, the robust Nehden material should not yet be referred to the species *I. bernissartensis*, all the more so since the illustrated Nehden ilia are somewhat deeper than those described from Bernissart (Fig. 3Bc, d), and the scapulae also differ in details (Fig. 3Aa, b). If anything, the robust Nehden ilia are more similar to that of the *I. seelyi* holotype (Fig. 3Cc—e). The robust Nehden material can be provisionally referred to *I.* sp. Assignment of the German material might be facilitated if the age of the quarry was better correlated with those of other pertinent sites. Although the Nehden quarry is probably closer in age to the Bernissart quarry and to *I. seelyi* than to *M. atherfieldensis*, this is not certain because the age ranges the first two quarries are set within

are broad, and do not entirely overlap either each other, or the horizon of the *M. atherfieldensis* holotype.

The Spanish teeth referred to *I.* sp. by Ruiz-Omeñaca et al. (2001) are Iguanodontoidea or Iguanodontidae *incertae sedis*. Iguanodont remains assigned to *I.* sp., *I. bernissartensis* and *M. atherfieldensis* from the various Barremian and Aptian locations of Spain and France (Weishampel et al., 2004) probably cannot be reliably assigned to specific species or even genera and should be conservatively reassessed.

The incompleteness of the *I. orientalis* holotype hinders determination of its taxonomic status and placement; the incomplete maxilla with 27 preserved tooth positions not being sufficient to alter this. Norman (1996) did not consider the differences that distinguish the scapulae of *I. bernissartensis* and the *I. orientalis* holotype taxonomically significant. The scapulae are actually so dramatically different that the two taxa should not be placed in the same genus, much less species (Fig. 3Aa, e). The *I. orientalis* scapula is much more like that of *M. atherfieldensis* and especially *D. bampingi* than it is to the neotype species of *Iguanodon* (Fig. 3Ac—e). Despite the similarity of the remains of *I. orientalis* to those of the just mentioned gracile iguanodonts, the holotype specimen is not adequate to either place it in the same genus as the gracile European material — a conclusion reinforced by their geographical distance and the uncertain time separation — or to use the species as the basis for a new genus. The species is a *nomen dubium,* with its validity indeterminate until the holotype can be compared to superior remains from the same location and horizon.

This reanalysis restricts *Iguanodon, Mantellisaurus* and *Dollodon* to a few million years in the Barremian and early Aptian portion of the Wealden Supergroup of Europe (Fig. 5), with just one species confidently attributable to each genus at this time. However, these genera's single species status is likely to be an artifact of lack of sufficiently diagnostic material, as at least some of the known material probably represents additional species referable to one or more of the genera. Chronospecies are especially probable. Additional species should not be assigned to *Iguanodon*, or to *Mantellisaurus* or *Dollodon*, unless sufficient anatomical and temporal evidence supports the placement.

In most respects *Jinzhousaurus* appears to be a moderately derived, standard iguanodont. The holotype skull's short, subtriangular rostrum and curved quadrate (new restoration, Fig. 2E) are most reminiscent of *M. atherfieldensis* which is close in time, but the deeper maxillary process of the premaxilla, far fewer teeth, lack of a down curve at the tip of the dentary, differing lacrimals and other details indicate they are not the same genus. Autapomorphies include frontals that do not participate in the orbit, and squamosals that contact one another. Description of the postcrania may better reveal its relationship to other iguanodonts.

Lack of the skull, poor dating and a short English text impair analysis of *Nanyangosaurus*. Also of concern is its small size, because if it is a juvenile rather than an adult as Xu et al. (2000) concluded, then some of its attributes, including exceptionally gracile limbs, may be growth related. The

large, hatchet shaped deltopectoral crest of the humerus appears to be a derived feature, as are other attributes discussed by Xu et al. (2000). It is not possible to properly assess the status of the taxon with the data on hand.

As explained by Norman (2002) *Probactrosaurus alashanicus* is a junior synonym of *P. gobiensis*, and *P. mazongshanensis* is not referable to the genus and is a *nomen dubium*. You et al. (2003) did not explicitly compare the two taxa, but the cranial and postcranial elements preserved in *Equijubus normani* and *P. gobiensis* are quite similar, and if the criteria utilized previously for iguanodont genera were applied they would be considered congeneric. The former has a longer diastema and shallower maxillary process of the premaxilla than the latter. But if additional remains show that *P. gobiensis* lacks the palpebral bar and has the distinctive lacrimal and jugal features present in *Eguijubus*, then the latter may be a subgenus of *Probactrosaurus*.

The diagnoses demonstrate that only the few, most distinctive iguanodont genera (*Lurdusaurus, Lanzhousaurus, Iguanodon* and *Ouranosaurus*) are definable by large sets of autapomorphies. Although *Dollodon* is easily distinguished from and cannot be assigned to *Iguanodon, Probactrosaurus* or even *Mantellisaurus*, it is difficult to discern any features specific to *Dollodon* not also found in other iguanodonts. Much the same situation applies to most iguanodont genera, which are usually distinguished and defined not by one or distinctive autapomorphies, but by the distinctive and unique combination of characters each possesses, even though the individual characters are widely distributed among other iguanodonts. Although advanced *Probactrosaurus* is distinct from more basal taxa, autapomorphies are largely limited to the gracile form of the arm and hand, yet its collective characters render it quite distinct from other advanced iguanodonts. The dorsal nasal trough of *Dakotadon* is an autapomorphy among known iguanodonts, but is also found in non-iguanodont ornithopods such as *Dryosaurus* and the near-iguanodont *Theiophytalia*. Some other iguanodont autapomorphies of *Dakotadon* are merely basal ankylopollexian or ornithopod characters not found in more derived iguanodonts. A number of the autapomorphies may be the result of incomplete preservation in the other taxa, such as the presence of an accessory palpebral in *Iguanodon*, and the entire absence of the orbital structure in *Equijubus*. Others may not be consistently present in taxa, especially when known from only one individual, such as the dorsal finger of the anterior jugal prong of *Equijubus*. Whether tooth position counts in the different species are consistently diagnostic is doubtful. Some autapomorphies are likely to prove to be present in yet undiscovered iguanodonts. These factors challenge the trend toward defining taxa based on autapomorphies, sometimes just one, alone.

Phylogenetic analyses of non-hadrosaurid iguanodonts in Sereno (1986, 1999), Norman (1990, 1998, 2002, 2004), Norman and Weishampel (1990), Godefroit et al. (1998), Head (1998, 2001), Kirkland (1998), Xu et al. (2000), Kobayashi and Azuma (2003), You et al. (2003, 2005, 2006) and Suzuki et al. (2004) are very inconsistent in their results, with differences in the placement of taxa often being extreme.

Such disparate results show that consensus has not been reached on the subject, and suggests that the cladograms are primarily reflections of the data sets being used in each case. Although a new analysis is beyond this study's scope, some comments on iguanodont phylogeny and their high level taxonomic consequences are pertinent.

In some of the above studies iguanodonts are at least partly paraphyletic, while in others they are a monophyletic sister clade to hadrosaurs. In particular Norman and Weishampel (1990), Norman (1990, 1998), Godefroit et al. (1998), Head (2001) and Kobayashi and Azuma (2003) conclude that *Iguanodon* and *Ouranosaurus* form a monophyletic sister group to more derived iguanodontoids and/or hadrosauroids, while Sereno (1986, 1999), Head (1998), Kirkland (1998), Xu et al. (2000), Norman (2002, 2004), You et al. (2003, 2005, 2006) and Suzuki et al. (2004) place *Ouranosaurus* closer to hadrosaurs than *Iguanodon*. In the same studies, *Altirhinus, Probactrosaurus* and *Ouranosaurus* contend for the position closest to hadrosaurs, with each getting the nod in at least one study. Sereno (1986, 1999) is unique in placing *Probactrosaurus* as a basal iguanodont, Norman (2002, 2004) is unique in placing it higher than fairly derived hadrosauroids such as *Eolambia* and *Protohadros*, and You et al. (2003, 2005) put it higher than *Equijubus*, a taxon which they consider the most basal hadrosauroid. In contrast, *Equijubus* is basal to *Iguanodon* in the strict consensus tree in Norman (2004). Insufficient coverage of pertinent characters and some apparent errors question the results. In Kobayashi and Azuma (2003), no dentary diastema is attributed to any species attributed to *Iguanodon*, or to *Probactrosaurus* which has one. You et al. (2003) did not score the length of the diastema. Turning to Suzuki et al. (2004, also see comments further above) a dentary diastema is present in *Dollodon, Probactrosaurus* and *Ouranosaurus* in addition to *Altirhinus*; the latter's dentary appears no more down curved than those of some other iguanodonts; dentary teeth posterior to the anterior edge of the coronoid are present in all known iguanodonts, not just derived examples; constriction of the scapula blade is common in iguanodonts; other cited characters are difficult to interpret, such as the shortening of phalanx I of manual digit III.

The data in Table 1 suggests that *Altirhinus, Probactrosaurus, Equijubus* and *Ouranosaurus* are all much more derived in the direction of hadrosaurs than is *Iguanodon*. Therefore neither *Probactrosaurus* nor *Equijubus* is a basal iguanodont. Between *Probactrosaurus* and *Equijubus* the latter has a slight phylogenetic edge in having a longer, hadrosaur-like diastema. In many regards *Mantellisaurus* and especially *Dollodon* approach or match *Altirhinus* in the possession of hadrosaur features, but the latter has the more derived teeth. Between *Ouranosaurus* and *Probactrosaurus* the African taxon has the duck-billed beak and long diastema, but *Probactrosaurus* shares with *Altirhinus* the incipient 3rd tooth row. So does *Equijubus*, which also lacks a palpebral bar; whether *Probactrosaurus* shares this hadrosaur-like condition cannot yet be assessed. A better understanding of the interrelationships of iguanodonts and basal hadrosauroids, including how many iguanodonts belong to the hadrosauroids because they are

more derived than *Ouranosaurus* (Sereno, 1986), requires a more accurate and extensive character assessment, but the small sample and limitations of cladistics may bar definitive results until the fossil record is much more comprehensive.

The status of high-level taxonomy in iguanodonts is correspondingly as unsettled as it is unsatisfactory. In Sereno (1986), Hadrosauroidea appear to be defined as the clade that includes *Ouranosaurus* and hadrosaurids, and is nested within the iguanodontoids. This definition is potentially unstable. As originally formed, Hadrosauroidea depends upon *Ouranosaurus* not being the closest relative of, and preferably more derived than, *Iguanodon*. If it turns out that *Ouranosaurus* is further from hadrosaurids than is *Iguanodon*, then the Iguanodontoidea and Hadrosauroidea switch positions, with the former clade nested within the latter. Hadrosauroidea collapses entirely if *Ouranosaurus* forms a clade with *Iguanodon*. Sereno (1998) redefined Hadrosauroidea to include all iguanodontoids closer to *Parasaurolophus* than to *Iguanodon*; this organization is more stable. If, as seems correct, *Mantellisaurus* and *Dollodon* are phylogenetically intermediate between *Iguanodon* and the *Ouranosaurus*-hadrosaur clade, then they are hadrosauroids according to the 1998 definition, but are not according to the 1986 version. As part of his dual system of two monophyletic stem-based taxa in each node-stem triplet Sereno (1986) segregated iguanodontoids (= Hadrosauriformes) into the Iguanodontidae and Hadrosauroidea. The inadequate result is strong taxonomic and anatomical asymmetry between the twin clades. The Hadrosauroidea contains many genera and a large degree of diversity in form and function. At least at this time a monophyletic Iguanodontidae may be limited to highly specialized *Iguanodon*, and there is little prospect that the number and anatomical diversity of genera that can be assigned to the group as defined by Sereno (1986) will ever be large. A similar problem applies to Sereno's (1986) node-stem triplet for Ankylopollexia in which a single-genus Camptosauridae contrasts to the enormous Iguanodontoidea (similar asymmetries afflict some of the other node-stem triplets in Sereno, 1986). It can be asked what is the point of retaining the little Camptosauridae and minimalist Iguanodontidae as laid out in the inelegant and topologically uninformative Sereno system. It is also perplexing that Sereno (1999) included an apparently multi-genus Iguanodontidae that spans much of the Early Cretaceous without explanation. The Iguanodontidae were present in *The Dinosauria* (Norman and Weishampel, 1990) where some iguanodonts appeared to form a monophyletic group, but is not mentioned in the *Dinosauria II* (Norman, 2004) where the iguanodont group is paraphyletic. We are left with the taxonomically awkward situation in which classic iguanodonts, such as *Iguanodon, Mantellisaurus* and *Dollodon*, belong to no formal, single-word group. The only cladistic designation for iguanodonts below the *Ouranosaurus*-hadrosaur clade is the unwieldy 'non-hadrosauroid iguanodontoids', in which the members are described by what they do not belong to as much as what they do belong to. In contrast, and because of the evolutionary accident that they represent a terminal clade, the many hadrosaur genera continue to be contained in the classic Hadrosauridae.

This sort of taxonomic arrangement is technically inconsistent, as well as discriminatory, towards taxa that do not happen to belong to modest sized, terminal monophyletic groups. Redefinition of the Iguanodontidae as a paraphyletic group lying between set boundaries within the basal, non-hadrosaur iguanodonts may offer a solution. If so, then a similar process would be necessary to accommodate other ankylopollexian families. The Camptosauridae is also absent from Norman (2004), and new families would need to be devised for nonhadrosaurid iguanodontians that may lie below (*Theiophytalia, Lurdusaurus*) or above (*Eolambia, Protohadros*) iguanodonts.

8. Conclusions

Prior to this study the common view of Early Cretaceous European iguanodonts was simplistic: that they consist of one genus spanning 20 million years or more, and are divisible into one robust and one gracile species in the Barremian and Aptian. However, in the modern world large herbivore families are taxonomically more complex. In contemporary Europe two similar yet distinctive deer genera, gracile *Capreolus* and heavier *Cervus*, often live in the same locale, and massive *Alces* may also be present. A wide array of cervids and/or bovids is often found in the same regions in India and Africa. There is no a-priori reason to assume the situation was different in the Mesozoic, and the analysis presented here indicates that the gracile and robust iguanodonts of Europe included multiple genera and species. During the Barremian and early Aptian the habitats of the Wealden Supergroup were inhabited by iguanodonts that were at the same time alike, yet also markedly different. One, *Mantellisaurus*, retained a generalized ornithopod form including the short arms and big pelvis associated with strong bipedalism. Although apparently more basal overall, *Iguanodon* was a drastically modified, massive, semi-quadrupedal ornithopod whose deep, powerfully muscled head and long, strong arms and great thumb spikes suggest it feed on heavy, coarse vegetation. *Dollodon* was a harbinger of derived iguanodontoids in being gracile, long snouted and weaker jawed, semi-bipedal, and featuring numerous hadrosaur-like features including a shallow tail. *Dollodon* may have been a hadrosauroid. *Mantellisaurus* may have been as well, and it appears to predominate numerically in England. *Iguanodon* is known from a much higher number of specimens than *Dollodon* at Bernissart, but at Nehden and in England it is in the minority compared to the gracile material. The differing proportions of stout versus slender do not appear to be due to differing taphonomy (Norman, 1987b), so it is more likely that divergent ecologies present at the respective locations were probably responsible. At this time only material from Bernissart can and should be assigned to *I. bernissartensis* and *D. bampingi*, and all other European material that is potentially assignable to either taxon is too incomplete, and potentially different in age, to be reliably referred to them. The only material referable to *M. atherfieldensis* is from the early Aptian of England; all other European material potentially referable to the genus is insufficiently complete, and usually too old, to be assigned to the species.

The early Early Cretaceous, European, and insufficiently diagnostic "*I.*" *hoggii* is removed from Jurassic *Camptosaurus*, and along with poorly described "*I.*" *dawsoni*, "*I.*" *fittoni* and "*I.*" *hollingtoniensis* is regarded as Ornithopoda *incertae sedis*. A long-ignored specimen that may or may not belong to one of the prior taxa appears to have combined hadrosaur-like jaws with stout spiked arms of exceptionally heavy construction at this early stage of the Cretaceous. The later, North American *Dakotadon* is a distinctive, very basal iguanodont. Asian "*I.*" *orientalis* is not a junior synonym of *I. bernissartensis* and is indeterminate. The removal of the Asian and North American taxa from *Iguanodon* means that evidence for a high degree of taxonomic similarity across the hemispheres is currently lacking among the iguanodonts. Instead the group was highly provincial at the genus level, and anatomically markedly diverse. Iguanodonts were much more variable than tyrannosaurids and exceeded hadrosaurids in this regard; they were less diverse than ceratopsids. As iguanodonts developed increasingly hadrosaurian forms, considerable mosaic evolution occurred, so derived, late appearing *Altirhinus, Ouranosaurus, Probactrosaurus* and *Equijubus* retained deep-bodied ilia not that different from *Camptosaurus*, while basal, strongly built *Iguanodon* evolved distinctive, shallow ilia. *Ouranosaurus* combined a duck-billed, hadrosaur-like skull with a broad, camptosaur-like manus. One Valanginian styracosternan appears to have retained a rather camptosaur-like form, at least one iguanodont from the same stage had a surprisingly derived, hadrosaur-like, anteriorly elongated mandible, and approached *Lurdusaurus* in the stoutness of the forelimbs. The late appearing but basal *Lurdusaurus* took stoutness to an extreme. The super-iguanodont *Lanzhousaurus* matched the biggest hadrosaurs and some sauropods in bulk. It is now apparent that dental batteries underwent much greater evolutionary experimentation among iguanodonts than hadrosaurs. Specifically — and in contrast to hadrosaurs — some iguanodonts had a low number of teeth; in *Lanzhousaurus* to allow a dentition made up of enormous teeth, in a long jawed Valanginian iguanodont to allow development of a hadrosaur-like diastema.

Acknowledgements

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