Remaking the Old into the New New. Names for Iguanodonts of Europe and North America by Gregory S Paul

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As we all know, in the early 1820s the first dinosaurs were recognized as ancient Mesozoic reptiles in southeastern England. The teeth of the herbivorous Iguanodon were first published in 1822 and named in 1825 and the predatory Megalosaurus was figured and named in 1824. Named by Gideon Mantell, the Iguanodon anglicus teeth may have been discovered by his wife Mary (exactly what happened is obscure). The type teeth were from early Early Cretaceous sediments that are now known to be about 138 million years old, of middle Valanginian age.

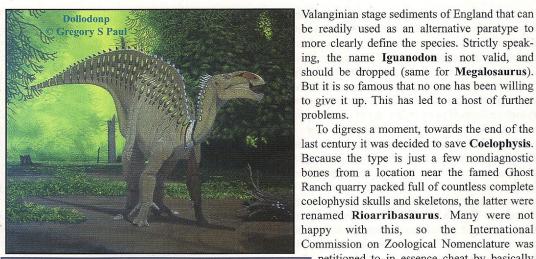
With folks now alerted that some really peculiar animals had been roaming about Ye Old England, parts of iguanodont skeletons soon started to show up from sediments of varying stages of the English Early Cretaceous. They were initially restored as a colossal, fully quadrupedal, rhino-like lizard with a spike on its nose, most famously as a still existing sculpture originally on display with other strange anti-deluvian beasts on the grounds of the Crystal Palace. They held a small banquet inside the great model as it was being constructed.

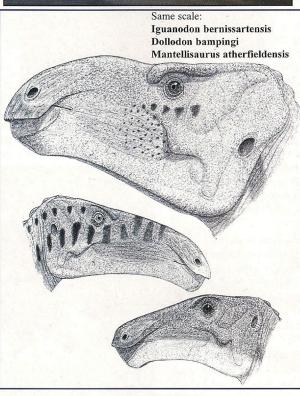
Eventually it was realized that iguanodonts were large ornithischian dinosaurs -- these days we understand that they were advanced ornithopods with well developed grinding tooth batteries closely related to the even more advanced duckbilled hadrosaurs of the Late Cretaceous. In 1834 Mantell described an incomplete, gracile skeleton from the Barremian-

Aptian boundary of some 125 million years ago that lacks the skull. The specimen was long assigned to I. mantelli even though that species too was based on teeth. The full nature of iguanodonts became clear in the late 1870s when Belgian coal miners at Bernissart came across a number of complete skeletons. These date from about 128-124 million years ago in the late Barremian or earliest Aptian stage; dating the quarry more exactly has proven difficult and even this date range was arrived at only recently. Almost all the Bernissart skeletons represent a robust species that were coined Iguanodon bernissartensis in 1881. Described in a fair amount of detail by Louis Dollo, these remains verified that the big spike was on the thumb rather than the nose, and that iguanodonts were semi-bipedal animals. When people think Iguanodon, they are usually thinking of the classic Bernissart species.

To say that there are problems here does not begin to cover the difficulties. Unlike mammals, dinosaur teeth are not sufficiently distinctive to be used as the holotype specimen to name species and genera. They can only be used to determine family level placement. These days it is no longer considered proper to name dinosaurs on teeth alone. A part of the skeleton that is distinctive to the genus and preferably the species is required - this, by the way, means that tooth-based Troodon is not valid, it should be Stenonychosaurus.

Nor are there complete iguanodont skulls and skeletons from the same





ing, the name Iguanodon is not valid, and should be dropped (same for Megalosaurus). But it is so famous that no one has been willing to give it up. This has led to a host of further To digress a moment, towards the end of the last century it was decided to save Coelophysis. Because the type is just a few nondiagnostic bones from a location near the famed Ghost

Ranch quarry packed full of countless complete coelophysid skulls and skeletons, the latter were renamed Rioarribasaurus. Many were not happy with this, so the International Commission on Zoological Nomenclature was

petitioned to in essence cheat by basically changing the type of the taxon from the original holotype to the same, oft published American Museum individual that was the holotype of Rioarribasaurus, making the latter the lectotype of C. bauri. Although somewhat controversial this was not all that radical in that the original and new types of Coelophysis were from much the same place and time, and there is a very good chance they really are the same species of dinosaur.

A few years ago it was decided to do something similar to rescue Iguanodon from the looming purgatory of nondiagnostic status. But without even one complete skeleton, or skull, from the same stratigraphic level in the general vicinity the situation was quite different from that of Coelophysis. It was though to be a good idea to petition the ICZN to shift the type from the British Valanginian teeth to the type of the later Belgian I. bernissartensis. The notion was that Iguanodon would then be based on the specimens that are most associated with the name. After a discussion that was not as thorough and controversial as it should have been, the request was approved.

One failure in the process was that in the original application, the age of the original type teeth was understated by saying that the Bernissart quarry was only "a little younger" than the I. anglicus which was incorrectly placed in the Hauterivian - oops -- and by suggesting that there may be a larger time gap between the latter and the holotype of the then Iguanodon atherfieldensis. But the actual time gap between the original teeth and the Belgian skeletons is 10 to 14 million years, and "I." atherfieldensis is little if any further away in time from the teeth. The mistake on the age of I. anglicus was not corrected in the ensuing back-and-forth discussion, instead the time issue was completely ignored. It would have been interesting to see what would have happened if the ICZN judges understood the full scope of the temporal separation. Because species tend to last only a few million years, it is virtually certain that the old and new type specimens are different species. Also, I. bernissartensis is a very specialized iguanodont, and it is most unlikely that it is the same genus as the much earlier type teeth.

In any case the insufficiently informed ICZN agreed to make the change, so Iguanodon is no longer an English based genus, it's new home is across the channel in Belgium. Perhaps it is an EU sort of thing. In any case the shift in types was extraordinarily radical in time, place, and almost certainly in phylogeny. Yet it is not easy to suggest an alternative for saving Iguanodon. The only good British skull and skeleton available as a new type, the holotype of "I." atherfieldensis, is no closer in age to I. anglicus than I. bernissartensis, is no more likely to be the same species or genus as the old teeth, and is not as familiar to the public as I. bernissartensis. It is easy to complain, not so easy to come up with a better idea.

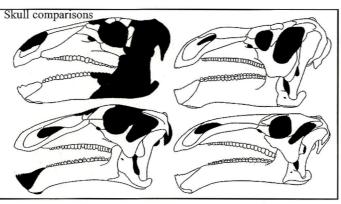
So the type species of **Iguanodon** is now a late Early Cretaceous robust iguanodont whose skeletal anatomy is well documented by numerous complete specimens. This has the advantage that we can now see

which other iguanodonts really are Iguanodon or not, something that could not be done as long as the name was tied to nothing more than a palm full of indistinctive teeth. So the next question is what other iguanodonts belong to the same genus. This brings us the other big problem. The name Iguanodon became so famous that it has been a taxonomic "waste basket" into which over the long years many remains from different times in the Cretaceous from Europe, Asia and even North America were tossed in to. In England a poorly preserved specimen from very early in the Cretaceous, the Berriasian, was titled I. hoggii. Much better but still partial fossils just a little older than the original "I." anglicus teeth became I. dawsoni, I. fittoni and I. hollingtoniensis. These 139 million year old ornithopods are too different to be in the same genus, but it is a real possibility that either or both I. fittoni and I. hollingtoniensis (which may or may not be the same species) are the same genus as Mantell's teeth -- yet they can no longer be assigned to Iguanodon since the ICZN ruling has moved the genus so much later in the Cretaceous. Also in England a rather slenderly built, modest sized iguanodont based on a good skull and much of the skeleton whose age of about 125 million years straddles the Barremian-Aptian boundary was designated I. atherfieldensis in 1925. Later one slenderly built skeleton

from Bernissart. IRSNB 1551, was placed in this species. In general, Barremian-Aptian iguanodont remains in Europe have of late been simplistically placed in either robust I. bernissartensis or gracile I. atherfieldensis. A poorly known Mongolian specimen of uncertain age originally designated I. orientalis was placed in I. bernissartensis. In 1989 a partial skull from South Dakota was given the name Iguanodon lakotaensis. This was presented as evidence of a close biogeographic connection between Europe and North America, the Atlantic ocean not being very wide back in those days.

Taken at face value **Iguanodon** at its maximum taxonomic lumping was roaming about the entire northern hemisphere (which is plausible), and spanned as much as 35 million years covering almost all of the Early Cretaceous (which is much less likely). In recent years there has been a tendency to move away from dumping new taxa into old names unless it can be justified, and the species of **Iguanodon** have been reduced by eliminating some of them. **I. hoggii** was placed in **Camptosaurus**, which itself was not the best move because the bones are too fragmentary to assign to any genus – especially one otherwise known only from the mid Late Jurassic -- or even family. All we can say is that **I. hoggii** is probably an Ankylopollexian ornithopod. The big nosed Asian skull incorrectly placed in **I. orientalis** was given its own genus, **Altirhinus**.

In my taxonomic research I am concerned that many dinosaur groups are oversplit at the genus level. For example the skeletons and skulls aside from the head crests and neural spine height of **Hypacrosaurus**, **Corythosaurus** and **Lambeosaurus** are very similar, and the variations in the crests and spines are exactly the sort of differences that make species distinct from one



another. Much the same applies to other dinosaurs such as Saurolophus and Prosaurolophus, or Centrosaurus, Styracosaurus, Einiosaurus Achelosaurus Pachycephalosaurus, and Chasmosaurus, Pentaceratops Agujaceratops, as well as Coelophysis and "Syntarsus". Some generic pruning is called for in these cases - and has occurred in the case of Coelophysis which now officially includes the later African form. But it is not a matter of knee jerk lumping. At the other extreme a host of big theropods of varying form were dumped into Megalosaurus

which is now limited to the type dentary, and perhaps Poekilopleuron. Crested Dilophosaurus sinensis was placed in the same genus as similarly crested Dilophosaurus wetherilli despite clear differences in the main body of the skull and the skeleton. Brachiosaurus (Giraffatitan) brancai has quite different dorsal vertebrae than Brachiosaurus altithorax, and of course a plethora of very different ornithopods were collected in Iguanodon. What is needed is some consistency in designating genera so that the degree of anatomical variation allowed within a given genus is much the same in all cases, and is broadly similar to that seen in modern, well established genera such as Varanus, Panthera, Canis, or Cervus. An example of where this has been successfully accomplished is Psittacosaurus, which includes a large number of distinctive species within the same basic skull and skeleton plan.

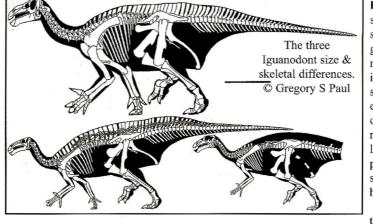
That paleontologists have resisted inventing an array of new genera for the psittacosaurs suggests that excessive splitting in some dinosaur groups, excessive lumping in other groups, and doing it right in some is a matter of habit that develops in different cases. Following the idea of getting things just right, I call trying to name genera on a more uniform basis the Goldilocks Principle of taxonomy.

I have long realized that **Iguanodon bernissartensis** and "I." atherfieldensis are too different for even an antisplitter like myself to be in the same genus. Not only is the latter much more gracile than the former – in of itself not enough to warrant generic separation -- there are some big differences in detailed anatomy. Most obviously, **Iguanodon bernissartensis** retains a rather primitive, camptosaur like shallow prepubic process of the pubis, while that of "I." atherfieldensis is very deep, and similar to that of hadrosaurs.

There are significant differences in the structure of the lateral process on

the scapula too. These differences are actually greater than seen in the entire Hadrosauridae. No way that they can be the same genus. So, back when Ronnie was president, I decided I would give a new name to I. bernissartensis, one that would give recognition to its describer Dollo. Never did get around to it, kept putting it off. This procrastination, the sort of intellectual idleness regularly condemned as slothful inaction, proved to be a very good thing that saved my taxonomic behind. Had I renamed the robust Bernissart iguanodont then, there is little doubt that the new generic title would have been deliberately targeted and killed by the ICZN ruling for Iguanodon the same way Rioarribasaurus was done in by the earlier ICZN decision in favor of Coelophysis. It would have been a mess. Let that be a lesson, sometimes it is better to be lazy.

But the ICZN ruling does nothing to solve the basic problem that more than one iguanodont genus is present in the Bernissart quarry, as well as late Barremian and early Aptian of Northern Europe. So I simply shifted my attention to "I." atherfieldensis and gave it a new name that honors the Mantells in a short paper in Horns and Beaks in 2006.



In doing so, I made a mistake. I assumed as have many others that the English type of Mantellisaurus atherfieldensis and the gracile Bernissart skeleton IRSNB 1551 are the same taxon. But as I continued my research in iguanodont taxonomy I noticed something funny about the ilia of these beasts. Despite all their other differences, the ilia of I. bernissartensis and IRSNB 1551 are alike in being shallow, even though the skeletons are usually preserved flattened from side to side rather than dorso-ventrally. This is different from all other iguanodonts which have deeper ilia more like those of camptosaurs. Hmmm. I became yet more suspicious as other differences between M. atherfieldensis and IRSNB 1551 became apparent. So I did what I should have a long time ago – I have after all, built up the most extensive library of technical dinosaur skeletal illustrations -- and did the first skeletal restoration of the type skeleton of M. atherfieldensis. The results fully verified my growing doubts of synonymy. While the arms of IRSNB 1551 were long enough for it to have run on all fours, those of M. atherfieldensis were so short they could be used only at the slowest speeds. The pelvis of the latter is very large, with the deep ilium. And the skulls are distinct, that of IRSNB 1551 being very elon-

gated, especially in the snout, and having a significant gap between the beaks and the tooth rows. Turns out that IRSNB 1551 is as different from Mantellisaurus atherfieldensis as it is from Iguanodon bernissartensis.

Back when "Iguanodon" lakotaensis was named, I realized it was markedly less derived than I. bernissartensis, the snout of the former is more camptosaur like. It too needed a new name.

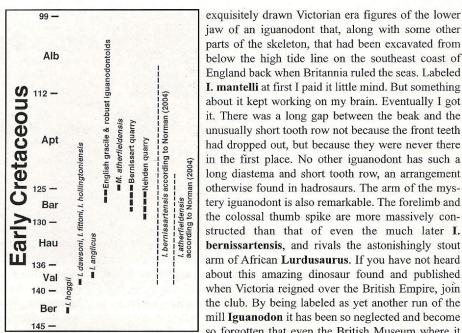
So I ended up conducting an overhaul of the entire group that has been published in Cretaceous Research (2008 29:192-216). The new name for the

gracile Bernissart skeleton is Dollodon bampingi, the genus name being in honor of Dollo. The North American skull is now Dakotadon lakotaensis. It is the first dinosaur named after the state of South Dakota.

The results of all the recent work mean that Iguanodon now consists only of robust iguanodonts restricted to Europe from a narrow time zone. Mantell's much earlier teeth no longer have anything to do with the genus. I. bernissartensis is officially limited to the Bernissart quarry at this time. Some robust remains from Germany can be assigned to Iguanodon, but it cannot be told if they belong to I. bernissartensis or another

species. Over in the former home of Iguanodon, England, the ilium of I. seelyi is similar to and may or may not be the same species as I. bernissartensis. Some other bones in England and Europe from the later Barremian and early Aptian may also be Iguanodon. A very long lower jaw. from England looks like that of **Dollodon**, and can be assigned to the genus. Mantell's partial skeleton can be provisionally assigned to Mantellisaurus atherfieldensis, as can other remains until they too are studied. Down in the old Valanginian "I." dawsoni (which may not be a proper iguanodont) "I." fittoni and "I." hollingtoniensis are not Iguanodon, and require research to decide what is what and assign new generic titles. Other names such as Vectisaurus and Heterosaurus belong to inadequate type specimens that can only be attributed to iguanodonts of uncertain identity. It is important that European specimens no longer be arbitrarily placed in a specific genus or species unless it is well justified, otherwise the fossils should be considered to be indeterminate iguanodonts. The same applies outside of Europe. The Asian I. orientalis is almost certainly not an Iguanodon and is indeterminate.

But wait, there's more! Sometimes I. hoggii is spelled with two i's, other times with one. So I decided to look up the original description by Darwin's bug eyed, intelligent design creationist opponent, Sir Richard Owen, from 1874 and make sure. I got the ancient volume out of the Hopkins library storage and verified the spelling. In the same paper there was one of those



jaw of an iguanodont that, along with some other parts of the skeleton, that had been excavated from below the high tide line on the southeast coast of England back when Britannia ruled the seas. Labeled I. mantelli at first I paid it little mind. But something about it kept working on my brain. Eventually I got it. There was a long gap between the beak and the unusually short tooth row not because the front teeth had dropped out, but because they were never there in the first place. No other iguanodont has such a long diastema and short tooth row, an arrangement otherwise found in hadrosaurs. The arm of the mystery iguanodont is also remarkable. The forelimb and the colossal thumb spike are more massively constructed than that of even the much later I. bernissartensis, and rivals the astonishingly stout arm of African Lurdusaurus. If you have not heard about this amazing dinosaur found and published when Victoria reigned over the British Empire, join the club. By being labeled as yet another run of the mill Iguanodon it has been so neglected and become so forgotten that even the British Museum where it

resides has lost track of its stratigraphic level, although it is clearly from quite early in the Cretaceous. Even worse, the scapula - one of the most diagnostic parts of iguanodonts - was never figured and has since been lost to pyrite's disease. What is left of this fascinating specimen requires research and a new name.

So it turns out that the iguanodonts of Europe are not just about Iguanodon, they were a much more diverse lot than previously realized. It is surprising that it has taken so long to figure this out. How these dinosaurs

were related to one another is obscure. Past cladistic studies have been contaminated by the tendency to combine features from multiple genera into Iguanodon and are obsolete. Although it will be interesting to run phylogenetic studies based on a more accurate tallying of the characters of the various genera, cladistic analysis has only a limited ability to address this problem because of limitations inherent to the methodology. A complex mixture of characteristics that leave each iguanodont genus more derived than the others in some regards and less so in others, it is a clas-

prepubic processes sic example of undirected mosaic evolution, and it is unlikely that the problem can be reliably sorted out. The removal of the South Dakota iguanodont from Iguanodon removes that particular piece of evidence for a close link between North American and European or Asian iguanodonts, although this may represent a lack of sampling that will be filled in by further discoveries out in the field. The other lesson is that there are still a lot of important and exciting discoveries to be made and science to be done by rummaging around in old technical papers.

The characteristics of the three main European species are summarized as follows. Iguanodon bernissartensis (8 m long, over 3 tonnes) Massively constructed, skull rather short and deep, no gap between beaks and main tooth rows, stout arms long so strongly quadrupedal, hand big, thumb spike enormous, ilium shallow, prepubic process of pubis shallow, feet big.

Dollodon bampingi (6.5 m long, 1.1 tonne) Lightly constructed, skull long and low, snout very elongated, gap between beaks and main tooth rows, slender arms moderately long so semi-quadrupedal, hand slender, thumb spike not large, ilium shallow, prepubic process of pubis deep.

Mantellisaurus atherfieldensis (adult size not certain, probably similar to Dollodon) Lightly constructed, skull low, snout moderately elongated, no gap between beaks and main tooth rows, slender arms too short to be used except when moving slowly so strongly bipedal, hand slender, thumb spike not large, ilium deep, prepubic process of pubis deep, toes longer than usual for iguanodonts.

