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Brontosaurus is back!

The iconic long-necked dinosaur was not Apatosaurus after all

Although well known as one of the most iconic dinosaurs, *Brontosaurus* (the 'thunder lizard') has long been considered misclassified. Since 1903, the scientific community has believed that the genus *Brontosaurus* was in fact the *Apatosaurus*. Now, an exhaustive new study by palaeontologists from Portugal and the UK provides conclusive evidence that *Brontosaurus* is distinct from *Apatosaurus* and as such can now be reinstated as its own unique genus.

Brontosaurus is one of the most charismatic dinosaurs of all time, inspiring generations of children thanks to its size and evocative name. However, as every armchair palaeontologist knows, *Brontosaurus* was in fact a misnomer, and it should be correctly referred to as *Apatosaurus*. At least, this is what scientists have believed since 1903, when it was decided that the differences between *Brontosaurus excelsus* and *Apatosaurus* were so minor that it was better to put them both in the same genus. Because *Apatosaurus* was named first, it was the one that was used under the rules of scientific naming.

In fact, of course, the *Brontosaurus* was never really gone - it was simply treated as a species of the genus *Apatosaurus*: *Apatosaurus excelsus*. So, while scientists thought the genus *Brontosaurus* was the same as *Apatosaurus*, they always agreed that the species *excelsus* was different from other *Apatosaurus* species. Now, palaeontologists Emanuel Tschopp, Octávio Mateus, and Roger Benson say that *Brontosaurus* was a unique genus all along. But let's start from the beginning.

The history of *Brontosaurus* is complex, and one of the most intriguing stories in science. In the 1870s, the Western United States formed the location for dozens of new finds of fossil species, most notably of dinosaurs. Field crews excavated numerous new skeletons mostly for the famous and influential palaeontologists Marsh and Cope. During that period, Marsh's team discovered two enormous, partial skeletons of long-necked dinosaurs and shipped them to the Yale Peabody Museum in New Haven, where Marsh worked. Marsh described the first of these skeletons as *Apatosaurus ajax*, the "deceptive lizard" after the Greek hero Ajax. Two years later, he named the second skeleton *Brontosaurus excelsus*, the "noble thunder lizard". However, because neither of the skeletons were found with a skull, Marsh reconstructed one for *Brontosaurus excelsus*. *Brontosaurus* was a massive animal, like *Apatosaurus*, and like another long-necked dinosaur from the Western United States, *Camarasaurus*. Because of this similarity, it seemed logical at the time that *Brontosaurus* had a similarly stout, box-like skull to that of *Camarasaurus*. However, this reconstruction was later found to be wrong.

Shortly after Marsh's death, a team from the Field Museum of Chicago found another skeleton similar to both *Apatosaurus ajax* and *Brontosaurus excelsus*. In fact, this skeleton was intermediate in shape in many aspects. Therefore, palaeontologists thought that *Brontosaurus excelsus* was actually so similar to *Apatosaurus ajax* that it would be more correct to treat them as two different species of the same genus. It was the second extinction of *Brontosaurus* – a scientific one: from now on, *Brontosaurus excelsus* became known as *Apatosaurus excelsus* and the name *Brontosaurus* was not considered scientifically valid any more.

The final blow to "*Brontosaurus*" happened in the 1970s, when researchers showed that *Apatosaurus* was not closely related to *Camarasaurus*, but to yet another dinosaur from the same area: *Diplodocus*. Because *Diplodocus* had a slender, horse-like skull, *Apatosaurus* and thus also "*Brontosaurus*" must have had a skull more similar to *Diplodocus* instead of to *Camarasaurus* - and so the popular, but untrue myth about "*Brontosaurus*" being an *Apatosaurus* with the wrong head was born.

But now, in a new study published in the peer reviewed open access journal PeerJ and consisting of almost 300 pages of evidence, a team of scientists from Portugal and the UK have shown that *Brontosaurus* was distinct from *Apatosaurus* after all - the thunder lizard is back!

How can a single study overthrow more than a century of research? "Our research would not have been possible at this level of detail 15 or more years ago", explains Emanuel Tschopp, a Swiss national who led the study during his PhD at Universidade Nova de Lisboa in Portugal, "in fact, until very recently, the claim that *Brontosaurus* was the same as *Apatosaurus* was completely reasonable, based on the knowledge we had." It is only with numerous new findings of dinosaurs similar to *Apatosaurus* and *Brontosaurus* in recent years that it has become possible to undertake a detailed reinvestigation of how different they actually were.

In science, the distinction between species and genera is without clear rules. Does this mean that the decision to resurrect *Brontosaurus* is just a matter of personal preference? "Not at all", explains Tschopp, "we tried to be as objective as possible whenever making a decision which would differentiate between species and genus". The researchers applied statistical approaches to calculate the differences between other species and genera of diplodocid dinosaurs, and were surprised by the result. "The differences we found between *Brontosaurus* and *Apatosaurus* were at least as numerous as the ones between other closely related genera, and much more than what you normally find between species," explained Roger Benson, a co-author from the University of Oxford.

Therefore, Tschopp and colleagues have concluded that it is now possible to resurrect *Brontosaurus* as a genus distinct from *Apatosaurus*. "It's the classic example of how science works", said Professor Mateus, a collaborator on the research. "Especially when hypotheses are based on fragmentary fossils, it is possible for new finds to overthrow years of research."

Science is a process, always moving towards a clearer picture of the world around us. Sometimes this also means that we have to step backwards a bit before we continue to advance. That's what keeps the

curiosity going. Hence, it is fitting that the *Brontosaurus* which sparked the curiosity of millions of people worldwide has now returned to do so again.

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Images:

Note: Full size versions of these images, plus additional images, are available here (http://goo.gl/gPqfpi)

Life restoration: "*Brontosaurus* as researchers see it today – with a *Diplodocus*-like head"
Credit: Davide Bonadonna, Milan, Italy. Creative commons license CC- BY NC SA.
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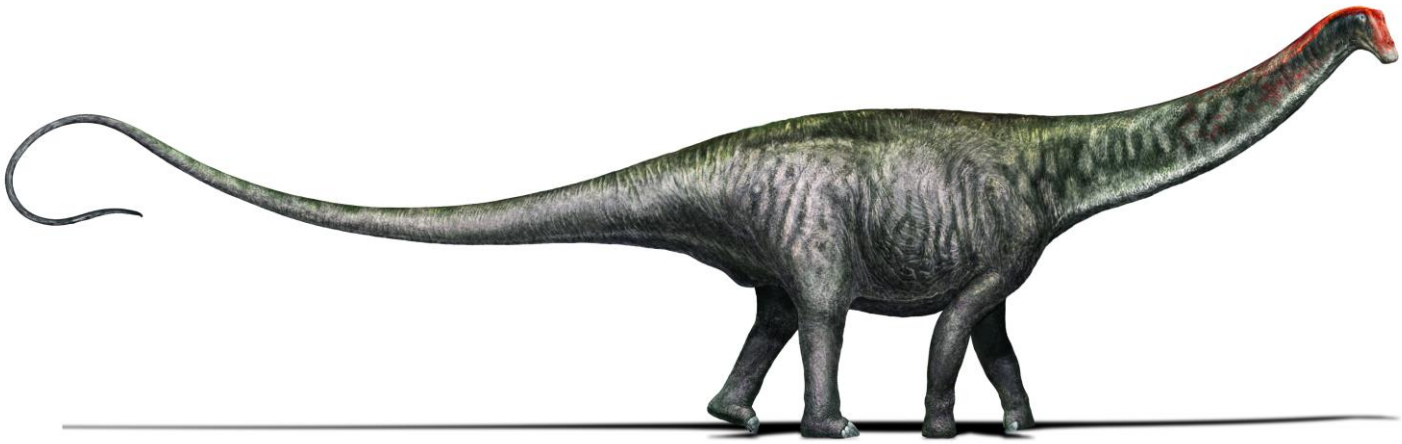

Infographic: "The history of *Brontosaurus* – one of the greatest stories in paleontology"
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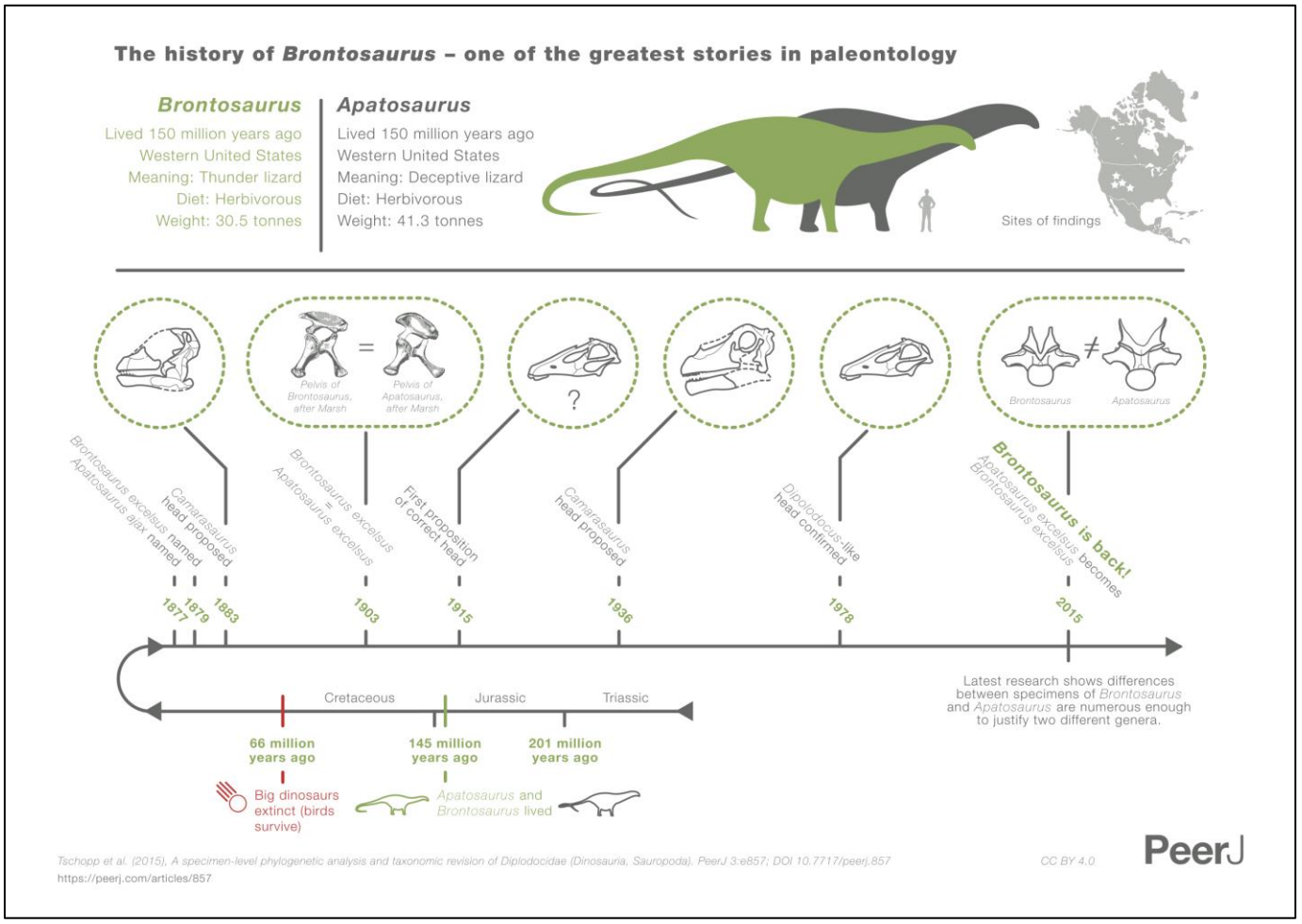

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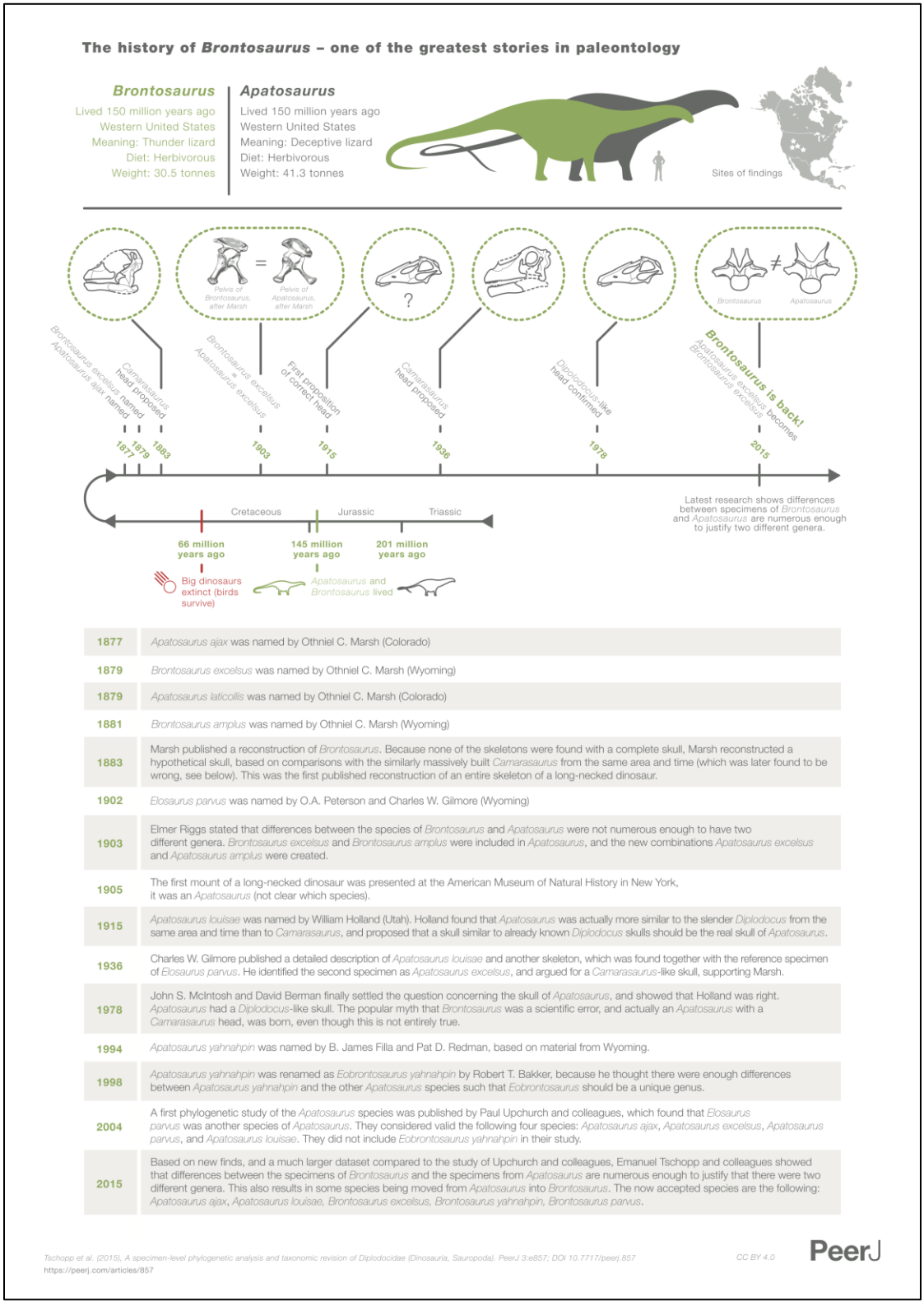

1877	*Apatosaurus ajax* was named by Othniel C. Marsh (Colorado)
1879	*Brontosaurus excelsus* was named by Othniel C. Marsh (Wyoming)
1879	*Apatosaurus laticollis* was named by Othniel C. Marsh (Colorado)
1881	*Brontosaurus amplus* was named by Othniel C. Marsh (Wyoming)
1883	Marsh published a reconstruction of *Brontosaurus*. Because none of the skeletons were found with a complete skull, Marsh reconstructed a hypothetical skull, based on comparisons with the similarly massively built *Camarasaurus* from the same area and time (which was later found to be wrong, see below). This was the first published reconstruction of an entire skeleton of a long-necked dinosaur.
1902	*Elosaurus parvus* was named by O.A. Peterson and Charles W. Gilmore (Wyoming)
1903	Elmer Riggs stated that differences between the species of *Brontosaurus* and *Apatosaurus* were not numerous enough to have two different genera. *Brontosaurus excelsus* and *Brontosaurus amplus* were included in *Apatosaurus*, and the new combinations *Apatosaurus excelsus* and *Apatosaurus amplus* were created.
1905	The first mount of a long-necked dinosaur was presented at the American Museum of Natural History in New York, it was an *Apatosaurus* (not clear which species).
1915	*Apatosaurus louisae* was named by William Holland (Utah). Holland found that *Apatosaurus* was actually more similar to the slender *Diplodocus* from the same area and time than to *Camarasaurus*, and proposed that a skull similar to already known *Diplodocus* skulls should be the real skull of *Apatosaurus*.
1936	Charles W. Gilmore published a detailed description of *Apatosaurus louisae* and another skeleton, which was found together with the reference specimen of *Elosaurus parvus*. He identified the second specimen as *Apatosaurus excelsus*, and argued for a *Camarasaurus*-like skull, supporting Marsh.
1978	John S. McIntosh and David Berman finally settled the question concerning the skull of *Apatosaurus*, and showed that Holland was right. *Apatosaurus* had a *Diplodocus*-like skull. The popular myth that *Brontosaurus* was a scientific error, and actually an *Apatosaurus* with a *Camarasaurus* head, was born, even though this is not entirely true.
1994	*Apatosaurus yahnahpin* was named by B. James Filla and Pat D. Redman, based on material from Wyoming.
1998	*Apatosaurus yahnahpin* was renamed as *Eobrontosaurus yahnahpin* by Robert T. Bakker, because he thought there were enough differences between *Apatosaurus yahnahpin* and the other *Apatosaurus* species such that *Eobrontosaurus* should be a unique genus.
2004	A first phylogenetic study of the *Apatosaurus* species was published by Paul Upchurch and colleagues, which found that *Elosaurus parvus* was another species of *Apatosaurus*. They considered valid the following four species: *Apatosaurus ajax*, *Apatosaurus excelsus*, *Apatosaurus parvus*, and *Apatosaurus louisae*. They did not include *Eobrontosaurus yahnahpin* in their study.
2015	Based on new finds, and a much larger dataset compared to the study of Upchurch and colleagues, Emanuel Tschopp and colleagues showed that differences between the specimens of *Brontosaurus* and the specimens from *Apatosaurus* are numerous enough to justify that there were two different genera. This also results in some species being moved from *Apatosaurus* into *Brontosaurus*. The now accepted species are the following: *Apatosaurus ajax*, *Apatosaurus louisae*, *Brontosaurus excelsus*, *Brontosaurus yahnahpin*, *Brontosaurus parvus*.

Tschopp et al. (2015), A specimen-level phylogenetic analysis and taxonomic revision of Diplodocidae (Dinosauria, Sauropoda). PeerJ 3:e857; DOI 10.7717/peerj.857
https://peerj.com/articles/857

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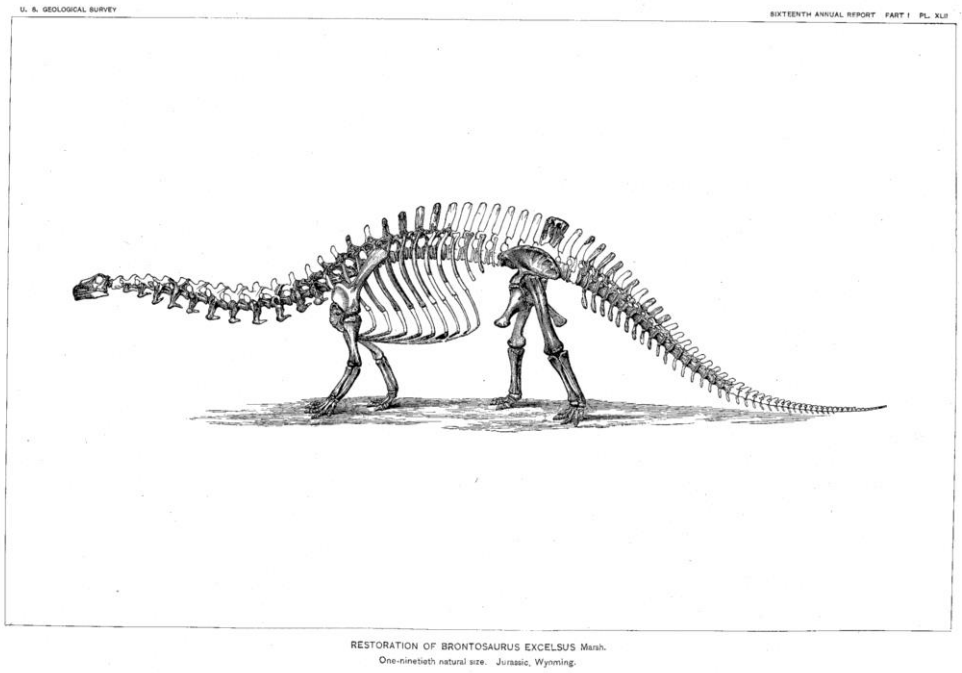
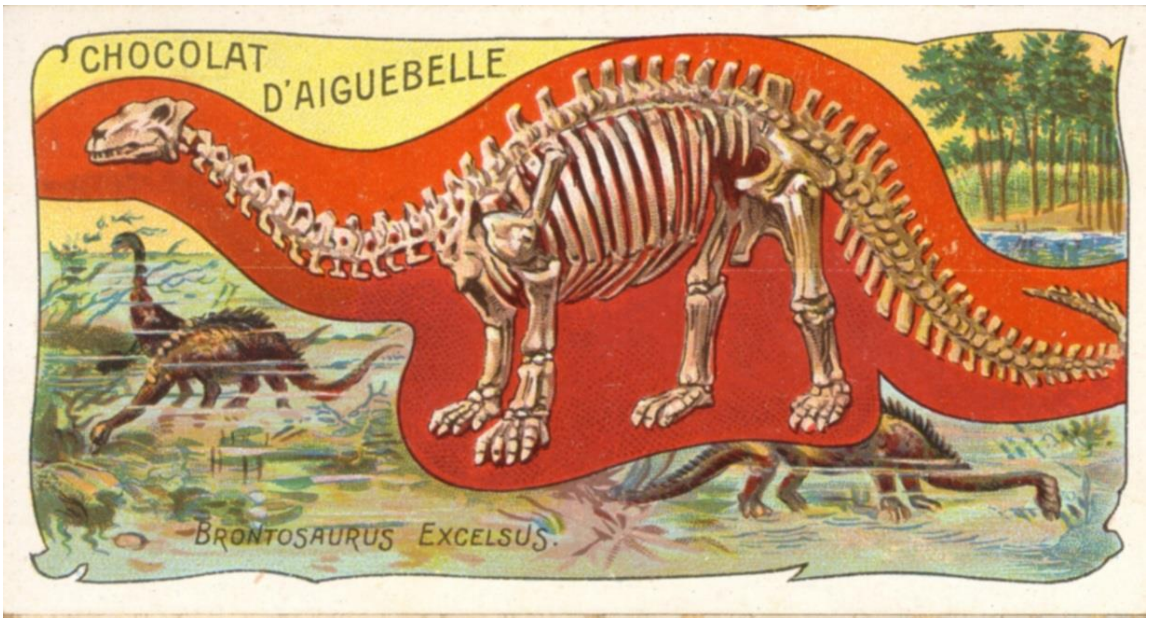
Historic image: "A reconstruction of the skeleton of *Brontosaurus excelsus* with the wrong, *Camarasaurus*-like skull". Published by OC Marsh, 1896, now in public domain, available here: http://www.copyrightexpired.com/earlyimage/bones/display_marsh_brontosaurus.htm



Historic life restoration: "*Brontosaurus* as researchers imagined it in the late 1800s: aquatic, and with a large, robust skull". Artist unknown, image in public domain, available here: http://www.copyrightexpired.com/earlyimage/bones/large/display_daiguebelle_brontosaurus.htm



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Abstract (from the article):

Diplodocidae are among the best known sauropod dinosaurs. Several species were described in the late 1800s or early 1900s from the Morrison Formation of North America. Since then, numerous additional specimens were recovered in the USA, Tanzania, Portugal, and Argentina, as well as possibly Spain, England, Georgia, Zimbabwe, and Asia. To date, the clade includes about 12 to 15 nominal species, some of them with questionable taxonomic status (e.g., '*Diplodocus*' *hayi* or *Dyslocosaurus polyonychius*), and ranging in age from Late Jurassic to Early Cretaceous. However, intrageneric relationships of the iconic, multi-species genera *Apatosaurus* and *Diplodocus* are still poorly known. The way to resolve this issue is a specimen-based phylogenetic analysis, which has been previously implemented for *Apatosaurus*, but is here performed for the first time for the entire clade of Diplodocidae. The analysis includes 81 operational taxonomic units, 49 of which belong to Diplodocidae. The set of OTUs includes all name-bearing type specimens previously proposed to belong to Diplodocidae, alongside a set of relatively complete referred specimens, that increase the amount of anatomically overlapping material. Non-diplodocid outgroups were selected to test the affinities of potential diplodocid specimens that have subsequently been suggested to belong outside the clade. The specimens were scored for 477 morphological characters, representing one of the most extensive phylogenetic analyses of sauropod dinosaurs. Character states were figured and tables given in the case of numerical characters. The resulting cladogram recovers the classical arrangement of diplodocid relationships. Two numerical approaches were used to increase reproducibility in our taxonomic delimitation of species and genera. This resulted in the proposal that some species previously included in well-known genera like

Apatosaurus and *Diplodocus* are generically distinct. Of particular note is that the famous genus *Brontosaurus* is considered valid by our quantitative approach. Furthermore, "*Diplodocus*" hayi represents a unique genus, which will herein be called *Galeamopus* gen. nov. On the other hand, these numerical approaches imply synonymization of "*Dinheirosaurus*" from the Late Jurassic of Portugal with the Morrison Formation genus *Supersaurus*. Our use of a specimen-, rather than species-based approach increases knowledge of intraspecific and intrageneric variation in diplodocids, and the study demonstrates how specimen-based phylogenetic analysis is a valuable tool in sauropod taxonomy, and potentially in paleontology and taxonomy as a whole.