Journal of Geek Studies

jgeekstudies.org

Steampunk dinosaurs and Victorian-era palaeontology

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When watching, reading or playing works of fiction, we are the type of biologists who get annoyed with silly mistakes. Like when a movie has a bird sound that's not appropriate to the region or that belongs to a different bird species than shown; common cases include the screaming piha, the loon and the bald eagle vs red-tailed hawk, which have become more of common knowledge of late (Vox, 2021; Eberwein, 2025). We understand that sometimes choices are made in detriment to real-world biology, like Robin's robin in *Honkai: Star Rail* (Salvador, 2024), and that is absolutely fine. Still, it can be quite disappointing when mistakes could have been prevented with a five-second Google search, like the other Robin's robin in *Fate/Grand Order* (Salvador, 2024; Salvador & Tomotani, 2024)[1] or the many issues with the recent dinosaur films (e.g., Igielman, 2022).

On the other hand, we cannot help but beam with happiness when creators hit a biological nail right on its head. That was the case with a dinosaur depiction in an anime we recently watched, Chapter 2 of *Princess Principal: Crown Handler* (by Actas, 2021). Granted, it is a very minor appearance with no relevance to the plot whatsoever, but still, there is such an interesting story behind it that we just had to write about it.

DINOS & DRAGONS

Princess Principal is set in Albion, a fictional steampunk analogue of early 20th-century Britain. The original anime series aired in 2017 and now the *Crown Handler* series is being released as six films (we're currently in the 4th one). The story follows a group of five girls doing spy things; during *Crown Handler* Chapter 2, they go to the theatre during an investigation. And here, the small details included on this scene makes all the difference (Fig. 1).

In front of the theatre there are two lizard-like statues. Chise doesn't know what they are, so Ange explains to her that they are extinct animals called dinosaurs. Seems straightforward enough, but there are a couple of things to unpack here. First, while the British public at that time was familiar with dinosaurs (more on that later), that was not necessarily the case elsewhere, including Japan, where Chise comes from.[2] Secondly, while the statues might look

[1] Not to mention the fact that FGO writers did not know that South America and Central America are two different things, and that Mexico is located in neither of them.

Cite this article as: Salvador, R.B. & Tomotani, B.M. (2025) Steampunk dinosaurs and Victorian-era palaeontology. Journal of Geek Studies 12(2): 127-136. https://doi.org/10.5281/zenodo.17559145

weird given our current understanding of dinosaurs, it is spot on for the period in which the anime takes place (more on that later as well). Of course, there are some nice "extra" touches, like the steam coming out of the statues' nostrils, which is at the same time very steampunky and in line with the dragon theme of the play at the theatre.

The dinosaur depicted in the anime is Iguanodon, and its weird lizard-like appearance with a horn on its nose was just the first iteration of one of the most revised and reinterpreted dinosaurs in the history of palaeontology.

Figure 1. The team arrives at the theatre and are greeted by two dinosaur statues. Images are screen captures of the film.

DISCOVERY AND NAMING

In the early 19th century, the British (and the European scientific community at large) were becoming acquainted with fossils of large reptilian animals, largely thanks to Mary Anning (Fig. 2), who was unearthing plesiosaurs and ichthyosaurs in Lyme Regis (Fallon, 2020; Salvador, 2021). Still, some fossils were very puzzling and didn't seem to fit well with other then known reptiles. Those included a handful of bones, teeth, and fragments that were later described as *Megalosaurus* (Buckland, 1824), *Iguanodon* (Mantell, 1825), and *Hylaeosaurus* (Mantell, 1833).

In 1842, the naturalist Richard Owen coined the name 'Dinosauria' for a new animal group that could house all those weird fossils, including carnivorous and herbivorous "reptilian" animals (Costantino, 2015).[3] That kick-started discussions and studies about such "new" animals, fuelled by more discoveries being made around the world. And *Iguanodon* has been in the centre of discussions ever since.

[2] While current paleontological advances started to become available in Japan during the Meiji era, alongside some stories like Julio Verne's gaining traction, the more "mainstream" dinosaur boom in Japan came in the 1980s with the amazing new discoveries that were happening in Fukui, now known as the Dinosaur Kingdom (Matsukawa et al., 2006; Fukui Station Dinosaur Area Portal Site, 2024). Technically, the first dinosaur discovered in Japan was *Nipponosaurus sachalinensis*, but it was found in Sakhalin (Nagao, 1936), which is now part of Russia.

[3] The name first appeared in 1841 in a talk to the British Association for the Advancement of Science. The proceedings of that meeting were published in the following year (Owen, 1842: 102).

Figure 2. Mary Anning and her fossil discoveries. Well, kinda. This is the artwork (by Riyo) for the Stage 3 ascension of Mary Anning in *Fate/Grand Order*, because we cannot have an article about British palaeontology and not talk about her. Source: Fate/Grand Order Wiki.

Figure 3. The original illustration of *Iguanodon's* teeth, with a comparative figure of an iguana's teeth. Source: Mantell (1825).

The first *Iguanodon* fossils came from Whitemans Green. They were rock-embedded teeth and were either found by Gideon Mantell and/or his wife Mary Ann (not Anning!) or acquired from the local quarry around 1820–1821 (Dean, 1999). At first, Mantell thought the teeth belonged to a large crocodile, but soon realized they belonged instead to a very large herbivorous reptile. That was a first, as no prehistoric reptilian herbivores were known so far (Osterloff, 2020). Among the known reptiles, the iguana had the most similar-looking teeth, although the fossils were many times larger. Thus, the new fossil species was named *Iguanodon* (that is, "iguana tooth") by Mantell in 1825 (Fig. 3).[4]

In the years that followed, Mantell kept looking for more fossils, but found only more teeth and isolated and fragmentary bones (Osterloff, 2020). Then, nearly a decade later, in 1834, mine workers found a more complete specimen of *Iguanodon* in Maidstone.[5] Mantell travelled to Maidstone to study the new specimen, which was used as the basis for the first attempt to reconstruct this extinct animal's skeletal structure –and also for the first artistic renderings of the species (Fig. 4). Still, the fossil was in a rather poor shape and led to some misinterpretations, the most infamous of which was the horn. *Iguanodon* was reconstructed as having a horn on its nose, like a rhino (remember the depiction in *Crown Handler*;

[4] Weirdly, Mantell did not provide the full binomial that is needed for a species scientific name (like *Homo sapiens*). That was later coined by Holl (1829): *Iguanodon anglicus*.

[5] This specimen is now considered to belong to a different species in a related genus, namely *Mantellisaurus atherfieldensis* (Norman, 2013).

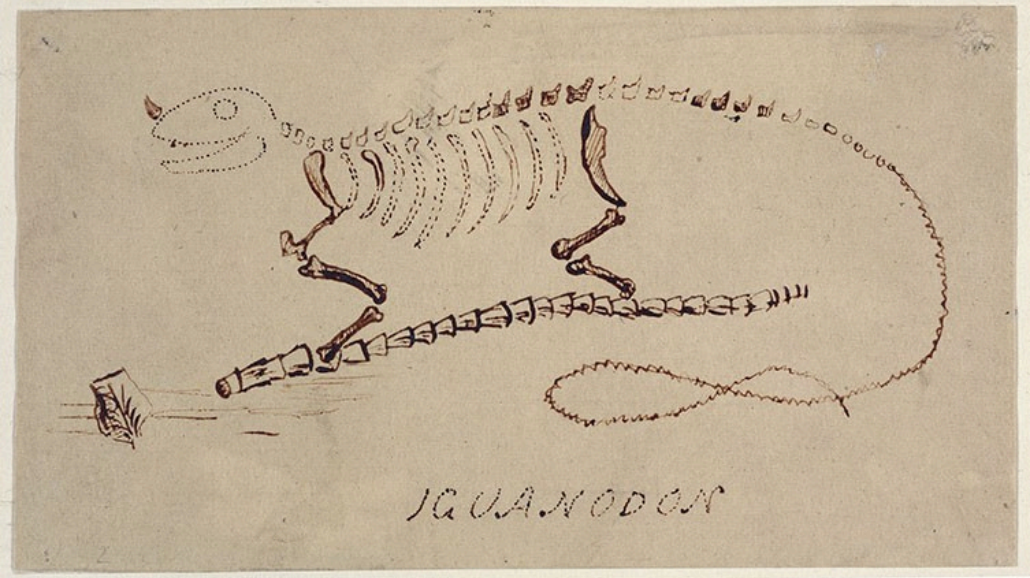

Figure 4. Mantell's reconstruction of *Iguanodon* would have looked like based on the Maidstone fossil and the anatomy of living reptiles. Source: Natural History Museum (public domain).

Fig. 1). Years later, better preserved fossils showed that the "horn" was actually a modified thumb, but that was not an easy thing to imagine back in the early days of dinosaur research. Speaking of which, in a sense it was Mantell who started scientific research on dinosaurs as he tried, along a series of published papers (e.g., Mantell, 1848, 1851a), to understand *Iguanodon* and imagine how it lived back in the Cretaceous Period.

THE CRYSTAL PALACE

By the late 1940s and early 1950s, Mantell was clashing against Owen regarding *Iguanodon*. Owen was a creationist and believed that the Biblical god had created dinosaurs to be elephant-like or rhino-like creatures.[6] Mantell, however, knew that couldn't be so, as *Iguanodon* had slender forelimbs and thus, should walk, move and live in a completely different manner (Mantell, 1851b; Dean, 1999). Mantell died in 1852, an event that resulted in Owen's interpretation of *Iguanodon* becoming accepted and established for the following decades, in no small part thanks to the Crystal Palace dinosaur sculptures.

Such sculptures were commissioned in 1852 to mark the Crystal Palace's move to its new location in London. They were made by Benjamin Waterhouse Hawkins, who counted with scientific advice of none other than Owen (McCarthy & Gilbert, 1994). When unveiled to the public in 1854, they were the world's first sculptures of extinct animals and should represent the latest scientific knowledge of Victorian palaeontology (Osterloff, 2023). They included species from 15 genera of extinct animals (only three of which are actual dinosaurs, by the way). Today, we know the sculptures reflect the many mistakes of early palaeontology, of which the most notable example is perhaps Owen's interpretation of *Iguanodon* (Fig. 5; the wrongly positioned horn/thumb was Mantell's fault, though). Although many people would

[6] Owen appears in *Assassin's Creed: Syndicate* (Ubisoft, 2015) as an antagonist in a quest line where the main characters work alongside Charles Darwin. You can read a bit more about him in Salvador (2019).

Figure 5. *Iguanodon* sculptures at the Crystal Palace. Left: before restoration (1995). Right: after restoration (2014). Sources: Wikimedia Commons, respectively (Casliber, 2006; public domain) and FunkMonk (2014; CC BY-SA 2.0).

make fun of such mistakes, that is part of how science advances and our present-day knowledge will no doubt look silly to researchers in the next century.

The sculptures are recognized as having historical importance and were restored in 2002, which attenuated the derpy look of the originals (Fig. 5). The dinosaur sculpture in *Crown Handler* also attenuated that derpiness by giving *Iguanodon* front teeth (Fig. 1), which made it (purposefully or not) look a bit more dragon-like.

IGUANODON 2.0

A better reconstruction of what *Iguanodon* would have looked like had to wait until the end of the 1870s, when nearly complete skeletons of over 30 individuals were discovered in a coal mine in Bernissart, Belgium (Norman, 1980, 2005). These belonged to a new species, *Iguanodon bernissartensis*. On top of the regular research on those new specimens, one skeleton was mounted for public display in Brussels by Louis Dollo (Fig. 6). With access to numerous fossils, Dollo could see that Owen's interpretation was incorrect (Dollo, 1883). Based on what was then known about the somewhat similar Hadrosaurus in North America, Dollo mounted the *Iguanodon* skeleton in a bipedal kangaroo-inspired posture and hypothesized that it was amphibious and used its tail to swim (Godefrolt, 2017).

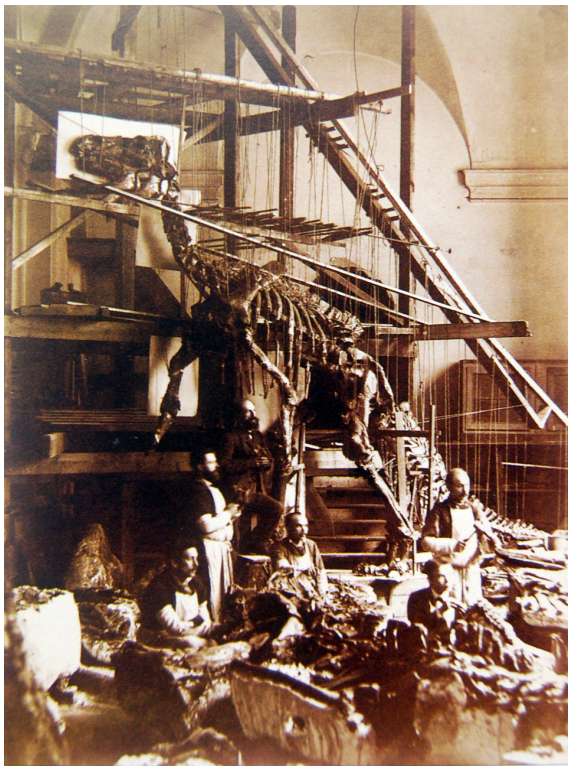

Figure 6. Skeleton of *Iguanodon bernissartensis* being mounted for display in the St. George Chapel in Brussels. Source: Wikimedia Commons (Aimé Rutot, 1882; public domain).

Importantly, Dollo was able to see that the "horn" was actually a modified thumb that looks like a spike (Fig. 7). To this day, palaeontologists still do not know what the hell is going on with this thumb. Some argue that it was used as a defensive weapon; others say it is a specialization for stripping leaves from branches, like the panda's "thumb". In any event, iguanodons' thumbs would have been even larger in life, as the bone could have been covered with keratin (Osterloff, 2020).

Figure 7. The hand of an *Iguanodon* specimen from the Natural History Museum (London, UK) showing the modified spike-like thumb. In all honesty, it does look like a horn or something similar. Source: Wikimedia Commons (Ballista, 2006; CC BY-SA 3.0).

After that, research on *Iguanodon* slowed down as interest in it waned, and wars, economic depression, and the rise of fascism changed the priorities in Europe away from dinosaurs. Then, as it is widely known, a "dinosaur renaissance" started around the 1960s, when new data and fresh research started to indicate that dinosaurs were not sluggish overgrown lizards but rather active warm-blooded animals (Bakker, 1986). Such reinterpretation started to show dinosaurs under a different light, as animals capable of complex behaviours like forming social structures and caring for their young (for instance, *Maiasaura* is the classic example of parental care; Horner & Makela, 1979). It took a while, but eventually, in the 1980s, the renaissance movement reached *Iguanodon*.

New research was done in skeletal anatomy, providing new ideas on topics like feeding mechanisms, posture and movement. Among the palaeontologists studying *Iguanodon*, David Norman was perhaps the most prolific and active (see, for instance, Norman, 1980, 1986). One major realization was that Dollo's kangaroo posture was impossible, because it required a flexible tail; the fossils clearly showed that the tail of iguanodons was straight and could not bend the way Dollo displayed. Thus, the new reconstructions have iguanodons as terrestrial animals walking with their body and tail held parallel to the

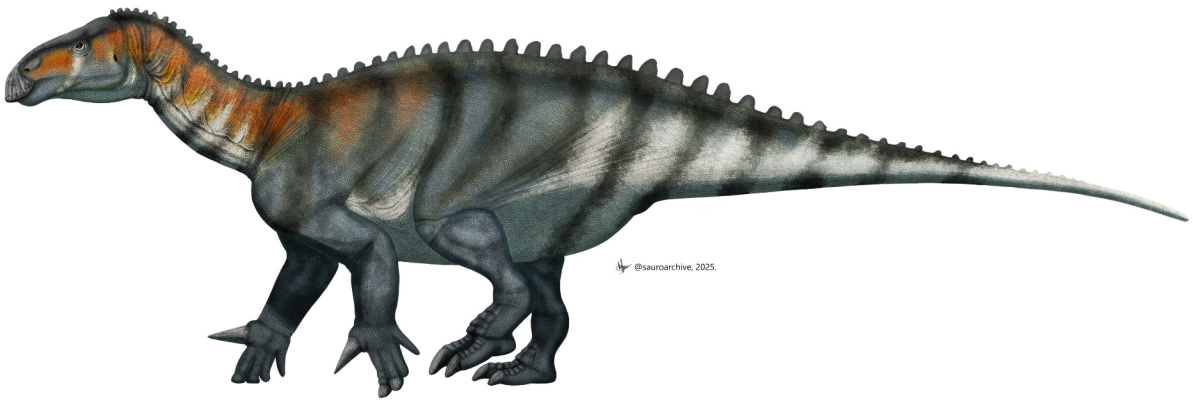

Figure 8. Modern reconstruction of *Iguanodon bernissartensis*. Source: Wikimedia Commons (Sauroarchive, 2025; CC BY 4.0).

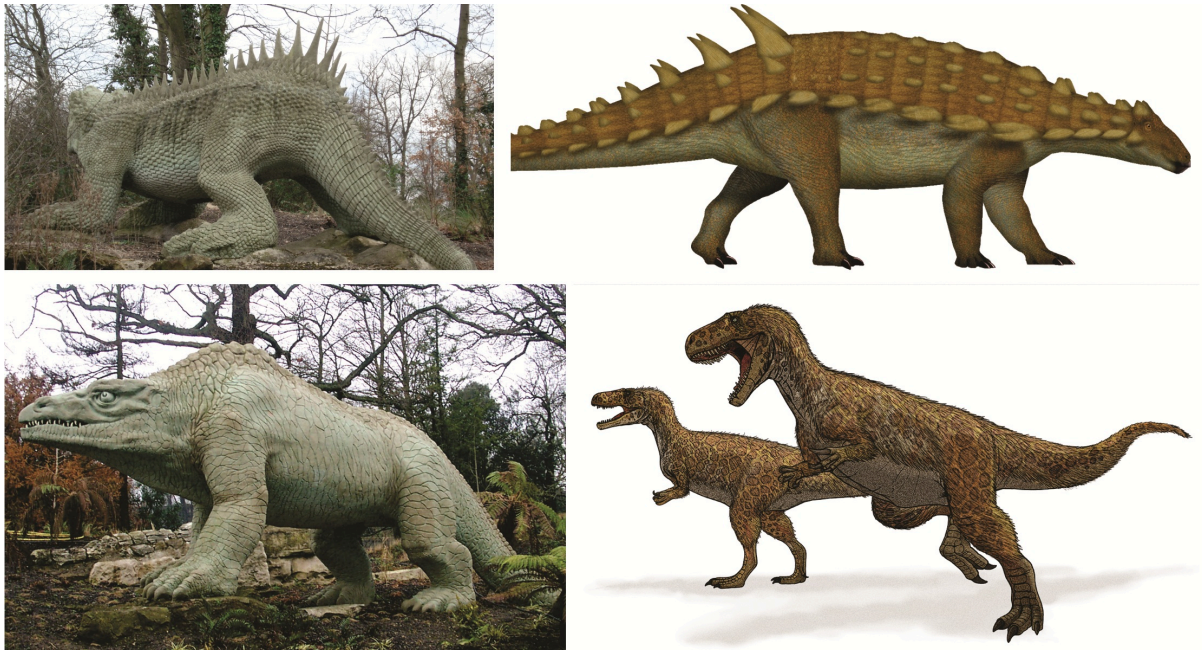

Figure 9. Crystal Palace dinosaur sculptures and modern interpretations of the animals. Top row: *Hylaeosaurus*. Bottom row: *Megalosaurus*. Sources: Wikimedia Commons (cropped), from top left respectively FunkMonk (2008; CC BY-SA 2.0), TotalDino (2023: CC BY-SA 4.0), CGP Grey (2005; CC BY 2.0), LadyofHats Mariana Ruiz (2006; public domain).

ground, and with arms offering further support to the body (Fig. 8). There were also discoveries about their behaviour, as rich fossiliferous deposits in Nehden, Germany, showed that iguanodons were gregarious animals (Norman, 1987).

Iguanodon was not the only one that went through reinterpretations over the decades. So, it is interesting to see how those other dinosaur reconstructions from the Crystal Palace compare to modern "post-renaissance" interpretations (Fig. 9).

FINAL THOUGHTS

Iguanodon, while not as well immediately recognizable to the public like T-rexes, stegosaurs and triceratopses, are still rather common in pop culture from Arthur Conan Doyle's *The Lost World* (1912) to Disney's *Dinosaur* (2000) and *Jurassic World Dominion* (Universal Pictures, 2022). They have long been present as collectibles too, starting perhaps with the cards in German chocolate bars during the 1900s–1910s (Fig. 10) and continuing to present-day gashapon miniatures (Fig. 11).

Box 1. A jumble of names

In the 200 years since its original description, the genus Iguanodon had many new species added to it. Some have remained in it, like *I. bernissartensis* and *I. galvensis* (described in 2015 from Spain; Verdu et al., 2015, 2018). Many have been transferred to other genera, like *I. atherfieldensis*, which became *Mantellisaurus atherfieldensis* (Paul, 2007) and includes the Maidstone specimen formerly thought to be *I. anglicus*. Such reassignments were due to anatomical features observed in the fossils and differences in the geological times in which they lived (e.g., Norman, 2010, 2013) – and due the penchant of vertebrate palaeontologists for oversplitting species and naming "new" species. Case in point, many putative new species described along the years have been synonymised with other previously known species (e.g., Norman, 2013).

Curiously, many fossils identified as the original *I. anglicus* were shown to belong to other species; *I. anglicus* itself is known only by teeth and it is considered a problematic species (a nomen dubium in the jargon). That led palaeontologists Charig & Chapman (1998) to select *I. bernissartensis*, represented by numerous complete skeletons, as the type species of the genus *Iguanodon* in detriment to *I. anglicus*, which was the first species described.

Figure 10. Painting by Heinrich Harder (c. 1916) of a group of iguanodons, part of a series of collector cards sold alongside chocolate bars. Source: Wikimedia Commons (public domain).

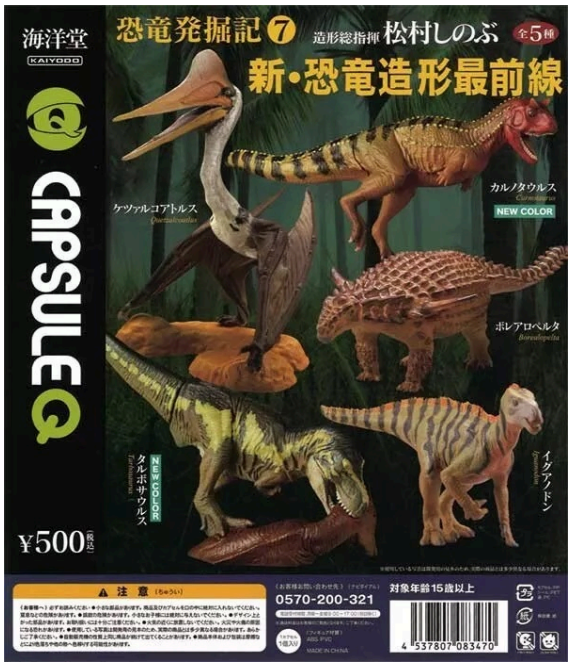

Figure 11. Advertisement of Kaiyodo's gashapon set from including an iguanodon (bottom right corner). Source: KAIYODO (2019).

Popular takes on iguanodons have largely followed the many changes in interpretation, from elephant-like to kangaroo-like, from terrestrial to amphibious, and finally to the modern reconstruction. While today's iguanodons are agile bipedal animals, we cannot help but think that there is a certain charm to the fat dragon-like reconstruction of the Crystal Palace and *Crown Handler*. Case in point, even the King of Monsters took inspiration from the old iguanodons (Tsutsui, 2004), so we are certainly not alone in thinking that.

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About the authors

Dr Rodrigo B. Salvador is a curator in the Finnish Museum of Natural History. While his past research was mostly in palaeontology, nowadays he is mostly studying the present-day fauna. He even had a brief stint studying dinosaurs but soon left that toxic research community behind. He loves steampunk and is always on the lookout for new titles to watch, play or read. By the way, could someone give these dinosaurs top hats and monocles, please? That should improve each and every palaeoart reconstructions.

Dr Barbara M. Tomotani is a researcher in the Arctic University of Norway who has actually not seen the anime. However, she is in this article not because she has done some research on extinct dinosaurs before and neither because she studies the living fluffball dinosaur known as *Parus major*; no, she is here because this year she spent hundreds of hours playing *Path of Titans* as a *Latenivenatrix*, which made her go through her many old dinosaur books.