DOI:
10.1007/s40656-018-0187-0

RECONSTRUCTING AN INCOMPARABLE ORGANISM

The Chalicothere in nineteenth and early-twentieth century palaeontology

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ABSTRACT

Palaeontology developed as a field dependent upon comparison. Not only did reconstructing the fragmentary records of fossil organisms and placing them within taxonomic systems and evolutionary lineages require detailed anatomical comparisons with living and fossil animals, but the field also required thinking in terms of behavioural, biological and ecological analogies with modern organisms to understand how prehistoric animals lived and behaved. Yet palaeontological material often worked against making easy linkages, bringing a sense of mystery and doubt. This paper will look at an animal whose study exemplified these problems: the Chalicotheres. Increasingly (although not unproblematically) recognized as a specific type from finds across North America and Eurasia from the early nineteenth century onwards, these prehistoric mammals showed short back legs terminating in pawed feet, long front limbs ending in sharp claws, a long flexible neck, and herbivorous grinding teeth. The Chalicothere became a significant organism within palaeontological studies, as the unexpected mix of characters made it a textbook example against the Cuvierian notion of "correlation of parts," while explaining how the animal moved, fed and behaved became puzzling. However, rather than prevent comparisons, these actually led to comparative analogies becoming flexible and varied, with different forms of comparison being made with different methods and degrees of confidence, and with the anatomy, movement and behaviour of giraffes, bears, horses, anteaters, primates and other organisms all serving at various points as potential models for different aspects of the animal. This paper will examine some of the attempts to reconstruct and define the Chalicotheres across a long timescale, using this to show how multiple comparisons and analogies could be deployed in a reconstructive and evolutionary science like palaeontology, and illustrate some of the limits and tensions in comparative methods, as they were used to reconstruct organisms which were thought to be incomparable to any modern animal.

KEYWORDS
Evolution; *Moschops*; mammals; Cuvier; correlation; analogy; homology.

INTRODUCTION

Of all the extinct animals uncovered and reconstructed by palaeontology in the nineteenth and early-twentieth centuries, some of the most problematic were the Chalicotheres.[1] Eventually classed as almost oxymoronic 'clawed ungulates,' the Chalicotheres combined teeth and jaws seemingly adapted for eating vegetation, with strangely proportioned limbs ending in large and fearsome claws. Described by one leading early-twentieth century palaeontologist as 'wonderfully aberrant' and 'as grotesque a creature as could well be imagined and, in advance of experience, no one ever did imagine such a beast (Scott 1913),' the Chalicothere was a problematic type, and a source of palaeontological doubt, difficulty and puzzlement. As a variety of fossil remains were slowly unified and consolidated into this order of large fossil mammals, which had lived across the Tertiary era in all continents bar Australia and Antarctica, different approaches and forms of comparison were brought in to understand these creatures. Across all of this, the language of strangeness persisted. Even after the apparent resolution of particular problems, the sense of doubt and difficulty remained acute. This paper traces these developments, examining how the reconstruction of the Chalicothere demonstrates some of the varied forms of comparison used in the nineteenth and early-twentieth century life sciences, and the varying degrees of confidence and authority which these could potentially deploy.

Palaeontology developed over the nineteenth and twentieth centuries as a subject which depended on comparisons to classify and reconstruct species and environments across geological time (Cohen, 2011; Rieppel, 2012; Rudwick 1976; Rudwick, 2014). The comparisons made by palaeontologists could take a variety of forms, and be made with a range of purposes and claims to authority. Some forms of comparison could be homological, arguing that the structure of an organism was identical in origin to that of another organism, and reflect either the same 'nature' or relatedness in an evolutionary manner. Other types of comparison could be more analogical, arguing that structures

[1] As this article will highlight, the taxonomic description of the Chalicotheres underwent considerable revaluation over the period being considered. This paper will broadly use the term 'Chalicothere' to refer to the family as a whole, and refer to lower taxonomic ranks by their genus or species names.

could be different in origin or nature, but serve the same function or purpose, and therefore be useful to reconstruct an organisms habits or modes of life. Additionally, the scale and purpose of the comparison – whether it was based on just key physical characteristics, on the amount fossil evidence available, on an attempted complete reconstruction of the animal, on an understanding of the animal 'in life' or in its environment, or of an entire evolutionary lineage – varied a great deal. Comparisons could be highly multivalent, building analyses and informing reconstructions or theories. Which form of comparison could be used in particular contexts, which characteristics were felt to have precedence over others when making these comparisons, and how much authority and truth underlay these claims, could vary significantly between palaeontological observers depending on their purposes, agendas, methods and theoretical conceptions.

A particularly important issue within this was authority, reliability and the risk of 'speculation.' As Lukas Rieppel has argued (Rieppel, 2015), nineteenth and early-twentieth century palaeontology was persistently plagued by problems of representation and authority. Palaeontologists were concerned with the need to assert the reliability of the claims they were making and the accuracy of their inferences from the fossil record. Yet they also deployed techniques from art, sculpture and imaginative conjectural reasoning to transform fragmentary fossil evidence into understandings of whole animals (Cohen, 2011). However, this was a tense affair, which was often foiled by the indirectness of much palaeontological evidence and accusations of other scientists (either from other disciplines, or rival palaeontologists), that the researcher was simply making things up or engaging in over-rash speculation. As the field also frequently depended upon appeals to public audiences for funds, resources and recognition, this tension could become particularly acute, as stoking the 'spectacular' or strange side of the discipline for public interest was often felt to lead almost by default to overrash speculation. Strong drives to reign in these potentially damaging elements of palaeontological research, as well as using accusations of over-hasty speculation to build one's own authority or belittle one's rivals, were a common feature within palaeontological discourse.

The reconstructions of the Chalicotheres across the long period from the 1800s until the 1930s illustrate these tensions between the need to reconcile different forms of comparison, and maintain authority through a language of methodological innovation and acknowledged doubt in the life-sciences. How to understand creatures that seemed to be unlike any known modern organism, and how to relate a series of anatomical parts that seemed to parallel pieces of different organisms threw many of these tensions into relief. This article argues that on the one hand, mixing and matching different forms of comparison played an important role in conceptualizing and asserting the validity of the scientific conclusions being made. These reconciliations occurred in a manner which shifted according to the practices of particular researchers, their institutional contexts, and the type, extent, and forms of palaeontological evidence which was being engaged with.

However, beyond this, there was another force at work which can be seen across the long duration being examined: the invocation of mystery, doubt and tentativeness of the conclusions being made. This could play an important role in both couching potentially speculative linkages and inspiring future research. The Chalicothere was not just important as a strange fossil organism that was problematic to interpret, but the very act of highlighting its strangeness, and noting the tentativeness of conclusions which needed to be made about it, could become a way of overcoming the risks of speculation and doubt. Through highlighting the continually ratcheting mysteries around the Chalicotheres, scientists could both engage in often quite tangential comparisons, while maintaining their credibility. This paper will follow these trends across a long period, from the initial researches and construction of the claws of the animal as a 'gigantic pangolin' by Georges Cuvier, to the first skeletal reconstructions produced in France and the United States, to the attempts by the Austrian palaeontologist Othenio Abel to reconstruct Chalicotheres in their early environments, and finally to ideas that living Chalicotheres could still be roaming the plains of East Africa in the 1920s. Across this period, the language of doubt and mystery, and the wide range of forms and subjects of comparison, could be related together, and allowed the tense relations between mystery, authority and speculation to be tempered and negotiated.

PART I: DEFINITION THROUGH COMPARISON

The earliest definitions of the Chalicotheres were closely connected with the initial development of palaeontological research in the early years of the nineteenth century. As Martin Rudwick and others have shown, this was a key period for the formation of the field, as fossils were identified as the remains of extinct animals, and placed within long periods of geological succession and hierarchies within nature. (Rudwick, 2008a, 2005).

The earliest discussion of fossils which were later to be included within the Chalicothere grouping were in the works of Georges Cuvier (Cuvier 1823, 193), the doyen of palaeontology and comparative anatomy in early-nineteenth century France, and often later presented as the founder of the discipline. (Bowler, 1976; Rudwick, 2008b) Cuvier developed a range of methods to understand and classify both living and fossil organisms, from the huge number of specimens of extant animals held in the Muséum d'histoire naturelle in Paris (either dead in its study collections or alive in its Menagerie), to the fossils, casts and illustrations of fossils which were accumulating in the museum stores. Cuvier saw the comparison of key characteristics, most notably those relating to the 'functions' of an organism, as the only reliable manner of classifying both known and unknown creatures.

In his *Recherches sur les ossemens fossile* of the early 1820s, Cuvier described a large claw found in Eppelsheim in the Rhineland, and used his comparative anatomical techniques to extrapolate the animal it ought to have belonged to. While the claw was only a fragment of the creature, it was an important one: Cuvier's method relied on a hierarchical mode of reasoning, which saw anatomical features which were related to functions, particularly the acquisition of food and the organism's interaction with the environment and other creatures, as being the most important for classification. Of the potential characters, claws –which could be used for digging, fighting or catching prey – were given a very value to both understand the creature and classify it. Cuvier analysed the large claw from Eppelsheim and expressly noted how 'nothing better proves the importance of the laws of comparative osteology than the conclusions which can be drawn from this lone fragment … this piece proves that animals existed at former times which are unknown today, disappearing by some sort of catastrophe from the lands they inhabited, and probably annihilated from the surface of the globe.' Through a detailed anatomical comparison with modern claws in the Museum collections, he noted how 'this claw has no other analogues in nature than that of the pangolin, and after the laws of coexistence, it cannot be doubted that the animal will be closely connected with this group of quadrupeds.' (Cuvier 1823, 194) The structure was the same as this modern creature, but much larger. He exclaimed, 'what size it must have been!' before calculating, based on the dimensions of modern pangolins who had claws one-ninth the size of the fossils, that the owner of the claw must have been at least 24 feet long.

Cuvier's argument that the claw was that of a gigantic pangolin illustrates important aspects of his reconstructive methods, and the use of analogy and comparison in early palaeontology. On the one hand, the argument followed the maxim that fossil animals could be reconstructed from single key bones owing to laws of analogy and homology (a subject recently treated in Dawson 2016). Through comparing the size of the claw of the small modern pangolin with the giant claw of its extinct equivalent, a ratio could be constructed to gain the whole size and likely look of the animal. While this gigantic pangolin was clearly strange and spectacular, it was still a recognizable type. There were laws of comparative anatomy, which enabled an extrapolation of the organism from the single claw, and its placement within a particular group of organisms.

This characterization also drew from notions of harmony within nature. Cuvier had made much of his reputation from analyses of the *Megatherium americanum*, a huge fossil South American quadruped with structural affinities to the living tree-sloth. If the past had seen gigantic sloths, why not gigantic pangolins? The notion was not just logical, but drew from assumptions of order and progress within the natural world. A key taxonomic category throughout the nineteenth century was the order of Edentata – 'the toothless ones' – which included the sloth, aardvark, anteater, and pangolin. Named for their reduced dentition, the Edentates were presented as the lowest placental mammals in taxonomies and hierarchies of nature. Whether their toothlessness was due to an original deficiency or was a later degeneration was something debated by palaeontologists and comparative anatomists. However, that the Edentates were a lower type compared to the more sophisticated ruminants, carnivores and proboscideans, who were all defined by complex and specialized teeth which were well-fitted to particular types of food, was strongly implied. This slotted them into notions of consistency across geological eras: the ground sloths showed that the Americas had previously been dominated by large Edentates, which had been swept aside in later ages. This gigantic pangolin demonstrated a European equivalent. Comparisons were therefore not just for reconstructing individual organisms, but could be used to understand much wider principles within the whole natural world.

The emphasis on claws and dentition as defining characters of organisms in comparative anatomy and reconstructive palaeontology fed into how another set of remains were interpreted. In the 1820s, the German palaeontologist Johann Jacob Kaup described fossil teeth and jaws found in Hessen that seemed to have belonged to a new form of 'pachyderm.'[2] This was named *Chalicotherium* – 'the gravel beast' – and described as about the same size as a Javan rhinoceros, and taken to represent a 'new genera of pachyderms which would be placed between *Anopolotherium* and *Palaeotherium*, and which has an affinity with … the tapir.' (Kaup 1832, 5) As with Cuvier's alignment of his fossil claw with the Edentates, these comparisons had strong associations: *Anoplotherium* and *Palaeotherium* were fossil mammals from the Paris basin studied and named by Cuvier, and described as the most ancient and undifferentiated mammals from the beginning of the Tertiary. Meanwhile, the tapir was also often presented as one of the most primitive and undeveloped of modern mammals. This meant that the *Chalicotherium* was marked as low on the scale of nature. Additioanlly, Kaup discovered claws similar to those of Cuvier's gigantic pangolin, but associated these with the *Dinotherium*, a huge mammal which he interpreted as a marsh-dwelling hippo-like creature, mixing together edentate and elephantine characteristics.[3]

Throughout the nineteenth century, further remains were discovered and classed as being like Cuvier's gigantic pangolin and Kaup's gravel beast, often closely together. Numerous jaws and teeth similar to those of *Chalicotherium* were found by the French scholars Albert Gaudry in his excavations in Greece, and Eduoard Lartet in Sansan in southern France. These were often found close to large claws and associated leg-bones, which Gaudry named as belonging to *Ancylotherium* ('the crooked animal') and Lartet as *Macrotherium* ('the large animal'). Both Lartet and Gaudry placed these latter remains within the Edentates (and highlighted them as the only Edentates to be found in Europe), but distinct enough to deserve their own genus. In a joint paper on the finds in Pikermi in Greece, Lartet and Gaudry noted how *Macrotherium* was actually 'closer to the sloths than the pangolins … [although] their form is very strange compared to all that is currently contained in nature.' (Gaudry & Lartet 1856) Beyond Europe, Hugh Falconer also described jaw fragments and teeth of an animal aligned with Kaup's *Chalicotherium* in the Siwalik Hills in India, describing them in 1846 as 'one of the most remarkable and aberrant pachyderms that has yet been met with, either in the fossil or recent state.' (Falconer 1868, 209) The wide geographic scope of palaeontology, and its spreading of information through publications and journal exchanges, ensured that these specimens could be compared across large geographic distances, and the family reconstructed at a distance (Anderson 2013; Podgorny 2013)

[2] The term 'pachyderm' was often used as general category for four-footed herbivores in this period.
[3] The *Dinotherium* would be understood by later scientists as a land-dwelling proboscidean and grouped with the elephants, lacking claw-like feet.

A major shift occurred in the 1880s and 1890s, when scholars began to more closely link the 'pachyderm' teeth and skulls with the 'edentane' claws, arguing that these in fact belonged to the same animal. The most well-documented case was made by Henri Filhol, a fossil collector from Toulouse who gained a stipend from Paris' Muséum d'histoire naturelle to continue the work of Eduoard Lartet in Sansan. Filhol described a diverse woodland fauna of primates, sabre-tooth cats (represented by a particularly fine skull of a *Machairodus*), rhinoceroses, cervids and several types of elephant. At the climax of his description, he featured his account of the *Chalicotherium*, and his resolution of an apparent mystery. He described studying *Chalicotherium* skulls and teeth held in the Muséum in Paris, and noted that – while they certainly had 'ungulate' and 'pachyderm'-like features, they also had edentane qualities, particularly in their undeveloped teeth. The *Macrotherium* similarly seemed to mix ungulate and edentane qualities in its limb-bones and claws. This common mixture of characters within these two sets of remains led him to a possible conclusion:

> I thought that we in palaeontology have perhaps made a truly notable confusion. Could it not be that the bones of that Edentate, which we name *Macrotherium*, belonged to *Chalicotherium*, and that we have up until now placed the head and body of the same beast in two different genera? … The bones of *Macrotherium* were extremely common in Sansan and, if the skeleton of *Chalicotherium* had never been found, the head of *Macrotherium* had also never been found. (Filhol 1892, 298-9)

Filhol raised this in his text as a conceptual possibility, deduced from the known fossil material. However, in his scientific practices, deduction in the museum was not enough: to fully back it up, fieldwork and the acquisition of relatively complete specimens was required. Continuing his narrative, Filhol noted how his prediction had indeed been proved during the excavations: 'my workers one day alerted me that they recognized, at the lower portion of the deposit, some very compressed bones belonging to a large animal.' (Filhol 1892, 299) This complete skeleton showed the claws of the *Macrotherium* united with the head of the *Chalicotherium*. This was therefore a single animal, of strange and mixed qualities.

This idea was not just presented by Filhol. In Lyon, Charles Depéret was readying to make similar claims based on his own researches, and the Swiss-British palaeontologist Charles

Forsyth-Major made similar analogies based on finds in Crete. As such, a number of scientists, independently and almost simultaneously, linked the teeth and claws as belonging to the same animal. The idea was accepted relatively quickly. A notice in *Science* in 1892 by the American palaeontologist Henry Fairfield Osborn (who was later to direct the American Museum of Natural History in New York) noted how *Chalicotherium* 'has attracted unusual attention of late, owing to the discovery by Filhol and independently by Forsyth Major that the foot-bones of *Macrotherium*, which has been considered an Edentate, really belong to *Chalicotherium*.' (Osborn 1892, 276)

The relatively quick acceptance of this alignment can partly be put down to the joint nature of the account, with both British and French scholars making the link. However, it also rested on shifts within palaeontology itself. On the one hand, more evolutionary, or at least developmental, perspectives, were beginning to take hold, which were frequently either postulating or actively searching for animals which could link different categories. While most attention focussed on dramatic instances of this, most notably animals that seemed to link reptiles and birds like *Archaeopteryx* or *Hesperornis*, or reptiles and mammals like the strange fauna of Permian South Africa, connections between different more closely related classes, like different forms of mammal, were also of great interest. An additional point was the increased valuation of fieldwork as a scientific practice in its own right, rather than something which simply supplied museum collections and provided raw material for scholarly conjectures. If remains were discovered alongside one another in the same site, then that was more convincing proof of the animal's structure than comparative deductions. The life of the past needed to be understood in the specific context of its geology and excavation.

The above story of early misidentification also became important in its own right: in fact, the story of the Chalicothere became a key warning within the discipline in the twentieth century, expressly used to counter the notion that single bones could used to reconstruct whole organisms. The narrative of the 'discovery' of *Chalicotherium* was frequently recounted by William Berryman Scott, Professor of Geology at Princeton, who would note how 'the tale of these discoveries ought to put an end to the foolish notion that the palaeontologist can reconstruct a lost animal from a single bone or tooth, but it will not. The idea has been exposed and confuted many times, but it is immortal and invulnerable and no doubt will long continue to flourish.' (Scott 1937, 461) The Chalicothere was used to explain the 'progress' of science as it accumulated material and corrected errors in old interpretations (even from grand old founders like Kaup and Cuvier). However, it also warned palaeontologists against over-eager speculation in their deductions. Scott's cautionary tale recognized a key tension within palaeontology: comparisons were essential for classification and reconstruction, but these always had to be tentative and made in a measured manner. Over-hasty speculation had to be combated for the discipline to maintain its credibility. As a result, confidence in interpretations needed to be balanced by a recognition that there were still mysteries and problems that the discipline could not yet solve, and that the conclusions of predecessors even as illustrious as Cuvier could be subject to later revision.

PART II: EVOLUTIONARY RELATIONSHIPS

As Scott's assertions should indicate, far from settling discussion on the Chalicotheres, the linking of the head and leg-bones were felt to raise more mysteries and problems, seeming to construct a chimerical animal with plant-eating teeth and large claws. Debate shifted to classification, and where exactly this creature could be placed on the 'tree of life:' was it an edentate, an ungulate, or something totally unique? As has been noted above, answering this question was connected with a greater emphasis on fieldwork and the increased prominence of evolutionary thinking within the life sciences more generally. Palaeontology could be used to provide the evidence for a measure of change, development and continuity in life's history, but also use the fossil record to show the ancestry and relatedness of different animals across time and space through comparative means.

Palaeontology's relations with evolutionary thinking were not unproblematic. The tense and often quite torturous engagement which palaeontologists had with Darwinian evolution during these years has been discussed in a number of works, most notably by Peter Bowler. (Bowler 1983; Bowler 1996) Deploying a range of evolutionary models – some derived from Darwin, but others from orthogenetic or Lamarckian conceptions – palaeontologists placed more attention on deducing evolutionary lineages and relationships deep in the geological past. The more evolutionary mode of thinking emphasized distinct forms of comparison from that of typologists like Cuvier, that the correct way of defining organisms was not due to structural similarities, but due to phylogenetic connections with other organisms. This meant that characters closely tied to 'function' were not the most suitable to compare to classify organisms. Instead, it was homological characters which could be traced back to common ancestors which were to be looked for, and these could have undergone considerable change over time in line with evolutionary processes. Rather than solve problems, this instead set up a new and more complex research programme, as deducing which characters were homological and shared with ancestors required a great deal of fieldwork, extensive collections, and comparison across the long duration of evolutionary history.

Figure 1: Filhol's Reconstruction of *Chalicotherium magnum*, from *Etudes sur les mammifères fossiles de Sansan* (1892). The bones in outline are hypothetical. Courtesy of the British Library.

Filhol had accompanied the account of his finds with a tentative reconstruction of the whole skeleton of *Chalicotherium magnum*, presenting the leg-bones and skull which he had successfully extracted, and filling the gaps in the body with speculated bones. He interpreted the animal in simple bridging terms, as linking the Edentates and the Pachyderms, and forming an important connection in the scale of nature – a view which seemed to draw from the more Lamarckian and progressivist evolutionary ideas which were predominant in the French context, and presented strongly by Albert Gaudry. (Gaudant 1991) Filhol's reconstruction, as the simplest compromise mixing the older interpretations of the bones with a developmental framework, was not widely accepted however. Charles Depéret expressly rejected the 'Edentane' qualities of the skeleton as just superficial similarities, which were not due to a common origin. Yet beyond this, European scholars were often unable to continue the study of this lineage in the early-twentieth century. The remains in European museums were highly fragmentary, and even Filhol's prize skeleton was badly crushed and incomplete, making full analysis difficult. Museum practices also played a role: the original fossils of Falconer's *Chalicotherium sivalense* were lost; and Kaup's specimens had been distributed across Germany, making consistent study difficult. While there were still large numbers of fossils in the Muséum in Paris, French scholars, and particularly Marcellin Boule, who succeeded Gaudry as the Curator of Palaeontology in 1902, wrote very little on the Chalicotheres, preferring to focus on the Ice Ages and human evolution. In this way, loss of objects and changing interests affected palaeontological research, whatever its claims to be based on the progressive accumulation of knowledge.

In the United States meanwhile, palaeontology was ramping up in scale. After the discipline reached a high scientific and public profile in the 'Bone Wars' between Othniel Charles Marsh and Edward Drinker Cope in the 1860s and 1870s, it became institutionalized in large metropolitan museums. As Paul Brinkman has illustrated, these underwent a second phase of expansion in the 1890s and 1900s, in what has been termed the 'Second Dinosaur Rush,' (Brinkman 2010) as large institutions backed by big money and philanthropy, like the Field Museum in Chicago, the American Museum of Natural History in New York and the Carnegie Museum in Pittsburgh competed to unearth and mount huge sauropod dinosaurs. While the public face of the discipline often focussed on spectacular reptiles, fossil mammals were also plentiful in American deposits, and the subject of a great deal of scientific interest. Mammals from all eras of the Tertiary were unearthed, and compared with finds in Europe, and Henry Fairfield Osborn and William Berryman Scott both produced popularizing books on the fossil mammals of the American continent. (Osborn, 1910; Scott, 1913)

In an 1893 paper Osborn turned his attention to *Chalicotherium*, which he called 'the most unique mammal of the Miocene period.' (Osborn 1893, 118) He drew attention to the Sansan specimen as 'taller than the grizzly bear,' and with limbs that not only ended in claws, but were strangely proportioned, being 'rather slender, and a striking peculiarity of this species is that the fore limb is nearly twice as long as the hind limb.' (Osborn 1893, 118) Reconstructing the animal's posture and locomotion was therefore very difficult, as it would have moved in a manner seemingly not paralleled by any living creature. Classifying the organism was also at a deadlock, and seemed impossible through strict comparative anatomy. He agreed with Depéret that the organism's 'Edentane' qualities were superficial, and due to parallel adaptations: 'the adaptations of the phalanges for prehension or digging involve an entirely different set of muscles from those employed in either the Cats or the Edentates. This genus has attained a somewhat similar functional result by a different route - a case of analogy but not of homology.' (Osborn, 1893, 123). Such comparisons might be able to describe how the animal had behaved in life, but could not inform a discussion of the classification of the organism.

The question of whether the organism was an 'ungulate' or an 'ungiculate' (a hoofed or unhoofed mammal) was left open. Osborn felt the prior suggestions and existing evidence was inadequate to answer this question. He argued that – rather than focus on individual characteristics – palaeontologists needed earlier examples of the lineage, and that 'we must wait for the discovery of the middle and upper Eocene Chalicotheriidae' (Osborn 1893, 119) to solve the problem. This was partly due to the puzzling nature of the Sansan specimen, but was also due to a more evolutionary agenda combined with a notion that authority needed to be based on large and extensive collections. Notably, Osborn did not want more complete examples of Miocene Chalicotheres to clarify comparisons with existing orders, but desired a preceding form, from the earlier geological era of the Eocene, to work out its evolutionary relationships. The problem could only be solved by going into the field and adopting an explicitly evolutionary agenda: to be valid for classification, comparisons needed to be based on much deep trends of development, and understood in phylogenetic manners.

The classification of the Chalicothere was therefore tied to a major expansion in fieldwork, and a search for productive palaeontological sites to excavate. One key locality for the excavation of fossil mammals was the holdings of a Nebraska farmer, Harold Cook, at Agate Springs. This was a particularly rich deposit of Miocene age, containing the remains of early elephants and mastodons, entelodonts and large sabre-toothed predators. It was also subject to a great deal of competition over excavation rights between the American Museum of Natural History and the Carnegie Museum, with Jeremy Vetter describing the conflicts between these two institutions over rights to excavate the site. (Vetter 2008) While the AMNH was rising to prominence as possibly the leading and most extensive palaeontological collection in North America (and potentially also the world), the Carnegie Museum in Pittsburgh, with the sponsorship of the industrialist and philanthropist Andrew Carnegie and under the directorship of W.J. Holland, was a developing rival, which made a huge splash in the 1900s with the mounting and international publicization of *Diplodocus carnegii*, a spectacular specimen of a Sauropod dinosaur (Nieuwland, 2010). For the Carnegie Museum, locating and analyzing further prize specimens was an important strategy to build the authority and profile of the institution. Here, an important role was played by the discovery of the remains of numerous specimens of *Moropus elatus* – an American Chalicothere – at Agate Springs. American Chalicotheres had up until then only been known from isolated remains, with the type specimen of *Moropus* in Yale only consisting of a few broken foot-bones. The remains discovered at Agate were much more extensive, with Olaf Peterson, director of the excavations, finding 'a great many bones belonging to the genus *Moropus* in a disarticulated condition' between 1905 and 1908, including 'the most perfect cranium of a chalicotherine animal which had thus far been found, surpassing in perfection any specimen in the collections of either America or Europe.' (Holland and Peterson 1913)

These fossils enabled the workers at the Carnegie Museum to make a major intervention in the thorny issue of the classification of the Chalicotheres, leading to a monograph on *The Osteology of the Chalicotheroidea* published in 1913 by Peterson and Holland. The monograph went through the history of Chalicothere research, describing all the known Chalicothere specimens around the world and giving a detailed account of the excavations at Agate. It concluded with a long discussion on the classification of the lineage and a full reconstruction of *Moropus elatus*, as both a complete mountable skeleton and a sculpted organism 'in life.' Like Depéret and Osborn, Holland and Peterson brushed aside any Edentane similarities as only superficial, and aimed to examine the animal as an entire organism. The classification was therefore based on its fully reconstructed anatomy rather than any individual diagnostic features. Taking the whole reconstruction into account, it was judged that 'perissodactyl characters predominate when the skeleton is viewed as a whole,' despite 'a number of anomalous features,' in particular the back-legs and pelvis, which were judged as quite 'ursine' (Holland and Peterson 1913, 376). Palaeontological reconstruction and comparative anatomy therefore combined to clearly place the lineage within a specific grouping – the Perissodactyls or odd-toed ungulates – which included the extant horse, tapir and rhino, and the huge extinct Titantotheres of deeper geological time in the United States. Perissodactyl qualities were particularly marked in the skull, the prize specimen of the excavations, which was judged as 'combining various features represented in the horse, the rhinoceros, and the tapir.' (Holland and Peterson 1913, 377) The final assessment was that '*Moropus* was a highly aberrant Perissodactyl,' with some 'affinities with the horses, Titanotheres, and Paleotheres, but quite distinct from all these and representing a wholly independent line of evolutionary development' (Holland and Peterson 1913, 378) – something visualized in the skeleton and sculpture, which seemed to combine tapir, horse and bear-like features.

Figures 2, 3 & 4: Skull, skeletal mount and reconstruction of *Moropus elatus*, from Holland and Peterson, *The Osteology of the Chalicotheroidea* (1913). Courtesy of the Wellcome Library, London.

Workers at the American Museum of Natural History reviewed Holland and Peterson's publication quite harshly, finding particular problems with the reconstruction of the whole animal. Henry Fairfield Osborn used another tactic to solve the classification of the Chalicotheres himself. Going deep into the fossil vaults of the AMNH, Osborn reanalyzed one of Edward Drinker Cope's specimens, the leg-bones and skull of *Triplopus amarorum* found in Wyoming in 1873. Rather than be an undifferentiated ungulate as Cope had argued, Osborn reclassified and renamed this as actually being an ancestral Chalicothere – '*Eomoropus*.' (Osborn 1913) Through comparing its features with later *Moropus* specimens, Osborn argued that this was the hypothetical ancestor that he had previously desired to discover, and had been lying in the museum's stores all this time. In this way, rather than fieldwork leading to the solving of the problem, this was a claim based on mastery over the largest collection of fossils in North America, and possibly the world.

However, while the Carnegie and AMNH reconstructions of the Chalicotheres illustrate competition between leading museums over specimens and the solution of scientific mysteries, the institutional conflict actually marked a growing degree of consensus. Osborn's conclusions were essentially the same as Holland and Peterson's: *Eomoropus* showed enough specific 'Chalicotherine' features to be the ancestor of *Moropus*, but was also closely connected with the earliest Perissodactyls, illustrating that it derived from a shared early common ancestor with horses, rhinos and tapirs. Osborn concluded his study by noting that these animals had developed their key 'specialist' qualities in the Eocene, which therefore 'justifies the establishment of the Chalicotheroidea as one of the five great branches of the Perissodactyl stock.' (Osborn 1913, 272) This was an interpretation which drew from Osborn's views of evolution, which presented lineages of organisms forming early in their evolutionary history, with generalized early ancestors dividing into a variety of lines through a process of 'adapative radiation.' While differences between these groupings were only minor early in their evolutionary history, they became locked on a track to form ever more extreme and specialist forms later in their development. Placing the Chalicothere within this order, and highlighting the extreme specialization and problematic position of its later forms, not only resolved the issue of its classification, but presented the extreme incomparability of the Chalicotheres as something that would almost be expected through Osborn's view of development.

PART III: THE LIVING CHALICOTHERES

Discussions on typology and classification of the Chalicotheres increasingly rested on the drive for complete reconstructions of organisms and evolutionary lineages, and the search for homologous comparisons. However, different types of comparison were required when palaeontologists attempted to reconstruct what the living animals would have been like. This was a major concern in early-twentieth century palaeontology, with the increased prominence of an approach often described as 'palaeobiology,' marked by an increasing emphasis on reconstructing fossil animals as living, breathing animals within past ecological communities. This not only required morphological analyses and comparisons with modern creatures, but also connected palaeontology with changing concepts in ecology and animal behaviour. It was also acknowledged to require a heavy dose of imagination, conjecture and artistic sense, in order to bring fossil bones to life. Here comparisons often became explicitly more speculative, and analogies with modern organisms believed to exist in similar environments (a method which had been explicitly rejected when developing evolutionary phylogenies) became a more viable technique. Notably, these analogies were always tentative and often accompanied by large caveats, reflecting the acknowledgment of the more conjectural nature of these comparisons. However, this return to analogy shows the persistence of varying modes of comparison within palaeontology, and the different claims to truth and authority which the field could present.

The mixture of physical characteristics and the lack of clear modern analogues to the Chalicothere made any attempts to understand its living habits incredibly difficult. This was quite pressing though, as the animal – while often only found through fragmentary remains – was far from rare. Chalicotherine fossils were identified from a vast stretch of time from the Eocene right up until the beginning of the Pleistocene, originating shortly after the extinction of the dinosaurs and continuing almost up until the present. Likewise, as palaeontological expeditions followed lines of imperial expansion and geological exploration, Chalicothere remains were found throughout the world: the Central Asiatic Expeditions of the American Museum of Natural History found Chalicothere bones in Mongolia in the 1920s; Ralph von Koenigswald discovered new forms in Indonesia in the 1930s; and from the 1920s onwards, geologists found Chalicothere fossils in east and southern Africa. Chalicotheres had existed for a long time throughout the world. They could therefore not easily be written off as just peculiar aberrant monstrosities, but needed to be understood as successful and adaptable animals.

One of the most detailed outlines of the problems in understanding the living Chalicotheres was presented by William Berryman Scott, in his *Land Mammals of the Western Hemisphere*, whose two editions were published in 1913 and 1937. He devoted several sections to 'the wonderful aberrant perissodactyls with clawed feet, the chalicotheres.' (Scott 1913, 238) Their diet could be explained through a relatively straightforward analysis of their dentition: 'from the character of the teeth, the long neck and fore limbs, it may … be inferred that they fed chiefly on the leaves of trees,' (Scott, 1913, 239). However, how they used their large claws was problematic. In a long passage, Scott went through the various analogical possibilities, eliminating most through a process of comparative deduction:

> Many suggestions have been offered as to the manner in which these great claws were employed. The teeth demonstrate that these animals could not have had predaceous habits, but must have been inoffensive plant-feeders. As no such herbivorous creatures are living now, it is impossible to reach a definitive solution of the problem ... It is inadmissible to suppose that these great chailicotheres could have been burrowers, or tree-climbers, or that they pursued and slaughtered prey of any kind, for, aside from the character of the teeth, such heavy and slow-moving beasts would have been utterly inefficient at work of that sort. No doubt, the claws were used, to some extent, as weapons of defence, as the existing South American Ant-Bear (*Myrmecophaga jubata*) uses his formidable claws; probably also some, if not all, of these clawed ungulates would employ the fore feet in digging for roots and tubers, as is done by the bears generally. Many years ago, the late Sir Richard Owen suggested with reference to the ground-sloths that the principal use of the fore feet, other than that of locomotion, was to draw down within reach of the long tongue and prehensile upper lip the branches upon which they browsed. This explanation may perhaps be applicable to all of these aberrant and exceptional groups of hoofed animals. (Scott 1913, 355-6)

This passage is interesting for the way in which it combines palaeontological and comparative anatomical analysis with discussions on potential ecological roles that animals could take, attempting to test them on the 'peculiar mix of characteristics' in the Chalicotheres. Scott's account also shows the long duration of particular animal analogies:

the main comparisons being made were with animals placed within the Edentates, notably giant anteaters and ground sloths. Even though the taxonomic relationship suggested by Cuvier and others was now rejected, the analogy was still being deployed to understand the similar morphology of the giant claws. Comparisons based on 'function,' not taking into account the evolutionary relationships or origin of the structure, remained valid when the aim of comparison was to understand ecology and lifestyle.

A slightly different approach was attempted by the Austrian palaeontologist Othenio Abel in his 'Studien über die Lebensweise von *Chalicotherium*' (Abel 1920). This outlined the increasingly global research on the animals, and broadly agreed with the Perissodactyl classification. However, in order to reconstruct the lifestyle of the Chalicotheres, Abel went beyond strict morphological analysis, instead linking his study of the bones with reconstructions of the environments in which the creatures had lived, and comparisons between different Chalicothere genera. Abel argued that there was clear separation between different forms of Chalicothere in both their anatomy and where they had lived. Miocene Greece and the US interior, with their elephants and mastodons, seemed to have been grassland savannah environments. Meanwhile, prehistoric southern France and India, with their fossil apes, deer and great cats, seemed to be woodland and rainforest. The Chalicotheres found in these two sets of areas were also physically quite distinct. The American and Greek forms, which Abel placed within the genus of *Chalicotherium*, seemed to be less specialized, with a narrow pointed skull, relatively short forelimbs, and well-developed claws. This indicated an animal which 'used its arms for scratching and digging, and its food must have been soft vegetable tubers and bulbs, with the wedge-shaped tapered skull and strongly-developed neck playing an important role in taking in food, and used for rooting around in the earth of the steppes.' (Abel 1920, 45)

Meanwhile the French and Indian forms, for which Abel revived the term *Macrotherium*, was more robust and had much longer forelimbs. This animal was interpreted as primarily living on fruit, berries and leaves, and used its longer arms in quite a different way:

> Here we must keep in mind the bears, with which these Chalicotheres must have had numerous similarities, which would have been particularly noticeable in the general look; the very striking length of the arms corresponds well with this idea ... We also observe arm lengthening in the arboreal Edentates, who also have a certain parallel with the *Macrotherium* types. (Abel 1920, 44-45)

The size of the animal meant that it could not ‘climb among the branches like the living sloth or tree-anteater,’ but instead used its arms to ‘bring leafy branches towards it mouth.’ (Abel 1920, 54) This account was accompanied by two illustrations, both by Abel himself, of representatives of the two genera, with *Chalicotherium pentelicum* depicted as an almost Aardvark-like creature digging for roots in the plains of Miocene Greece, while the forest-dwelling *Macrotherium magnum* was a much more bear-like animal. Abel’s account is interesting for the ways in which it attempted to reconcile some of the competing interpretations of the creature’s lifestyle – digging or forest-dwelling – and for bringing in new elements of comparison, that of the whole ecosystem and between different forms of Chalicothere. The animal analogues Abel deployed were quite conventional, with bears, sloths and anteaters being again brought in as the clearest counterparts, but were interpreted in terms of niche and habit. The geological past was now understood as diverse and shifting, with the animals adapting to different environments and lifestyles across geological time. Comparison therefore could not just define the animal’s features, but also its environment.

Figure 5: Reconstructions of the plains-living *Chalicotherium pentelicum* from Abel, ‘Studien.’ Courtesy of the British Library.

Figure 6: Reconstruction the forest-dwelling *Macrotherium magnum* from Abel, ‘Studien.’ Courtesy of the British Library.

Possibly the strangest course in attempts to understand the Chalicothere occurred in the 1920s, when geological exploration was connected with indigenous traditions in colonial territories and the media. In 1923, E. J. Wayland, Director of the Ugandan Geological Survey and a keen palaeontologist, sent some mysterious fossil remains found in East Africa to the London Zoological Society. The find was reported on in *Nature* by C. W. Andrews, a prominent palaeontologist employed by London’s Natural History Museum, and interpreted as belonging to a Chalicothere. (Andrews 1923, 696) Andrews noted that these remains had been found in very recent geological layers, dating from at most a few thousand years ago. They had also been found alongside the remains of hippos and okapi, which were also associated with Chalicothere remains in Miocene Greek sites.

This raised a possibility, again informed by more speculative comparative reasoning: if this animal had survived until such a recent date, could it still be living somewhere in Africa? Andrews argued that this recentness meant that the Chalicothere might still be alive, and if so 'it will be a discovery of greater interest than the Okapi,' a creature which had been first reported to great sensation in 1901, and was also often described in similarly chimeric ways as the Chalicothere. While 'cryptozoology' – the idea that hidden animals, often conceptualized as survivals from prehistoric periods, still survived in remote regions of the world – is often associated with its upsurge from the mid-twentieth century (Regal, 2013), in the 1900s it could remain a fairly respectable notion, presented by established scientists like Andrews. The claim was reinforced with an additional source – African folklore – being reported alongside alongside East African stories of the 'Gereit' or the 'Nandi Bear,' a mysterious and ferocious clawed animal which attacked people in the night and resembled a giant, oddly-shaped hyena. Andrews mentioned this legend in his report, and argued (using a more prosaic comparison) that if the creature were nocturnal, that would explain its elusiveness: 'it does not seem at all improbable that, in such a country, even a large nocturnal animal might escape notice for a long time: even in England few people have ever seen a badger in the wild state.' (Andrews 1923, 696)

This idea was of great interest in the wider media. The British periodical *The Illustrated London News* contained several reports linking the 'Nandi Bear' with the Chalicothere in the 1920s and 1930s. William Pycraft's regular 'World of Science' column accompanied the announcement of Wayland's finds, and featured a great deal of dedicated discussion. This built up, in atmospheric detail, the conjectures around the creature:

> It would be well to remark that for some long time past stories of a strange beast, a veritable bogey, have been current among the Nandi people – a beast that walks by night, seeking whom he may devour. … Hitherto, sportsmen and naturalists alike have been inclined to regard these dread stories as due to an over-lively imagination and a love of the mystical. … It would now seem that they rest on a very solid foundation, for the claw just found is quite certainly that of an animal believed to have become extinct tens of thousands of years ago, and answers well to the creature which has so long disturbed the peace of mind of the Nandi. (Pycraft 1923)

However, Pycraft's discussion was not just building up an aura of scientific mystery and African wildness. It also raised a deductive comparison with potentially similar animals to reconstruct what the 'Nandi Bear' may actually be like. Speculating on the use of the animal's claws in a similar manner to Scott, he noted how:

> The supporting bony core, it will be noticed, was deeply cleft, after the fashion seem in the similar cores of the mole, the ant-eater, and the bandicoot. In all these creatures the claws in the living animal are of great size and used for digging – sometimes for tearing down the nests of termites and ants, or for digging up roots. They may on occasion, it is worth noting, be use for defensive purposes, after the fashion of the existing American ant-bear, which can inflict terrible wounds. (Pycraft 1923)

Again this was a potentially dangerous animal. However, reflecting on the 'very low-crowned' teeth, it was further deduced that it would have been a browser on leaves. This altered perceptions of the creature completely: 'if these deductions are correct, then the poor "Gereit" has probably been much maligned, and it will proved, when captured, to be one of the mildest mannered beasts that ever bit a head off! … it has bred an atmosphere of distrust and earned a reputation for ferocity which is quite foreign to its nature.' (Pycraft 1923) This was accompanied by a reconstruction from the *Illustrated London News*' resident palaeontological artist, Amédée Forestier, depicting the Chalicothere as an ant-eating creature digging in termite-mounds. However, with the headline 'Possible Quarry for the Future Big-Game Hunter in Africa' this put matters firmly in the scope of imperial exploration. The Chalicothere remained a creature of wonder and mystery, and from this it drew its interest.

CONCLUSION

The story of the discussion and reconstruction of the Chalicothere across the nineteenth and twentieth century raises a number of issues around the use of comparison in the modern life sciences. Different forms of comparison could be used for different claims, relating combinations of practices, specimens, and underlying conceptions. Those forms of comparison thought to be based on the core 'nature' and taxonomic position of the animal were often made with a strong degree of confidence, and claims to truth and authority. However, the precise criteria of what this entailed varied considerably between different researchers – ranging from Cuvier's notion that the essence of a creature could be deduced from functional characteristics and key anatomical features like teeth and claws, to the more evolutionary concepts presented later by Henry Fairfield Osborn and others that comparisons needed to be made across geological time to establish phylogenetic relationships. The contrast between these forms of comparison, and the different forms of taxonomy that they entailed, demonstrates shifts in the life sciences in the nineteenth and twentieth centuries, moving from fairly static models of typology to more evolutionary ones.

However, these taxonomic comparisons based on deep anatomical structures and evolutionary relationships were not the only ones being made. Throughout this long period, there was also a consistent use of more analogical reasoning, to understand the animals in life, in terms of how their anatomical features fitted together and how the creatures may have lived and behaved. This was more speculative and conjectural, and in the case of the Chalicotheres required the usage, deployment and mixture of a range of different animal analogies and types of comparison, with palaeontologists basing these on animals with similar anatomical features, in similar taxonomic classes, or believed to have similar lifestyles or live in similar environments. These forms of comparison often required a considerable degree of imagination and artistic deployment, as well as knowledge and understanding of the modern natural world and wider geological history, mixing and integrating different approaches and styles of thinking. These analogical approaches were very often admitted to be fairly speculative or conjectural by their proposers, and so were couched in a language of strangeness.

Across all of the different modes of comparison, there was a strong idea that all these conclusions were tentative, subject to debate or later correction, and that over-hasty generalizations needed to be guarded against. Yet this was not necessarily regarded as a problem, but was instead – as in Scott's warning story around the principles of correlation and Cuvier's methods – regarded as a natural instance of scientific work. The strangeness and incomparability of the Chalicotheres enabled them to serve as testing organisms through which a range of comparisons could be deployed, presented and related together. In some respects, attempts to understand the animal threw the difficulties of palaeontology's claims to be an authoritative science into relief, emphasizing the problems and mysteries of drawing conclusions from fragmentary fossils. However, highlighting these unknown issues and the range of methods needed to solve them could be a way of both inspiring further research, building up claims to authority, or justifying and rationalizing potentially speculative deductions. With a range of methods, from natural history, geology, myth, environmental science, and ecology being brought together, attempts to reconstruct the Chalicothere integrated varied comparative and disciplinary threads. Understanding the strange clawed ungulate was a way of testing the limits of different forms of comparison, and grappling with the tensions between conjectural reasoning and claims to truth and authority in the life and evolutionary sciences.

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