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Celebrating Dinosaurs: their behaviour, evolution, growth and physiology

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Abstract

Dinosaurs have attracted varying degrees of scientific and public interest since their initial description in 1824. Interest has steadily increased, however, since the late 1960s when the Dinosaur Renaissance began, and when the Canadian Journal of Earth Sciences started to publish. Since then, there has been a feedback system (international in scope) promoting increased scientific activity and ever-increasing public attention. This has led to ever more dinosaur discoveries internationally; increased numbers of museums and parks displaying dinosaurs; more publications, blogs and other media on dinosaurs; and (most importantly) increased numbers of people and institutions doing research on dinosaurs. About 30 new species of dinosaurs are now being described every year, adding to the more than 1,000 species already known. Furthermore, it is now acknowledged by most biologists and palaeontologists that modern birds are the direct descendants of dinosaurs, and that they are classified as part of the Dinosauria. Recognizing that there are more than 11,000 species of living dinosaurs has given us a better understanding of many aspects of the biology of non-avian dinosaurs. Along with technological improvements, this has revealed new – and often surprising – facts about their anatomy (bones, soft tissues and even colours), inter-relationships, biomechanics, growth and variation, ecology, physiology, behaviour, and extinction. In spite of the intensity of research over the last six decades, there is no indication that the discovery of new species and new facts about their biology is slowing down. It is quite clear that there is still a lot to be learned!

Key Words: Dinosaurs, History, Anniversary, Research

Introduction

Dinosaur bones and other fossils have been recognized and recovered by humans for centuries (Dong 1997; Spalding 1993; Sarjeant 1997; Major 2011), although initially they may have been attributed to mythological animals like dragons or gryphons, or to animals that were supposedly still alive but living in unknown corners of the Earth. The 'scientific' discovery of dinosaur bones came much later, and the first finds are usually considered to be the collection between 1818 and 1821 of teeth and bones from gigantic, extinct reptiles in southern England. *Megalosaurus* (Buckland 1824) and *Iguanodon* (Mantell 1825) were the first genera of dinosaurs named, and became two of the three dinosaurs that Owen (1842) used to erect the Dinosauria.

Dinosaurs have received a lot of attention because their scientific discovery, and much of that has been within the last half of that two century period. There was an initial period when public and scientific interest was insatiable, but two world wars, political turmoil, and the great economic depression of the 1930s put a damper on those interests. The period between 1930 and the late 1960s was a time when there was relatively little research being done, especially in relation to changes in concepts of what dinosaurs were (Buffetaut 1997). But things were happening that led to a resurgence in scientific interest in dinosaurs during what ultimately became known as the Dinosaur Renaissance (Bakker 1975). For example, fieldwork in Mongolia by Soviet expeditions (1946-1949) and Polish-Mongolian expeditions (1963-1971) led to many exciting discoveries (Lavas 1993). In China, C.C. Young (Yang Zhongjian) collected and named many dinosaurs during this period (Dong 1997), and Richard C. Fox started collecting dinosaurs for the University of Alberta in Dinosaur Provincial Park. And almost certainly, books by Colbert (1968) and Kielan-Jaworowska (1969) describing these and other expeditions had their impact on the initiation of the Dinosaur Renaissance.

The public always maintained an interest in dinosaurs, and from 1930 to 1970 they remained among the most popular exhibits in museums worldwide, and the stars of books, cartoons, comic books, movies and toys (Glut 1980). The Sinclair Refining Company helped keep dinosaurs in the public eye by using a sauropod as its logo, by sponsoring the first animatronic models at the World's Fair in 1932-1934 and life-size models at the New York World's Fair in 1964, and by various promotions with giveaway toys, books and brochures.

Scientific interest started to recover in the late 1960s, and the "Dinosaur Renaissance" was in full swing by the early 1970s (Bakker 1975; Desmond 1975). Robert Bakker was in fact the focal point for creating the "Dinosaur Renaissance" in that he changed the way we looked at things with his ability to think differently and develop new approaches, his unorthodox appearance, his enthusiasm and ability to inspire others, and his willingness to debate conventional ideas. New ideas about dinosaurs emerged and this created even more interest by the public, and expanded into new regions internationally. He was an amazing inspiration to younger palaeontologists, even if they did not agree with everything he said. On certain subjects (such as warm-blooded dinosaurs, classifying birds as dinosaurs, and even suggesting that non-avian dinosaurs were feathered) he was greatly outnumbered by his colleagues, but in the long run, many of his ideas have prevailed. As dinosaur research increased, a feedback loop developed in that more public interest led to more funding for a science that was grossly underfunded. This in turn led to more research on dinosaurs, which led to more exciting discoveries, which led to more media attention, which led to more public attention, which led to more funding, which led to more research and discoveries. In the 1970s, it seemed like the feedback loop could not go on forever, but it has continued to this day, albeit with ebbs and surges in intensity.

Dinosaurs have long been icons for science in general, and have been a major influence on career and research choices for students. There is perhaps no better example for the power of this influence than the second major surge in the "Dinosaur Renaissance" caused by the release of the movie of "Jurassic Park" in 1993. The book by Michael Crichton (1990) had created a considerable buzz when it was released, but it did little to prepare us for what would happen when the movie was released several years later. Public and media interest in dinosaurs surged like it never had before. For example, attendance at the Royal Tyrrell Museum of Palaeontology shot up by 40% after the release of the movie, and we had as many as three film crews a day at the museum during the summer of 1993. But more importantly, it also had a major impact on public education, which surprised me. Although Steven Spielberg – the director and producer of the movie – was concerned with the accuracy of what was being presented about dinosaurs, many of the scientific ideas about dinosaurs were subtle in their presentation. Yet the public seemed to get it, and overnight the questions we were getting as palaeontologists from the public changed. During the 1970s and 1980s, those of us who specialized in dinosaurs thought we were doing a good job getting the ideas through to the public that dinosaurs were warm-blooded, that dinosaurs were the direct ancestors of birds, that some dinosaurs had more intelligence than they were generally credited for, and that dinosaurs had social interactions on par with modern animals (Schweitzer and Lessem 1997). But we realized after the release of the movie that Hollywood had reached a much bigger segment of the population with these ideas, and that suddenly we were being asked questions that were more relevant to our current understanding of the biology of dinosaurs than had been portrayed in older movies like King Kong, which was released in 1933 (Glut 1980).

Before the Dinosaur Renaissance began, dinosaurs were particularly popular in western cultures, where they often formed the most popular displays in museums (such as the American Museum of Natural History, Canadian Museum of Nature, Carnegie Museum of Natural History, Field Museum of Natural History, LA County Museum, the Natural History Museum in London, the Royal Ontario Museum, and the Yale-Peabody Museum of Natural History to name a few), parks (including Dinosaur National Monument, and Dinosaur Provincial Park), and amusement parks (including the Crystal Palace in London). Over the last 60 years, their popularity has grown internationally and new museums with major dinosaur exhibits have opened in Argentina (including Museo "Carmen Funes" in Plaza Huincul, and Museo Paleontológico Egidio Ferulio in Trelew), Canada (including the Philip J. Currie Dinosaur Museum in Wembley, the Royal Tyrrell Museum of Palaeontology [Fig. 1], and the *T. rex* Discovery Centre in Eastend), China (including Erenhot Dinosaur Museum in Inner Mongolia, the Henan Geological Museum in Zhengzhou, the Liaoning Paleontology Museum in Shenyang, and the Zigong Dinosaur Museum in Sichuan), France (Espéraza Musée des Dinosaures), Germany (Museum für Naturkunde der Humboldt Universitat in Berlin, and the Senckenberg NaturMuseum in Frankfurt), Japan (Fukui Prefectural Dinosaur Museum [Fig. 2]), Mongolia (the Natural History Museum in Ulaanbaatar, and the Gobi Museum of Nature and History in Dalanzadgad), Portugal (Lourinha Museum), Russia (Orlov Museum of Paleontology), Spain (the Jurassic Museum of Asturias), Switzerland (Aathal Dinosaur Museum), Thailand (The Sirindhorn

Museum), the United Arab Emirates (a new billion dollar dinosaur museum will soon open in Abu Dhabi) and the United States (Children's Museum of Indianapolis, Museum of the Rockies, New Mexico Museum of Natural History, Rocky Mountain Dinosaur Resource Center, Wyoming Dinosaur Center) (see Chure 1997 for a more extensive list). Whereas major dinosaur displays used to be concentrated in the higher population centres around the World, there has been a shift in North America towards the west, and internationally towards Asia, Australia, Europe and South America. More than ever before, there are more opportunities for people to be inspired by these amazing animals, which has led to more children internationally pursuing careers in palaeontology, and seeing jobs open up in their own countries. This of course has led to geometric increases in discoveries of dinosaur sites and new taxa, and to the recruitment of students into the field. Not surprisingly, there are now more universities around the world where one can study palaeontology (including dinosaurs).

A good place to chart the growth of the interest in dinosaurs since the beginning of the "Dinosaur Renaissance" is by looking at the 60-year history of the Canadian Journal of Earth Sciences. The journal was established in 1963, although the first issue of the first volume was not released until 1964. Ironically, the first article was by David M. Baird, who many years later became the first director of the Royal Tyrrell Museum of Palaeontology. However, in 1963, Baird was employed as a geologist, and the article he wrote was on gypsum-anhydrite deposits and had nothing to do with either dinosaurs or palaeontology. There were in fact no scientific articles about dinosaurs in the first three volumes of CJES. Langston (1967) has the honour of being the first palaeontologist to publish a dinosaur paper (about a beautiful skull of *Pachyrhinosaurus*) in the journal. Interestingly, his article was preceded by one by Dale Russell (1967a), who succeeded Langston as the dinosaur researcher at the National Museum of Canada (now the Canadian Museum of Nature). The latter article (Russell 1967a) did not have anything to do with dinosaurs, although it was about Cretaceous vertebrates. A different man with the same surname, Loris Shano Russell, published the second dinosaur article in CJES the following year (Russell 1968). For the next few years, the journal published up to two dinosaur articles per year (Heaton 1972, 1973; Norford 1973; Russell 1969, 1970, 1972; Waldman 1969) as the 'Dinosaur Renaissance' gained a foothold. There was nothing about dinosaurs in the eighth volume (1971) of CJES. On average then, there was less than one dinosaur article per year during the first decade of publication. In contrast, the current decade of issues (Volumes 51-60) is not finished but the number of dinosaur related papers already numbers more than 40. In part, this is because of special issues of CJES (Fig. 3) that are mostly (Burns et al. 2014; Currie 1993, 1996, 2001; Currie and Koppelhus 2010) or partially (Gardner et al. 2015; Mallon et al. 2021) focussed on dinosaurs or related topics.

Dinosaurs were still not being worked on by many palaeontologists during the 1960s and early 70s. Most were members of the Society of Vertebrate Paleontology, and attended the annual meetings. The dinosaur sessions were generally relatively small, both in terms of numbers of talks and attendance. However, in 1988, the annual meeting was hosted by the newly opened Tyrrell Museum of Palaeontology in Drumheller. The conference is generally relatively large and many of the meetings from around that time had attracted more than a thousand delegates. This is a number that would have been impossible for a town the size of Drumheller (with a population of about 7,000 people) to host. But delegates were willing to suffer some inconveniences, and some stayed in hotels that were more than an hour from

Drumheller. The Museum itself was also pushed to the limits to run the technical sessions, as the theatre was only designed to hold 250 people. Some of the collections' storage spaces were temporarily cleaned out and set up to seat larger audiences. Previous SVP meetings had larger sessions for fossil mammals and topics other than dinosaurs, so these topics were given the larger rooms. However, everything turned around at that 1988 meeting, and more people wanted to listen to the dinosaur talks. Consequently, we needed to change the auditorium for the dinosaur session to accommodate the largest audience of the conference. And since that year, the dinosaur sessions at the SVP meetings have steadily increased in the numbers of talks and attendance. In most recent meetings, almost a third of the talks (2 of the 6 scientific sessions) have been focussed on dinosaurs.

Without a doubt, palaeontology has always been influenced by its parents geology and biology. For the first century and a half, geology was the dominant parent of palaeontology as scientists focused on finding new localities, new formations and new specimens. There is no question that two major developments in geology (the refinement of radiometric dating and the acceptance in the late 1960s of continental drift) probably also had a major influence on the development of the dinosaur renaissance. The description of new species, the identification of associated floras and faunas, and recognition of evolutionary trends were of course more biological problems, but were a consequence of finding the specimens. Feedback between the two disciplines constantly refined the search for new sites, and the recovery of information from both sites and specimens. As collections became larger in public institutions, the need to go out and find new material was less important. Nowhere is this better manifest than the development of "taphonomy", the study of what happens between the death of an organism and its ultimate internment in the sediments, or more simply worded as the transition of remains from the biosphere into the lithosphere. The concept was defined by the Russian scientist Efremov (1940), who led the Mongolian Palaeontological Expedition of the Academy of Sciences of the USSR from 1946 to 1949 (Efremov 1954; Kurochkin and Barsbold 2000). One of the earliest taphonomic studies (Efremov 1955) involving dinosaurs was a locality in Mongolia that is referred to as the Dragon's Tomb (Fig. 4). Here, multiple well-preserved skeletons of *Saurolophus* were buried *en masse* (Efremov 1958; Bell et al. 2018), which amongst other things, suggests that they were herding at the time of their death. The significance of taphonomic studies towards understanding the palaeoecology of dinosaur-dominated faunas spread to North America. Dodson did one of the first taphonomic studies when he spent the summers of 1968 and 1969 in Dinosaur Provincial Park collecting sedimentological data from dinosaur quarries that had been marked by Sternberg (1950). The taphonomic work was a prerequisite for undertaking a palaeoecological study of the dinosaur fauna of what was called the Oldman Formation at that time (Dodson 1971).

By the end of the 1960s, the biological parent of palaeontology was having a greater impact on studies of dinosaurs. Today, the majority of dinosaur palaeontologists either graduate from biological programs at universities, or with a double major in biology and geology.

How Many Non-Avian Dinosaur Species Are Known?

The number of recognized dinosaurs is constantly increasing, although it should be pointed out that the number of genera and species will never be agreed on by all workers.

There are many reasons for this. First, many (in fact most) taxa are based on specimens that are incomplete, and the recovery of additional material can sometimes reveal inconsistencies with the original interpretation of characters. As will be discussed later, palaeontologists (and other biologists) can have different tendencies to be splitters (who emphasize differences to create new taxa) or lumpers (who interpret differences as variation, or perhaps preservational distortion; these people tend to synonymize taxa). There are many other reasons for different palaeontologists to accept different taxon counts, but over time the taxonomic number does increase with additional discoveries and research (Benton 2008a, 2008b). Nevertheless, without a full understanding of genetic composition, which may never be possible for any non-avian dinosaur species, taxonomy will always be an uncertain endeavor. And taxonomic instability is even true to a lesser extent with living animals.

When the name Dinosauria was created, Owen (1842) based it on three genera (*Hylaeosaurus*, *Iguanodon* and *Megalosaurus*), although other genera that ultimately turned out to be dinosaurs were known at that time (*Cetiosaurus*, *Poikilopleuron*, *Streptospondylus*). During the 1960s, fewer than three dinosaur genera were being described per annum (Olshevsky 1991), and an estimated 170 genera had been named as of 1969 (Dodson 1994). By 1989, 540 genera (and about 800 species) had been described. However, many of these names were based on incomplete or inadequate material, and the number of valid genera was estimated to have been only 285 (Dodson 1990). This number increased by 51 (to 336) over the next seven years (Holmes and Dodson 1997), at an average rate of 7.3 genera per year. And then during the following 15 years, the average annual rate of description had more than doubled (Wang and Dodson 2006) so that the total number of genera recognized as valid rose to 527. At the species level, Benton (2008a) found that at the end of 2004, 1401 species had been named, but only 726 of them were regarded as valid. Although there has not been a recent summary of the number of dinosaurs known at present, online estimates suggest there are now about 900 genera (and more than 1,000 species), which if true suggests that 25 to 30 new animals are being described annually. Although the calendar year 2022 was not over when this was being written, about 30 new dinosaur genera had already been published.

To most people, it sounds like we know a staggering number of dinosaurs. However, most people are also unaware that there are more than 6,000 living species of mammals, more than 10,000 living species of reptiles, and close to 11,000 extant birds (which are, as will be discussed, living dinosaurs). Considering that non-avian dinosaurs dominated the world for almost 150 million years, and that they lived in virtually every terrestrial ecosystem available to them on every continent, then a thousand known species seems like a very small number. Extrapolating the rate of dinosaur discovery using logistic accumulation curves, Wang and Dodson (2006) predicted that the number of new dinosaurs being described will approximately double over the next century, after which the rate of recovery will be much lower. The majority of known non-avian dinosaur fossils do come from very specific environments, however, such as the coastal lowlands of the Western Interior Seaway, or the fluvial and aeolian environments of central Asia (Jerzykiewicz et al. 2021). Because the majority of environments that non-avian dinosaurs would have been living in had little or no potential of preserving living organisms as fossils, then the number of dinosaur species recovered will never be more than a fraction of the number that must have existed.

Changes in Research Volume over the last Sixty Years

At the beginning of the Dinosaur Renaissance, there were fewer than a dozen palaeontologists employed worldwide to do research on dinosaurs. In fact, the 1960s was a very quiet time for the publication of research on dinosaurs. About 40 people published at least one dinosaur paper each during the 1960s (see the bibliography in Weishampel et al. 1990), but of these only a dozen (Bonaparte, Casamiquela, Colbert, Langston, Lapparent, Rozhdestvensky, Dale Russell, Loris Russell, Ostrom, Prasad, Raath, Riqles, and Young) published more than one research paper on dinosaurs during that decade. Luckily, those people started taking on graduate students, and their research productivity started to increase the number of publications on dinosaurs by the end of the decade (1969).

Over the last decade, several hundred publications appear each year on dinosaurs. Although the prime purpose of papers by Dodson (1990), Holmes and Dodson (1997), Wang and Dodson (2006) and Benton (2008a, b) were to look at the rate of description of new dinosaur taxa, the data of the numbers of dinosaur taxa are strongly correlated with the number of publications on dinosaurs in any given year. In addition to the sheer number of publications coming out, there are some significant differences in how the research is being done. First, the turnover at the peer-reviewed, scientific journals is much faster than it was even a decade earlier. Once a paper is submitted, each step of the review process now has a tight deadline. Secondly, on average more people are involved in putting together each manuscript, and carrying it through to publication. At the beginning of the Dinosaur Renaissance, the vast majority of research papers by vertebrate palaeontologists were authored by one or two authors. In 2022, about 200 papers on dinosaurs were published in peer-reviewed journals. On average, between four and five people authored each paper; eleven papers were authored by a single person, 35 were credited to two authors, and as many as 18 people co-authored each of the rest. The authorship tends to be more multidisciplinary and multinational than it used to be. These trends are not restricted to dinosaur palaeontology, but can also be seen in most scientific disciplines.

Role of Technology in the Accelerated Rate of Dinosaur Discovery

Its no secret that everyone who likes dinosaurs when they are young do not become vertebrate palaeontologists. Childhood ambitions aside, most people end up with jobs in the “real world”. However, many remember their influence and become volunteers at museums or go on dinosaur digs. And some offer their help in different ways. One consequence is that people who have access to new technologies or techniques are happy to offer their services to people who are working on dinosaurs. And consequently dinosaur researchers are often able to try these things out before anyone else, and frequently there are either no charges, or reduced charges. A special issue of the Anatomical Record is entitled “Paleobiology in the 21st Century” and showcases the broad spectrum of research being done in vertebrate palaeontology. As pointed out by the special editors Hedrick and Dodson (2020), we have a baseline understanding of anatomy, relationships, biology, and macroevolutionary trends, and using newly developed quantitative techniques and new technologies, dinosaur palaeontologists can now ask more complex questions and refine our understanding of dinosaur evolution.

Although access to better roads, more reliable vehicles, helicopters and heavy equipment have improved certain aspects of fieldwork, most of the work finding and collecting dinosaurs is still done respectively on foot and using hand tools. Although geophysical technological advances have produced amazing results in geology and archaeology, the use of ground penetrating radar is still a dream in palaeontology, notwithstanding its portrayal in the Jurassic Park movies. It has been experimented with (Gillette 1994; Meglich 2000), and under the right circumstances should work fine. Unfortunately, it is too difficult to get the equipment into the field and set up properly, and in most cases produces images that are too poor to distinguish bones from nodules, rocks and other inclusions in the sediments that have similar densities to the fossils. It is still faster and more efficient to rely on the tried and tested techniques of people using picks and shovels. Global positioning systems (GPS) have certainly improved the ability to pinpoint sites (MacDonald et al. 2005) with greater efficiency and accuracy, and drones are making a huge difference in mapping the distribution of skeletons (Fanti, Cantelli et al. 2018). Quarry mapping has improved dramatically using high resolution GPS (Brown et al. 2021), lidar and photogrammetry (Matthews et al. 2016). Geochemical fingerprinting of specimens and sediments (Fanti, Bell, et al. 2018) is now possible because of portable XRF (X-ray Fluorescence) analysers (Fig. 5).

Technological progress has probably had a greater impact on the study of dinosaurs after they have been collected. Histological studies – the thin sectioning of bones and teeth for subsequent microscopic examination – were first done for dinosaurs almost a century ago (Moodie 1928, Nopcsa 1933). These studies rose to prominence in the early years of the Dinosaur Renaissance when they were used to study tooth replacement, growth rates and even physiology of dinosaurs (de Ricqlés 1974, Reid 1997). Although histological studies in their simplest form require relatively unsophisticated equipment, they have been improved recently by micro-CT scans, synchrotrons (Funston et al. 2021) and even X-ray Fluorescence. The number of papers that include histological studies have increased dramatically over the last twenty years, and it has reached the point where some histological work needs to be done for each paper submitted, if only to determine how old the dinosaur was when it died.

Although we often forget that computers and the internet were not available to most researchers until the 1980s or 1990s, there is no question that both have had an enormous impact on research productivity. However, they have also allowed other types of programs and equipment to develop. CT (Computerized Tomography) scans, for example, have provided a non-invasive, non-destructive technique to study the interior anatomies of fossil bones for more than thirty years now, and the analytical software just keeps getting better. The combination of CT scanning technology powered by synchrotrons (Fig. 6) has increased the details of what can be studied to the same degree that Scanning Electron Microscopes improved the scale of imagery seen under conventional optical microscopes (Dyer et al. in press; Nirody et al. 2022).

Until recently, photographs of dinosaur specimens were usually unsatisfactory when published. Part of the problem was the low resolution of the published photographs, and the tendency to print them in black and white because of the cost of printing colour plates. Stereo pairs were an improvement in that they allowed the reader to see three-dimensional features that could not be seen well on two-dimensional photographs. However, they were a problem to photograph and print properly, and many people could not see the three-dimensional qualities without special equipment. Anaglyph stereo imaging was a variant that used colours to distinguish the right and left images of a stereo pair that were superimposed (Gatesy et al.

2005). Although easier for the reader to see the images in three dimensions, nevertheless they still had to be printed in colour and required having the coloured stereo-glasses. Digital photos were not widely used until shortly after the year 2000. Digital photography has now surpassed the resolution of imagery possible with conventional (film) cameras by being able to layer and merge images to eliminate depth of field problems, or even produce three-dimensional models that can be studied, measured or manipulated on computer screens. Photogrammetry has been used to record whole fossil sites to map the distribution of footprints or bones, or simply as a way to study and illustrate individual footprints, bones and teeth.

At the beginning of the Dinosaur Renaissance, statistics, bivariate analyses, and even simple forms of multivariate analyses were all being used to analyze similarities/differences between fossils to determine taxonomic or ontogenetic differences. With the increasing availability of more powerful, desktop computer hardware and software, more complex morphometric studies could be done easier. Good examples include principal component analysis (Pei and Xu 2022).

Computers have greatly enhanced the ability to produce models that visually show the movements that were calculated either mathematically or from physical or digital models (Thompson and Holmes 2007). By producing animations or physical models, the data can be constrained to show what was possible at either extreme of movement at each joint. Visualization is important to show how bite forces calculated for oviraptorids (Meade and Ma 2022) suggest that these animals had very powerful bites. This supports the idea that they were herbivorous and exploiting tough vegetation.

Anatomy and Taxonomy

Many of the modern studies of dinosaur palaeobiology were initiated by the large number of dinosaur skeletons that had been collected and identified worldwide. According to Russell (1967b) and Béland and Russell (1978), about 250 articulated dinosaur skeletons had been collected from the region around what is now Dinosaur Provincial Park (Fig. 7). One of the greatest resources for the new studies done on dinosaurs at the beginning of the Dinosaur Renaissance was a topographic map produced by C.M. Sternberg (1950). One hundred and twelve quarries had been staked/mapped (Tanke 1994), and their geographic and stratigraphic positions were marked on the topographic map (Sternberg 1950). Of these, about 100 quarries had produced dinosaurs (the balance are crocodiles, turtles and other miscellaneous sites). In other words, about 40% of the dinosaur excavations could be revisited and checked for additional information and specimens. This gave a census of dinosaurs from a single place and time period that was used for initial palaeobiological (Dodson 1971; Bakker 1972; Farlow 1976a; Béland and Russell 1978) studies at the beginning of the Dinosaur Renaissance. Since the Sternberg map was published in 1950, many of the lost quarries have been identified (Tanke 2020) and many new skeletons have been excavated (Currie and Russell 2005). At present, 275 quarries have been staked in the Dinosaur Provincial Park region, 90% of which produced dinosaurs that were collected and are catalogued in public institutions. Because of questions related to possible collecting biases, another category of specimen identification was initiated in Dinosaur Provincial Park for articulated (or associated) but uncollected specimens (Currie and Russell 2005). Although these skeletons are not staked physically, their geographic and stratigraphic positions are known and they can be visited at any time. Close to three hundred sites with uncollected skeletons have been identified over the past four decades, but over the years many have been excavated (and their numbers have been turned into quarries). For example, U097 was a badly eroded hadrosaur postcranial skeleton found in 1992 by a University of Calgary graduate student (David Trexler). In 2011 (Tanke and Russell 2012), it was realized that this is probably the skeleton that goes with the holotype of *Corythosaurus excavatus* – a skull at the University of Alberta collected in 1920 by George Sternberg (Bramble et al. 2017). The skeleton was excavated in 2012, and the site number was changed from U097 to Q259 [Fig. 8]. There are still more than 100 dinosaurs with U numbers in the Park area, that have been at least identified and in many cases measured. In this way, it is hoped that some of the criticisms of collecting biases can be overcome.

The 1960s and 1970s saw a revolution in techniques used in taxonomic studies. Phylogenetic systematics (cladistics) rose as the most logical way to evaluate relationships of organisms without the interference of human prejudices and biases. An emphasis on the distribution of derived characters had always existed in classification systems, but was often obscured by other similarities that were primitive and had no significance to understanding relationships other than inheritance from common ancestors. The documentation of character states became ever more important in dinosaur studies; so much so that most papers were considered as incomplete if they did not include at least one cladogram. Dinosaur phylogenies were a major focus of debate during the decades on either side of the year 2000, but have settled down now that many data matrices (with thousands of coded characters) are available for most taxonomic levels. Computerization revolutionized phylogenetic systematics by allowing researchers to compare hundreds or even thousands of characters in similar numbers of taxa to produce better understandings of the evolution of characters and the inter-relationships of dinosaurs. Theoretically, the coding of character changes is supposed to remove human biases, and given the amount of data that is being analyzed this is largely true. Over time, more taxa are discovered to fill in gaps, more characters are added into the analyses, and mistaken codings are corrected. So although no phylogenetic analysis is the final word, there is a progression towards a better understanding of relationships. As character matrices became larger and more complex, the computer programs and algorithms used for analyses evolved into those used by most palaeontologists today (Mesquite, PAUP, TNT). After many years of drastic changes and realignments of relationships, a certain amount of stability has finally settled onto our understanding of dinosaur relationships. However, because of the stratigraphic and geographic holes in the fossil record, no taxonomic system will ever be accepted by everyone. Every new discovery (be it a new taxon, or a new anatomical feature not previously recognized in a well-known dinosaur) has the potential of changing our understanding of the interrelationships of major clades of dinosaurs. At no time was this more obvious than when a paper was published by Baron et al. (2017; see also Norman et al. 2022) questioning the interrelationships of what had been accepted for more than a century as the two major clades of dinosaurs – Ornithischia and Saurischia.

On a somewhat smaller scale, but nevertheless interconnected, are the different tendencies of palaeontologists to name dinosaur species. Late in the 19th Century, dinosaur studies were dominated by “splitters”, palaeontologists like E.D. Cope and O.C. Marsh, who assumed that every new specimen recovered potentially represented a new species of dinosaur, regardless of how complete or incomplete it was. Many of these were synonymized in short order when it was recognized that the material was inadequate to define any animal to the species level, or when it was recognized that they were the same animals as previously named species (Benton 2008a, 2008b). However, complete skulls and/or skeletons continued to be classified as different species on the basis of anatomical differences that could well have represented preservational differences, and/or individual, ontogenetic or sexual differences. A more biological approach emerged with the Dinosaur Renaissance, and large numbers of specimens were reassessed using statistical programs. Dodson (1975) did one of the most influential studies when he analyzed 36 specimens of 12 species of lambeosaurine hadrosaurs from the Campanian strata of Dinosaur Provincial Park, and found that many of the distinguishing characters could be accounted for by ontogenetic or sexual variation. On the basis of his research, he "lumped" the 12 species into three species, which is a lot more reasonable for what was considered as a single ecosystem spanning a relatively short period of geological time. His work influenced many other vertebrate palaeontologists, and for some time the tendency was for palaeontologists to lump taxa, rather than split them. Ironically, subsequent work has shown (Ryan and Evans 2005; Evans 2007; Mallon et al. 2012) that there are probably multiple faunal levels in Dinosaur Provincial Park, and several of the lambeosaurine species "lumped" by Dodson have been resurrected as valid.

In recent years, the proliferation of new discoveries, often from geographic areas or stratigraphic levels that were previously not known, plus a growing sense that it is more conservative to name new taxa if partial specimens are complete enough to be supported by phylogenetic analysis, has led to an acceleration of the naming of new dinosaurs. Whether or not we have entered a new phase of "splitting" is irrelevant in that the presentation of ideas so that they can be analyzed by others is an important part of the process. As pointed out by Benton (2008a, 2008b), the quality of the specimens being used to create new names is much better today than it was before the beginning of the Dinosaur Renaissance.

Are Dinosaur Skeletons Ever Complete?

After animals die, there are many things that can happen to their bodies. They can lie on the ground and decompose until even the bones are destroyed. More likely, they will be eaten by other animals, and a tyrannosaur would even destroy the bones by biting right through them or stepping on them. Sometimes the body will get buried (and fossilized) quickly enough after death to remain intact. Although this was probably a rare occurrence in a river system, it does happen (Fig. 9), and many virtually complete skeletons have been found in places like Dinosaur Provincial Park in Alberta, or the Nemegt Basin in Mongolia. In lakes, particularly those where volcanic ash settles out of the air and becomes part of the sediment, then whole skeletons can also be buried and preserved intact. A good example is the Jehol Fauna of northeastern China. The Solnhofen Limestones of Germany are derived from fine-grained deposits in lagoons, and preserved the exceptional *Archaeopteryx* specimens. Animals buried upright by sandstorms as whole skeletons in life positions are not uncommon in the Djadokhta and equivalent formations of China and Mongolia. But dinosaur skeletons do not have to be complete to be scientifically informative. Some bones and teeth are so distinct that there is no hesitation about identifying them when you find them.

The completeness of a dinosaur skeleton can also be correlated with the size of the animal. Small animals have a reasonable chance of being found as complete skeletons, often with preservation of soft tissues, in lagerstätten like the Jehol beds (Yixian Formation) of northeastern China or the Solnhofen Limestones of Germany, or even in aeolian beds like the Djadokhta Formation of Mongolia. However, taphonomic biases in fluvial deposits like the Dinosaur Park Formation of Alberta (Brown et al. 2013) and the Nemegt Formation of Mongolia (Jerzykiewicz et al. 2021) work against the preservation of small individuals (both immature specimens of large species and small-bodied species). In Dinosaur Provincial Park, skeletons of dinosaurs smaller than 60kg (estimated live body mass) are rarely found. There are exceptions like a juvenile *Chasmosaurus* (Currie et al. 2016) that even included skin impressions on one side of the body, and a *Saurornitholestes* (Currie and Evans 2020) that was virtually complete and lacked only a few bones that had been destroyed by erosion. Overall, however, small taxa are greatly underestimated in their diversity and abundance (Brown et al. 2013), and that there is an incomplete understanding of even well-known palaeoecosystems like the Dinosaur Park Formation. Curiously, the correlation between skeletal completeness and body size is not apparent in the Jurassic beds of the Morrison Formation (Leach et al. 2021).

Details of Soft Anatomy and Colour

Dinosaur 'skin' was found associated with skeletons as early as 1852 (Pittman et al. 2022) and with footprints since 1991 (Currie et al. 1991). One of the most spectacular early discoveries was a 'mummified' *Edmontosaurus annectens* skeleton recovered in Wyoming in 1910 (Sternberg 1909; Osborn 1912). But although this specimen was amazing when it was discovered and described, little or no skin had been recovered from the head. It was therefore surprising when a mummified specimen of the related *Edmontosaurus regalis* was discovered (Bell et al. 2014) with a fleshy 'cockscomb' on top of its skull and some different skin features on the neck region [Fig. 10]. Other studies on *Edmontosaurus* have revealed additional details (Drumheller et al. 2022; Libke et al. 2022). And although it was originally thought that only the outer surface of the skin was being preserved as impressions, recent analyses have revealed that in some cases there is still the original layering and structures (Barbi et al. 2019) of the skin, endogenously derived organics (Manning et al. 2009), evidence of sensory structures (Pittman et al. 2022) and even melanosomes (Zhang et al. 2010) – the structures that provide much of the colour in skin. The new interest in dinosaur skin came from careful re-examination of both specimens known for a long time, but also from the ability of technologies (including SEM, laser ablation, Laser-Stimulated Fluorescence, synchrotron) to provide greater details. Bell et al. (2022a, b) were even able to identify an "umbilical" scar (the first known from any pre-Cenozoic amniote) and a crocodile-like cloaca on a specimen of *Psittacosaurus* using Laser-Stimulated Fluorescence. Preservation of soft anatomy even provides evidence of how scavenging may be necessary for the preservation of certain soft-tissues (Drumheller et al. 2022).

Stimulated by the buzz caused by the release of Jurassic Park in 1993, many labs turned their attention to looking for genetic material in fossils. The search intensified with the report of the discovery of blood vessels in *Tyrannosaurus rex* (Schweitzer et al. 2005, 2007; Schweitzer, Suo et al. 2007). Broadly termed molecular palaeontology, these studies have been successful in showing that fossilization can include not only hard tissues like bone, but can also include osteocytes, layers of the skin, collagen fibres, muscle fibres, melanosomes and other tissues that were not visible by unassisted optical observation (Schweitzer et al. 2019; van der Reest and Currie 2020; Schroeter et al. 2022; Tahoun et al. 2022). If we ignore for the moment the feathered theropods of northeastern China (they will be discussed later), soft tissues (including in some cases possible genetic material) are now known for the theropods *Citipati* (Moyer et al. 2016), *Shuvuuia* (Schweitzer et al. 1999) and *Tyrannosaurus rex* (Schweitzer et al. 2005), the sauropod *Dreadnoughtus* (Voegele et al. 2022), the ankylosaur *Borealopelta* (Brown et al. 2017), and the hadrosaur *Brachylophosaurus* (Schroeter et al. 2017; Ullmann et al. 2022). Dinosaur feathers in amber, with colour shading, have been reported from Alberta (McKellar et al. 2011, 2012). There have been several reports of small dinosaurs trapped in Cretaceous amber from Myanmar, including a feather-covered tail (Xing et al. 2016). Shades of Jurassic Park!

Biomechanics

It was not that long ago that our understanding of how dinosaurs moved was coloured by a belief that these animals were overgrown versions of living reptiles. This was blatantly obvious as late as the 1950s in artwork, movies and even museum displays that portrayed dinosaurs with sprawling limbs and tails that dragged on the ground (Glut 1980). A major shift came in the 1960s and 1970s, when it became obvious that sprawling limbs could not hold up the great weight of a sauropod dinosaur, or that the tail functioned better as a counterbalance than as an additional appendage. The reconstruction of *Deinonychus* by R.T. Bakker in Ostrom (1969) heralded in the age of dancing dinosaurs (Bakker 1987) in dinosaur imagery, but also marked an increase in sophistication of the study of dinosaur biomechanics. More focussed studies of anatomy examined the direction and range of movements possible at the joints. Dinosaur trackways revealed the sequence of how the animals were actually stepping when they were alive, and gave a sense of how fast they may have been walking or even running.

Over the last sixty years, biomechanical studies have looked at cranial mechanics (including the analysis of jaw movements in ceratopsians, hadrosaurs (Williams et al. 2009), theropods and other types of dinosaurs), vertebral support and flexion, centres of gravity (Alexander 1989; Henderson 1999, 2006), and limb mechanics (Senter 2006; Senter and Robins 2006; Moore et al. 2022). Ceratopsian front limb posture is a great example of a long-standing debate of a biomechanical problem (Russell 1935; Bakker 1987; Johnston and Ostrom 1995; Paul and Christiansen 2000; Senter 2007) with two diametrically opposing interpretations. Some felt that the front limbs of ceratopsians were sprawling when they walked, others felt that the front limbs were held upright. The reality appears to have been somewhere between the two extremes (Rega et al. 2007; Thompson and Holmes 2007).

Growth and Variation

When dinosaur specimens were originally recovered, there was a failure to acknowledge that dinosaur species had growth series, individual variation and even sexual differences. There were exceptions of course, such as Dollo (1882), who mentioned the probability of ontogenetic and sexual variation in the *Iguanodon* specimens from Bernissart. The simplistic view for most workers, however, was that every specimen recovered probably represented a new species. Because of the large sizes of most dinosaur adults, and that they hatched from eggs that limited the size of the juveniles, there is a huge disparity between juvenile and adult sizes. The differences in body proportions meant that juveniles and adults can look surprisingly different, which can be further emphasized by anatomical features that only develop with approaching maturity.

With the recovery of large numbers of specimens from specific localities, however, then multiple morphs of single species could be recognized for the first time. One of the best examples is *Protoceratops*, collected by the Central Asiatic Expeditions of the American Museum of Natural History in Mongolia. Approximately 60 specimens were excavated between 1922 and 1925. Furthermore, eggs and nests of eggs were recovered from the same site (the Flaming Cliffs, now better known as Bayan Zag) that were also assumed to be *Protoceratops*. Unfortunately, this assumption associating the *Protoceratops* skeletal material with eggs is now known to be incorrect. Brown and Schlaikjer (1940) described the variation of the skulls and skeletons that had been collected, showing every growth stage from young to old individuals (Fig. 11). Subsequent expeditions to Bayan Zag and other Gobi localities have produced hundreds of additional specimens of protoceratopsians (Maryańska and Osmólska 1975; Dong and Currie 1993), including a nest of fifteen hatchlings (Fastovsky et al. 2011), which have led to numerous analyses of growth and variation (Kurzanov 1972; Dodson 1976). The eggs that were originally identified as protoceratopsian were subsequently shown to belong to oviraptorids, and the mystery of protoceratopsian eggs was resolved with the discovery of a nest of a dozen soft-shelled eggs with *Protoceratops* embryos (Norell et al. 2020). *Protoceratops* eggs had never been found before because the eggshells simply had not been preserved!

The eggs that were originally referred to *Protoceratops* from Bayan Zag had an association with another skeleton that told a story of life and death in the Gobi. On July 13th, 1923, the skeleton of a theropod dinosaur was found on top of a nest of what was supposedly *Protoceratops* eggs (Andrews 1932, 1943). This dramatic association was from the beginning thought to represent an example of a predator having died in a sandstorm caught in the act of stealing eggs from the nest of another species of dinosaur. The dinosaur was named *Oviraptor philoceratops* (Osborn 1924), which means “the egg thief that loves ceratopsian eggs”. The interpretation persisted for more than 70 years, until some remarkable discoveries were made in China (Dong and Currie 1996) and Mongolia (Norell et al. 1994) that showed another nest of eggs with an oviraptorid on top, and an oviraptorid embryo inside of what had previously been identified as a protoceratopsian egg. When we found the former in 1990, we immediately felt there was something wrong with the original interpretation of the *Oviraptor* and nest that had been found in 1923. Although it was possible that an egg-eater might remain with its food even when its life was threatened by being buried in a sandstorm, it seemed much more likely that it would only stay with the eggs if in fact its maternal or paternal instincts told it to protect its own eggs, which is a well-studied behaviour known as broodiness in living birds. The pose of the dinosaur on top of the eggs also supported the idea of brooding rather than feeding (Dong and Currie 1996). Other remarkable and well-preserved oviraptorid embryos have now been discovered (Weishampel et al. 2008; Xing et al. 2021). In the meantime, many complete and nearly complete nests of the same type of eggs had been (and continue to be) discovered, particularly in China and Mongolia (Yang et al. 2019). Seven nests straddled by associated adult skeletons are now known from Mongolia (Norell et al. 1995; Clark et al. 1999; Fanti et al. 2012; Norell et al. 2018) and China (Jin et al. 2020; Bi et al. 2021). They overwhelmingly show the egg-laying behaviour of oviraptorosaurs, as well as their possible brooding behaviour (Hopp and Orsen 2004). An oviraptorid skeleton with a pair of eggs in the pelvic canal (Sato et al. 2005) confirmed what had already been determined from the paired arrangement of eggs in nests, some of which are up to three metres in diameter with some of the largest eggs and embryos known for dinosaurs (Pu et al. 2017). Even egg colour and brooding temperatures have been determined for some oviraptorids (Wiemann et al. 2017; Tanaka et al. 2018). Hatchling (Lu et al. 2013) and adult (Wei et al., 2022) forms are known for some species of oviraptorids, including *Yulong* (Fig. 12). The life cycles of other dinosaurs – including sauropods (Fernández et al. 2022) – are also well understood because the fossil record includes eggs, nests, nesting sites and all stages of growth.

People are often surprised that dinosaur eggs are relatively small compared with the gigantic sizes of some adult dinosaurs. Egg sizes are controlled to a large extent by the shells that enclose the growing embryos, and this is particularly true of the hard-shelled eggs of non-avian and avian dinosaurs. Maximum egg size is determined by how thick the shell becomes. The bigger an egg becomes, the thicker the shell has to be to support the weight. And the thicker the shell, the more difficult it is for the growing embryo to breathe through the pores in the shell, and the more difficult it is for the embryo to break out when it is ready to hatch. The disparities in sizes from hatchlings to adults became ever greater as the adult sizes increased. Imagine then that when the titanosaurid sauropods hatched from the volleyball-sized eggs in Argentina (Chiappe and Dingus 2001) and India (Dhiman et al. 2022), the hatchlings had to increase their body lengths by more than twenty times to reach adult sizes. And although non-avian dinosaur eggs are relatively small compared to body size with the eggs of modern birds (Varricchio and Jackson 2003), they are large compared with those of living reptiles. There are changes (such as changing the shape of an egg from a simple sphere to an elongate oval, or resorbing the eggshell from the inside of the shell as the embryo gets larger) that push the limits of theoretical egg size, but the largest known dinosaur eggs are only half a metre long (Pu et al. 2017).

Ecology

Trying to understand the palaeoecology of dinosaurs was an early line of research in the Dinosaur Renaissance, fortunately because of the large databases of specimens from places like Dinosaur Provincial Park (Béland and Russell 1978, 1979), the Djadokhta and Nemegt Formations of Mongolia (Osmólska 1980), and the Morrison Formation in the western United States (Dodson et al. 1980; Foster 2020). Although early studies noted some interesting stratigraphic and geographic trends (Sternberg 1950; Béland and Russell 1978), additional data from other sources – including bonebeds (Currie and Koppelhus 2010), footprints (Currie et al. 2003), microvertebrate sites (Dodson 1988) – soon provided evidence that either supported or refuted earlier palaeoecological conclusions.

Non-avian dinosaurs were highly adaptable animals that inhabited virtually all habitable terrestrial environments from north to south polar regions (Bell and Snively 2008; Rich and Vickers-Rich, 2000). Although most dinosaur fossils are recovered from fluvial environments of coastal lowlands (Dodson 1997), other environments where dinosaur fossils have been preserved include arid regions (Jerzykiewicz et al. 2021), islands (Sander et al., 2006), lakes (Benton et al. 2008) and polar regions (Rich and Vickers-Rich, 2000). However, these sites do not represent more than a small percentage of all of the environments where dinosaurs could have lived, because many (if not most) environments do not have the potential of preserving animals and plants as fossils, and therefore leave no fossil record. Furthermore, even environments that have good potential for fossil preservation nevertheless have preservational biases that make it difficult to interpret palaeoecological signals. It is therefore important to understand that there are always preservational biases that need to be accounted for. Common species in most environments have a better chance of being preserved, for example, and rare species rarely (if ever) enter the fossil record. If the sample size is small, then it is less likely that the proportions of fossil species recovered will represent the true percentages of the populations. Ideally, one would like to check the findings against some other type of resource. For example, the Nemegt Formation of Mongolia is unusual in that the numbers of dinosaur skeletons recovered suggest that the tyrannosaurid *Tarbosaurus* may have numbered almost half of the large dinosaurs living in the region during the Late Cretaceous (Currie 2016). It is highly unlikely, however, that any environment could support such a high percentage of large carnivores, so there is clearly some kind of a bias that favoured preserving so many skeletons of the tyrannosaurid. Confirmation of the existence of a preservational bias came with the discovery of footprints in the Nemegt Formation (Fig. 13), which suggested that hadrosaurs were far more common than tyrannosaurids in that environment (Currie et al. 2003). The Nemegt Formation also clearly shows a bias towards the preservation of large bodied animals. The recovery of rare remains of small animals (Funston et al. 2018a, b) can be compensated for through the use of rarefication curves. In Dinosaur Provincial Park, the same kind of bias exists towards the preservation of large skeletons, but isolated bones, bonebeds and microvertebrate sites have been instrumental for providing identifications of the smaller animals in the Cretaceous ecosystems of that region (Dodson 1973; Brinkman et al. 2007).

More recently, isotopes of calcium (Cullen et al. 2020; de Rooij et al., 2022; Martin et al., 2022), nitrogen (Ostrom et al. 1993), oxygen, and strontium (Cullen et al. 2022) have been analyzed in dinosaur bones to determine the local palaeoclimatic conditions (He et al. 2022), diets and changes in diets (Martin et al. 2022), niche-partitioning in the ecosystem (Cullen et al. 2022), trophic levels (Ostrom et al. 1993), and even the possibility of migration in some extinct dinosaurs.

Feathered Dinosaurs and the Origin of Birds

When the first skeleton of *Archaeopteryx* was discovered in 1861 (Owen 1863), in essence the relationship between non-avian and avian dinosaurs should have been solved. In fact, Huxley published two articles (1868, 1870) that clearly pointed the way to our present understanding of the ancestry of birds. These ideas were accepted and elaborated on by palaeontologists like Franz Nopcsa (Weishampel 2022). However, Heilmann did a series of articles in Danish that were eventually published in English as a book (1927). Although he clearly showed that dinosaurs and birds were closely related, he excluded the former from the ancestry of birds because of the loss of several features in their skeletons, such as the clavicles (wishbone). Ironically, the absence of a clavicle was in fact proven wrong several years before the book by Heilmann appeared in English by the discovery of a ‘wishbone’ in *Oviraptor*. The bone had been misidentified as an interclavicle (Osborn 1924; Barsbold 1976), however, and it was more than 50 years before Barsbold (1981) recognized that the oviraptorid “interclavicle” was in fact a wishbone.

After Heilmann (1927) proposed that dinosaurs and birds were close relatives that shared a common ancestor, many researchers searched for the ideal direct ancestor of birds. For the fifty years, debates focused on whether the direct ancestor of birds was a 'thecodont' (like *Ornithosuchus*), a lepidosauromorph or a crocodylomorph. With the discovery of *Deinonychus*, however, the debate once again included dinosaurs, and Ostrom (1973) did an eloquent appraisal of the characters showing that the relationship was based on far more than the comparisons done by Huxley more than a century earlier. The ancestry of birds was one of the most hotly debated topics in vertebrate palaeontology during the last 25 years of the twentieth century.

Many of those who supported the idea that dinosaurs were the direct ancestors of birds felt that feathers had to have evolved in non-avian dinosaurs for some purpose other than flight. Consequently in the 1970s, artists started to reconstruct dinosaurs like *Deinonychus* with feathers (Bakker 1975). But the debate raged on with more palaeontologists and ornithologists favoring any possible ancestor other than dinosaurs. This started to change dramatically in 1996 with the discovery of the first feathered dinosaur (*Sinosauropteryx*, Fig. 14) in northeastern China (Ji and Ji 1996; Chen et al. 1998; Currie and Chen 2001; Benton et al. 2021). As the debate continued to intensify about whether they were really feathers, or whether the animals were dinosaurs or birds, more feathered dinosaurs were discovered and described. For me, the turning point was the discovery of several specimens of *Caudipteryx*, a turkey-sized dinosaur with long, bird-like feathers behind the arms and at the end of the tail (Ji et al. 1998; Currie 1998). It did not matter whether it was classified as a non-avian or avian dinosaur because it had all of the characters expected for a transitional form. And unlike *Sinosauropteryx*, which had relatively simple feathers that some argued were not feathers at all, *Caudipteryx* had feathers that were indistinguishable from those of modern birds. Although some persist in arguing that birds are not derived from non-avian dinosaurs, their arguments have increasingly fallen on deaf ears as ever more species and specimens of feathered dinosaurs were discovered in other parts of the world, including China (Norell and Xu 2005; Benton et al. 2021), Mongolia (Schweitzer et al. 1999), and even Alberta (Zelenitsky et al. 2012; van der Reest et al. 2016). Feathers are of course only one of the anatomical features that unite dinosaurs and birds, and as pointed out by Gauthier (1986), there are far more characters in the skeletons that define the relationship between these two groups. Nevertheless, the discovery of feathered dinosaurs had a huge impact on the public perception of dinosaurs, and has been hailed one of the greatest palaeontological discoveries of the latter half of the twentieth century. And whereas dinosaurs had long been thought of as an evolutionary dead-end group, this perception changed with the realization that the Dinosauria is still one of the most successful vertebrates alive today, and is represented by more than eleven thousand living species of birds.

Physiology

Although researchers (Owen 1842, Wieland 1942; Russell 1965) started thinking about dinosaurs as being possibly warm-blooded more than 150 years ago, the idea received little attention until the description of *Deinonychus* (Ostrom 1969). Ostrom (1969) suggested dromaeosaurid theropods may have been more agile and active than previously thought, but it was his student R.T. Bakker (1968, 1972) who took the idea forward to convince the world that dinosaurs were warm-blooded (endothermic). This escalated into a number of major controversies (Thomas and Olson 1980) at the beginning of the Dinosaur Renaissance.

The physiology of an animal determines how much and what that animal eats. There have been numerous attempts to determine how much food the average sauropod must have eaten, but in fact there are too many variables to make such calculations with confidence. In contrast, the dietary preferences of most dinosaurs are relatively easy to interpret in general terms by looking at their anatomy, particularly that associated with teeth, jaws, hands and feet. The teeth and claws of most carnivorous dinosaurs clearly show adaptations for killing and processing their prey for example, whereas the teeth and jaws of herbivores are clearly adapted for processing plants. Large herbivorous dinosaurs (such as sauropods) may also have had gastroliths within the digestive system to assist with grinding up plants after they had been swallowed, or broad abdominal regions that probably had broad expansions of the gut that were used as fermentation vats (as in ankylosaurs). In recent years, anatomical clues for determining diets have been supplemented by the study of isotopic signatures of the bones.

Many lines of reasoning have been used to determine whether non-avian dinosaurs were ‘cold-blooded’ (ectotherms) or ‘warm-blooded’ (endotherms). Most people thought of dinosaurs as giant, cold-blooded reptiles until the beginning of the Dinosaur Renaissance. However, the microscopic bone structure in dinosaurs (Reid 1997) was characteristic of warm-blooded animals with high metabolic and fast growth rates. The upright posture of most dinosaurs (Seymour et al. 2012), and walking speeds calculated from trackways both suggested that at least most theropods and bipedal ornithopods were endothermic. Bakker (1968, 1972) suggested that predator-prey ratios indicated that the carnivorous theropods were endothermic (endothermic predators generally are greatly outnumbered by their prey, which can make up 90-95% of the animals in an ecosystem. If there were too many carnivores, then they would decimate their food resources and perish by starvation). The predator-prey ratios of dinosaurs in ecosystems like Dinosaur Provincial Park approximated those of modern ecosystems dominated by large mammals today.

Endotherms require high rates of ventilation to supply oxygen to the muscles for higher and more constant levels of activity. The soft anatomy associated with respiration is virtually never preserved in non-avian dinosaur skeletons. However, during the last 60 years in particular, osteological correlates (such as sinuses in the skulls of non-avian theropods, and pneumatic bones associated with the anterior parts of the skeletons of sauropods and theropods) have revealed the presence of bird-like air sacs that in most cases would have been associated with bird-like respiratory systems (O’Connor and Claessens 2004).

Histology suggests that most dinosaurs were fast-growing animals, although maximum growth rates can be calculated with confidence for relatively few forms because of the rarity of the earliest and latest growth stages (Myhrvold 2013). A tyrannosaur, for example, seems to have had fast growth from the time that it hatched, but increased that growth rate during its “teenage years”. Late during that period, the growth rate slowed down as it approached adult weight (and presumably attained sexual and/or somatic maturity). The timings of growth rates seem to have been similar in all of the Late Cretaceous tyrannosaurids, although *T. rex* became so much larger by having a much higher growth rate during its “teenage” growth spurt, when it was putting on up to 758kg/year in body weight (Erickson et al. 2004, 2015). ‘Sue’ (FMNH PR2081, Erickson et al. 2004) and ‘Scotty’ (RSM P2523.8) are two of the oldest *T. rex* specimens known, and both animals seem to have died in their late 20s (Persons et al. 2020). Although there has been some argument concerning specific results of the technique (Myhrvold 2013), overall it did not change the conclusion that *T. rex* reached its gigantic size by accelerating its midlife growth rates.

There are other lines of evidence used to suggest dinosaurs were warm-blooded, including brain size, and creative thinking seems to bring out more ways to test the idea all of the time. More recently oxygen isotope ratios in different parts of the body have been used to suggest that some large theropods and ornithischians were homeothermic (Barrick et al. 1996; Barrick and Showers, 1999), which is also supported by fossil biomolecules from deep in the family tree of dinosaurs (Wiemann et al. 2022). To this day, it is controversial as to whether or not all dinosaurs were warm-blooded, but since the discovery of feathered dinosaurs in 1996 most palaeontologists seem to accept that at least the feathered 'coelurosaurs' were warm-blooded. After all, why would their bodies be insulated if it were not to control body temperature.

Behaviour

Speculation on the behaviour of dinosaurs began almost as soon as dinosaurs were discovered. Originally those who discovered the bones must have engaged in some wild speculation as they tried to imagine what such large animals must have been like. This must have been particularly true for those people who were collecting dinosaur footprints, because the trackways themselves were showing what the dinosaurs were doing when they were alive. In his first book, C.H. Sternberg (1909) occasionally lapsed into descriptions that imagined the behaviour and environments of fossils that he was excavating. This expanded into a full three chapters of the second book (1917), which may have been influenced by publication of the earliest science fiction books with dinosaurs by de Mille (1888), Doyle (1912) and Burroughs (1914). De Mille was a Canadian author, and the book was published eight years after his death. He included the first three known dinosaurs (*Hylaeosaurus*, *Iguanodon* and *Megalosaurus*), plus some of the marine reptiles that had been described up to that time.

Behaviour is of course a very broad topic that takes in an almost infinite array of potential topics. It covers everything from mating (Tanke and Currie 2000; Brown et al. 2021) and nesting behaviours (Dong and Currie 1996, Varricchio et al. 2009), to fighting and foraging/hunting behaviours (Farlow 1976b, Currie 2000, Currie and Eberth 2010), to migration (Currie 1992), to social behaviour and so much more.

The idea that certain dinosaurs moved in herds has been speculated on for a long time because of the discovery of accumulations of bones (both articulated and disassociated) of single species of animals like *Iguanodon* (Dupont 1878; Dollo 1882) and *Plateosaurus* (von Huene 1928), and of sub-parallel trackways of numerous individuals of single species (Bird 1944; Ostrom 1972). Sternberg (1970), Currie and Sarjeant (1979), and Horner (1982) are some of the early reports of bonebeds, nesting sites and trackway sites that suggest gregarious behaviour in dinosaurs. These reports proliferated throughout the intervening years and now include most major groups of dinosaurs, including allosaurids (Madsen 1976; Coria and Currie 2006), ankylosaurs (Burns et al. 2015), ceratopsids (Langston 1975; Currie and Dodson 1984; Ryan et al. 2001; Currie et al. 2008), coelophysids (Colbert 1989), dromaeosaurids (Ostrom 1969; Maxwell and Ostrom 1995), hadrosaurids (Rozhdestvensky 1957; Varricchio and Horner, 1993), megaraptorans (Currie and Azuma 2006), ornithomimids (Kobayashi and Lu 2003; Varricchio et al. 2008; Cullen et al. 2014), oviraptorosaurs (Funston et al. 2016; Funston et al. 2020), sauropods (Lockley 1991), spinosaurids (Fabbri et al. 2022), troodontids (Varricchio 1995), and tyrannosaurids (Currie 2000; Currie et al. 2005; Currie and Eberth 2010; Titus et al. 2021) are just a few of the dinosaur families that have evidence for one or more species that seem to have been gregarious. There is no reason to think that all dinosaurs were gregarious all of the time, but there is at least enough evidence to show that they were gregarious under at least some circumstances or at certain times of the year.

Migration is one way to explain herding behaviour (Currie 1989, 1992), and if one uses the simplest interpretation of the word ‘migration’ as the movement from one area to another, then there is absolutely no question about dinosaurs having migrated. However, the usual sense of the word suggests that migrating animals move on set paths on an annual basis. We know from bonebeds that many species of dinosaurs – especially ceratopsians, ornithopods and sauropods – died in massive groups (sometimes thousands of individuals) that suggest they were living in herds up until the times of their deaths. There are also footprint sites (Ostrom 1972; Currie and Sarjeant 1979; Henderson et al. 2022) that show gregarious behaviour in ornithopods, sauropods and theropods. There are no terrestrial ecosystems (either extinct or extant) known that could survive the presence of hundreds or thousands of multi-tonne herbivores for more than very brief periods of time. Therefore, we can assume that the gigantic monodominant bonebeds of *Centrosaurus*, *Edmontosaurus*, *Maiasaura*, *Pachyrhinosaurus* (Fiorillo and Tykoski 2022), *Saurolophus*, *Styracosaurus*, and other animals represent herds of these animals that encountered catastrophic conditions when they were passing through the regions. Packs of tyrannosaurs and other carnivores may either have formed when the herds of herbivores were passing through the specific ecosystems, or may have actually been following the herds. Some speculate that these herds were moving in relatively restricted areas, whereas others have postulated that the annual migration cycles may have encompassed hundreds or even thousands of kilometers. Unfortunately, there are very few cases where we can track the ranges (either temporal or geographic) of single species of dinosaurs. Part of the problem is identifying species with confidence. For example, we know that the geographic range of specimens identified as *Edmontosaurus* extend from Colorado and Wyoming to Alaska, and monodominant bonebeds have been found within most of this range. However, how many species (or even genera) are represented within this range? Most people (Campione and Evans 2011) agree that there were at least two species – *Edmontosaurus regalis* in Late Campanian to Early Maastrichtian times, and *Edmontosaurus annectens* in Late Maastrichtian times. However, there is also disagreement (Mori et al. 2015; Takasaki et al. 2020) about whether the Alaskan edmontosaurin should be considered as a different genus and species (*Ugrunaaluk kuukpikensis*) or not, not to mention that up to a dozen species have been proposed for the clade generally accepted as *Edmontosaurus regalis*. The related genus *Saurolophus* has an even more extensive range, extending from California (Bell and Evans 2010; Prieto-Marquez and Wagner 2013), up through Alberta (Bell 2011) and across into Mongolia (Rozhdestvensky 1957; Dewaele et al. 2015; Bell et al. 2018). Without knowing the genetic continuity of either genus across their ranges, it is impossible to even speculate whether or not herds were migrating within subsets of their total ranges. Various lines of analysis have been employed to try and tease out the most logical explanations for the monospecific bonebeds, but there are still no solutions to understanding the distances covered by migrating herds. Nevertheless, the acceptance that dinosaurs did collect into herds was a major step ahead in the last half century, and perhaps we will find the answers in careful anatomical, histological, geochemical or other analyses.

Pathologies have been used extensively to determine behaviour in some dinosaurs, and have been able to show face-biting interactions between tyrannosaurs (Tanke and Currie 2000; Brown et al. 2021), intraspecific combat in ceratopsians (D'Anastasio et al. 2022), cannibalism in some theropods (Longrich et al., 2010), and even reproductive behaviour (Dhiman et al. 2022)

Extinction

The extinction of non-avian dinosaurs has been a source of speculation ever since dinosaurs were first discovered. In the first half of the 19th Century, many people (including scientists) did not believe that any animals had ever gone extinct. Consequently, when they started to find dinosaur bones, they assumed that dinosaurs must still be alive somewhere in the world. It was an explicit charge of the Lewis and Clark Expedition of 1802 that they were to try to find any evidence of animals that were supposed to be rare or extinct, because Thomas Jefferson had an interest in finding a living mastodon in the American West. As exploration penetrated into the "darkest corners of the planet", there were occasional reports of dinosaur-like creatures as late as the 1960s, but these were put aside into a speculative field often referred to as Cryptozoology.

Over the years, dinosaur extinction has been considered one of the great mysteries of Natural History, and the number of hypotheses proposed to explain their disappearance has been truly impressive (Benton 1990). Nicely summed up by American humorist William Jacob Cuppy in his book "How to Become Extinct" (1941), "The Age of Reptiles ended because it had gone on long enough and it was all a mistake in the first place. A better day was dawning at the close of the Mesozoic Era. There were some little warm-blooded animals around which had been stealing and eating the eggs of the Dinosaurs, and they were gradually learning to steal other things, too. Civilization was just around the corner".

One of the basic problems in explaining dinosaur extinction, has always been the fact that there are relatively few places in the world that document the end of the Cretaceous, but the theories proposed for dinosaur extinction (and other K-Pg extinctions) are attempting to explain a universal phenomenon.

By the 1960s, a new approach emerged with the discovery of an iridium anomaly at the end of Cretaceous deposits in both marine and terrestrial beds around the world. It was assumed initially that the widespread occurrence of concentrations of this rare-earth element indicated a catastrophic event from an extraterrestrial source (possibly a supernova, or more likely an asteroid that collided with our planet). Other potential sources, such as volcanism, have been proposed as alternative explanations for the iridium anomaly, or possibly as events triggered by asteroid impact(s). Regardless of the source of the iridium, the anomaly provided an almost universal marker horizon that represented a very narrow window of time.

The idea of the collapse of Cretaceous faunas and floras being caused by an extraterrestrial event has received widespread but not universal support in the intervening years. More controversial is whether dinosaurs became extinct gradually over a long period of time, or whether extinction caught them at a time when they were still increasing in diversity.

Again, one of the limitations of any of these arguments is how universal they are when there are relatively few sites that document good terrestrial faunas and floras leading up to the K-Pg boundary. The most hotly contested areas are the terminal Cretaceous beds that were on the western margins of the Western Interior Seaway, extending from Mexico to Alaska. The stratigraphic succession in Alberta seems to suggest a steady but gradual reduction in dinosaur diversity from Campanian to late Maastrichtian times (Sarjeant and Currie 2001). Without question, preservational and collecting biases are major problems at all sites, as are different interpretations of the taxonomic status and diversity of many dinosaurs. Rarification curves have been used to suggest that there is no reduction of diversity within Maastrichtian times, but it is still evident that other analyses support the idea that dinosaur diversity was declining in North America overall (Condamine et al. 2021).

Currently, the majority of people working in the field favour the idea that an extraterrestrial event (an asteroid crashing into the Yucatan Peninsula) led to a worldwide collapse of marine and terrestrial ecosystems, which in turn caused the extinction of non-avian dinosaurs and many other organisms. DePalma et al. (2019) have proposed that one site (Tanis) in North Dakota documents what happened immediately after the impact. Although a few people argue in favour of the survival of some dinosaurs (Fig. 15) in Palaeocene refugia (Fassett 2009; Fassett et al. 2011), the evidence has been disputed by others (Lucas et al, 2009).

We are unquestionably closer to understanding the extinction of non-avian dinosaurs, but there are still many aspects that will require considerably more research in future years. And the recognition of birds as part of the Dinosauria by most scientists shows that dinosaurs did not perish completely at the end of the Cretaceous, and that more species (11,000 plus) are known to be alive today than the sum of all fossilized forms!

Dinosaur Palaeontologists in the 22nd Century

We have seen the massive changes that have taken place in dinosaur palaeontology over the last 60 years since the beginning of the Dinosaur Renaissance. These changes have been driven by new discoveries, new technologies, changes in how manuscripts are reviewed and published, and public interest in the subject. But the changes are also being driven by changes within the palaeontological community itself.

First and foremost, dinosaur palaeontology is more international than it ever has been. In part, this is because progressively more students were coming to universities in North America and Europe during the 1980s and 1990s. However, now this trend is reversing as trained palaeontologists establish research and education programs in the countries of their birth. These trends are particularly evident in Argentina and China, where the majority of dinosaur experts in those countries are now trained in the countries of their birth. And the reputations of their dinosaur experts are just as strong, if not stronger, than those of experts from North America or Europe. Xu Xing, for example, is a Chinese specialist on dinosaurs who has published more papers in Nature and Science than any other dinosaur specialist. And although a few westerners go to those countries to do degrees, it is more likely that Argentinean and Chinese graduates who specialize in dinosaurs will take jobs in North America or Europe.

At one time research in the field was dominated by male palaeontologists, and there are few female names amongst the research papers on dinosaurs from the 1960s and 1970s.

However, changes were afoot during those decades as more women became involved with major expeditions and research projects. This is particularly true of the Polish-Mongolian Paleontological Expeditions that were led from 1965 to 1971 by the dynamic Zofia Kielan-Jaworowska (1969, 2013). The vast majority of dinosaur research papers that came out of those expeditions were written by female palaeontologists Magdalena Borsuk-Bialynicka, Teresa Maryańska, and Halszka Osmólska – and the last two in particular continued to be major influences on dinosaur research from the 1980s until they finished their careers. Although males continue to dominate the research positions for dinosaurs, there are now more females doing research on dinosaurs than there were males during the entire 1960s. A partial but impressive list of highly influential women (with doctorates, strong publication records, and students) working on dinosaurs includes Jennifer Anné (Children's Museum of Indianapolis, USA), Victoria Arbour (Royal BC Museum, Canada), Emily Bamforth (Philip J. Currie Dinosaur Museum, Canada), Alida Bailleul (Chinese Academy of Sciences, China), Karen Chin (University of Colorado, Boulder, USA), Julia Clarke (University of Texas, USA), Anusuya Chinsamy (University of Cape Town, South Africa), Kristina Curry-Rogers (Macalester College, USA), Stephanie Drumheller-Horton (University of Tennessee, USA), Victoria Egerton (University of Manchester, UK), Catherine Forster (George Washington University, USA), Zulma Gasparini (Universidad Nacional de La Plata, Argentina), Eva B. Koppelhus (University of Alberta, Canada), Susannah Maidment (Natural History Museum, UK), Angela Milner (Natural History Museum, UK), Jingmai O'Connor (Field Museum of Natural History, USA), Ariana Paulina-Carabajal (Instituto de Investigaciones en Biodiversidad y Medioambiente, Argentina), Emily Rayfield (University of Bristol, United Kingdom), Patricia Vickers-Rich (Monash University, Australia), Emma Schachner (Louisiana State University, USA), Mary Schweitzer (North Carolina State University, USA), Angelica Torices-Hernandez (Complutense University of Madrid, Spain), Tat'yana Tumanova (Orlov Museum of Paleontology, Russia), Allison Tumarkin-Deratzian (Temple University, USA), Jasmina Wiemann (Yale University, USA), Holly Woodward-Ballard (Oklahoma State University, USA), Lindsay Zanno (North Carolina Museum of Natural Sciences, USA), and Darla Zelenitsky (University of Calgary, Canada). Over the years I have supervised more than a hundred research projects (Postdoctoral, Doctoral, MSc, and senior undergraduate theses), of which more than a third were completed by women. Unfortunately, surveys done over the last decade suggest that the number of jobs occupied by men in the field of vertebrate palaeontology has remained at about 80% over the last decade. And it seems as if jobs for women in dinosaur palaeontology have remained in close synch with the number of jobs in vertebrate palaeontology.

Summary

Over the last 60 years, all aspects of scientific and public interest in dinosaurs have exploded. The number of known dinosaurs has more than doubled within that time period, and about thirty new species of dinosaurs are discovered every year. The number of dinosaur museums, travelling displays, parks and protected areas continue to increase, and public interest continues to be stimulated by a multi-billion-dollar movie, media, and toy industry founded on our interest in dinosaurs. More importantly, however, the number of paid positions for people to do research on dinosaurs has gone from half a dozen more than 150. About 20% of these researchers are women. Internationally, the increased number of researchers (and their students) are recovering new specimens (which reveal not only new species but incredible facts about their biology), and publishing hundreds of research results in peer-reviewed scientific journals. The research teams have become more multidisciplinary and multinational over the years. There has been a shift from single authored to multi-authored papers, and the papers are coming out faster than ever before. Although dinosaurs included some of the largest animals that ever walked the earth, there has been a shift from looking at the gigantic skeletons overall to working on progressively smaller parts of even the largest specimens, using technologies like synchrotrons, CT scans, and X-ray Diffraction to learn things about dinosaur activity levels, behaviour, physiology, growth and variation, and even colour. But regardless of our increased understanding of dinosaur diversity and the number of species described, we have a long way to go. Dinosaurs are the icon of palaeontology, and to a degree of Science in general. New discoveries will continue to fuel interest in the Earth Sciences, and will continue to recruit new scientists from the young at heart.

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Figures

Figure 01. Royal Tyrrell Museum of Palaeontology (opened in 1985) as seen from the west side of the Red Deer River Valley. The badlands surrounding the museum expose strata of the Horseshoe Canyon Formation, and dinosaur skeletons have been recovered within several hundred metres of the building. Photo by P.J. Currie.

Figure 02. Fukui Prefectural Dinosaur Museum, Japan (opened in 2000) is one of the largest museums devoted to dinosaurs. The Museum, shaped like a gigantic dinosaur egg, is about 25km from the Katsuyama dinosaur site. Photo by P.J. Currie.

Figure 03. Two special issues of the Canadian Journal of Earth Sciences that were largely focussed on dinosaur research. The issue to the left is Volume 33, Number 4 from 1996, and was titled “Results from the Sino-Canadian Dinosaur Project, Part 2”. The cover art is by Donna L. Sloan, and shows a nesting oviraptorid burying her eggs as a sandstorm approaches. The artwork was done before the first feathered dinosaur fossil was found, and would be drawn differently today. Volume 47, Number 9 (2010) on the right was “A century of discoveries in the Late Cretaceous *Albertosaurus sarcophagus* bonebed of Alberta.” The *Albertosaurus* painting by Michael W. Skrepnick shows the aftermath of a different storm, where numerous bodies of the tyrannosaur have accumulated at the bottom of a stream after a catastrophic death event.

Figure 04. The Dragon’s Tomb at Altan Uul 2 in Mongolia. The photograph, taken in 2016, shows the partially excavated quarry where more than a dozen skeletons of *Saurolophus angustirostris* have been excavated, mostly by a Russian expedition in 1949. The drawings (from Jerzykiewicz et al. 2021) show the reconstruction of an adult skeleton (A), skulls of a juvenile (B) and adult (C, D) individual, and a reconstructed drawing of the articulated skulls and skeletons of six individuals of *Saurolophus*, as mapped in Efremov (1955). Photograph by P.J. Currie, and drawings by Matt Rhodes.

Figure 05. Portable XRF machine for reading the geochemical composition of fossils and the surrounding sediments. This was used to “fingerprint” dinosaur bones in the Nemegt Formation of Mongolia to help determine what sites poached specimens (which never have locality data when they are seized by authorities) may have come from. (Bell et al. 2018). Photograph by P.J. Currie.

Figure 06. Synchrotron X-ray microtomography of MOR 268 (left dentary from the lower jaw of a hatchling-sized tyrannosaurid from Montana). Abbreviations: mg, Meckelian groove; pit, pit at the anterior end of the Meckelian groove; spl, splenial. Teeth are numbered d4 to d10 and have been coloured blue. Modified from Figure 7 of Funston et al. 2020.

Figure 07. The badlands of Dinosaur Provincial Park (Alberta, Canada) are one of the richest dinosaur sites known. They were declared as the first UNESCO World Heritage Site established for palaeontological resources, have produced hundreds of original skeletons that are in more

than thirty institutions internationally, and have exposed millions of bones and teeth from bonebeds and microvertebrate sites. Photograph by P.J. Currie.

Figure 08. Two views of Quarry Q259 in Dinosaur Provincial Park. It seems that the specimen was originally uncovered in 1920 by George Sternberg. Rather than collecting the whole specimen, however, he only collected the skull, which went to the collections of the University of Alberta in Edmonton. It was eventually described as the holotype of *Corythosaurus excavatus*, and it was assumed by most researchers that it had been found without a skeleton. However, the quarry was found in 1992 with the by now badly eroded hadrosaur postcranial skeleton. In 2011 (Tanke and Russell 2012), a newspaper from 1920 was found in the talus below the quarry, and it was realized that this is probably the skeleton that goes with the holotype of *Corythosaurus excavatus* (Bramble et al. 2017). The skeleton was excavated in 2012, and re-united with the skull at the University of Alberta. Photographs by P.J. Currie.

Figure 09. An almost complete skeleton of the tyrannosaurid *Gorgosaurus libratus* found in Dinosaur Provincial Park in 1991. The head was pulled back over the hips, and the tail was pulled forward, as the muscles and ligaments dried out along the top of the backbone. This is the typical ‘death pose’ that a lot of dinosaurs are found in, and can also be evident in carcasses of modern animals as well (particularly those with long necks). Photograph by P.J. Currie.

Figure 10. Oval clusters of polygonal basement scales on the neck an *Edmontosaurus regalis* (UALVP 53722) from the Wapiti Formation of Alberta. Photograph by Phil Bell.

Figure 11. The Flaming Cliffs (Bayan Zag) of Mongolia have produced hundreds of specimens of *Protoceratops*, in the past 100 years. The *Protoceratops* skull was found thirty km away at Tögrögiin Shiree in 1986, and represents what Brown and Schlaikjer (1940) referred to as a large male individual. Photos by Philip J. Currie.

Figure 12. The skull of *Yulong mini*, a chicken-sized oviraptorid hatchling from the Late Cretaceous of Henan, China (Lu et al. 2013). The upper part of the figure is a photograph of the left side of the skull, whereas the lower part is a three-dimensional computer image produced by photogrammetry. The original computer image can be rotated in any direction for study. It looks a little taller than the specimen photograph because the view is slightly more ventral. The photograph was taken by Philip J. Currie, and photogrammetry was done by Dale Winkler (Southern Methodist University).

Figure 13. The Nemegt Formation of Mongolia has interbedded levels that either preserve dinosaur skeletons or dinosaur footprints. The dinosaurs in each of these two types of levels suggest two different compositions for the dinosaur fauna living in that area during the Late Cretaceous. In the footprint levels, hadrosaurs (lower left) greatly outnumber the ichnites of carnivorous dinosaurs (lower right). In the levels between the footprint layers, however, the tyrannosaur *Tarbosaurus* is much more common than the hadrosaur *Saurolophus*. Multiple lines of evidence suggest that there is some kind of preservational bias that favours the

recovery of tyrannosaurid skeletons between the footprint concentrations. Photos by Philip J. Currie.

Figure 14, lower left. The first feathered dinosaur recognized was *Sinosauropteryx prima*, which was found in 1996 in Liaoning in northeastern China. The specimen was split so that half is on one slab of rock (in Beijing at the National Geological Museum of China), and the counterpart (in this photo) is in the Nanjing Institute of Geology and Paleontology (Currie and Chen 2001). Upper right. Elongate feathers behind the arm of *Caudipteryx zoui* are too short to have been used for flight (Ji et al. 1998), but may have been used for display, or protecting eggs in the nest. *Caudipteryx* is also from the Early Cretaceous of northeastern China, but was related to oviraptorid dinosaurs. Pebbles in the lower right of the photograph are a mass of gastroliths for grinding up the vegetation that it swallowed to help it process food. Photos by Philip J. Currie.

Figure 15. Hadrosaur femur found in the Paleocene Ojo Alamo Formation of New Mexico. Some argue that such a large bone (1.07m long) cannot be reworked from the underlying Cretaceous rocks, whereas others feel the evidence is not convincing as long as there is a remote possibility of transport. Photograph by P.J. Currie.

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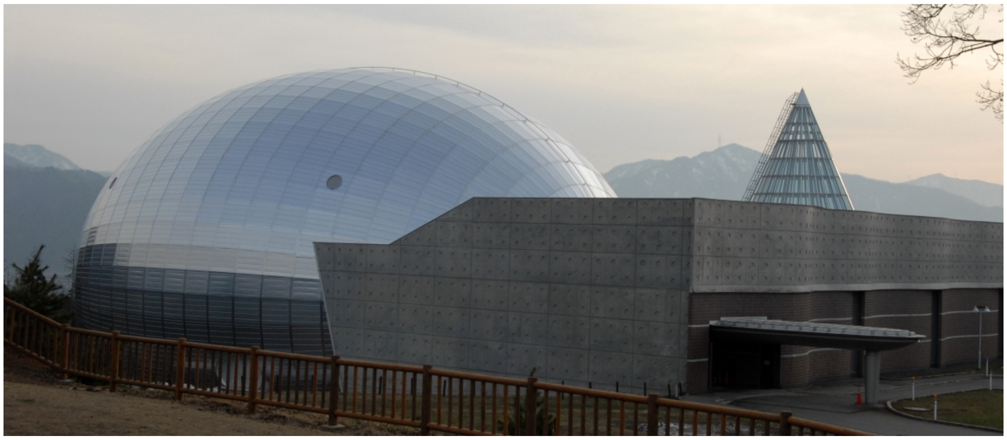

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327x141mm (300 x 300 DPI)

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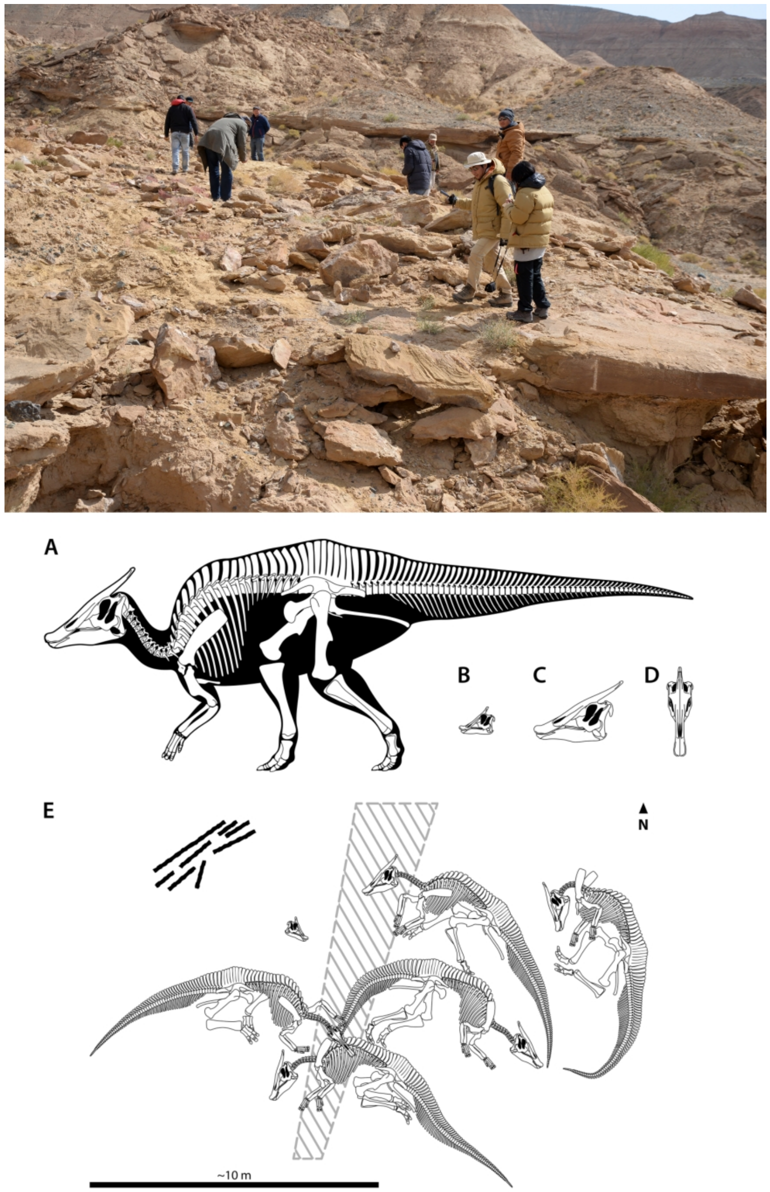

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127x199mm (600 x 600 DPI)

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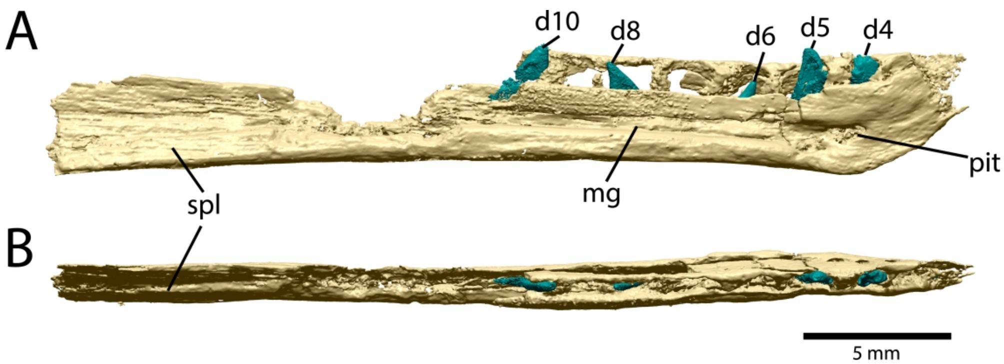

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314x110mm (300 x 300 DPI)

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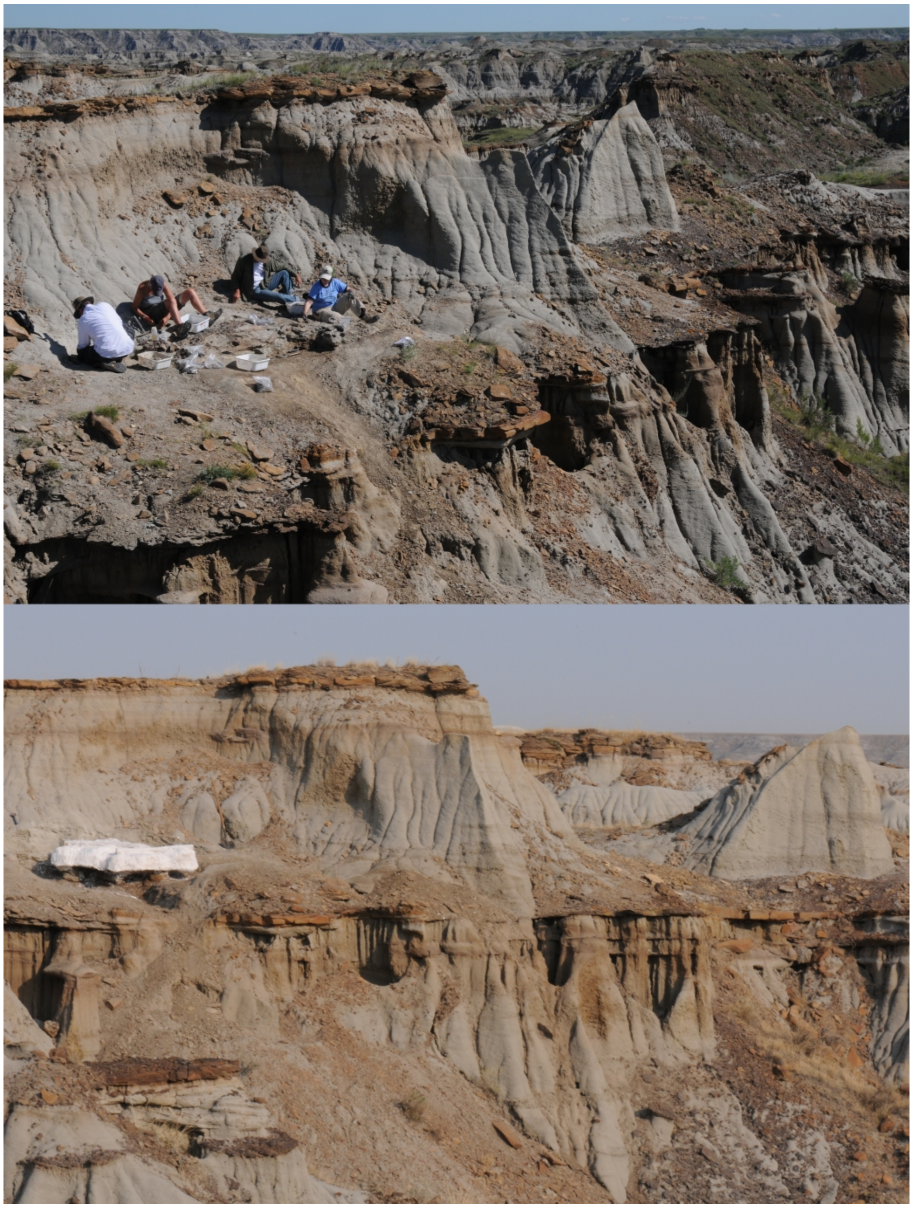

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181x239mm (600 x 600 DPI)

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101x71mm (600 x 600 DPI)

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133x84mm (600 x 600 DPI)

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161x199mm (600 x 600 DPI)

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226x320mm (300 x 300 DPI)

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127x173mm (600 x 600 DPI)

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105x207mm (600 x 600 DPI)

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144x380mm (240 x 240 DPI)