

Introduction: on systematics and morphological variation

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In recent years, dinosaurs have captured the attention of the public at an unprecedented scale. At the heart of this resurgence in interest is an increased level of research activity, much of which is innovative within the field of paleontology. Whereas earlier studies emphasized basic morphology and taxonomy, modern studies develop our understanding of what dinosaurs were like as living animals. More than ever before we understand how their bodies worked, how they behaved, how they interacted with their surroundings and with each other, and how they changed over time. Nevertheless, these studies still rely on certain basic building blocks, including knowledge of anatomy and taxonomic relationships.

One of the aspects that we understand better than before is ontogenetic, sexual, and individual variation within a species. This helps us to evaluate our understanding of dinosaurs as biological species. Studies in progress are giving us a good understanding of all forms of variability for one or more species of each of the major groups of dinosaurs, including theropods (Chapters 6, 7), hypsilophodonts (Horner and Weishampel 1988), hadrosaurs (Horner and Makela 1979; Dilkes 1988; Horner and Weishampel 1988), iguanodonts (Norman 1987), protoceratopsians (Brown and Schlaikjer 1940; Kurzanov 1972; Dodson 1975b; Maryańska and Osmólska 1975), ceratopsians (Chapters 16, 18; studies in progress on *Centrosaurus* and *Pachyrhinosaurus*), and ankylosaurs (Maryańska 1971; studies in progress on new *Pinacosaurus* material from China).

A major shift occurred late in the nineteenth and early twentieth centuries, spurred on in part by the revolution that occurred in biology (Allen 1969). At that time, experiments in genetics produced some insights into variation seen in the natural world. Gilmore was

one of the first to recognize the importance of this research when he raised the possibility that not all of the species of *Camptosaurus* he recognized years earlier were valid, "... *C. medius* ... may eventually be found to represent the female of the larger *C. dispar*, and that its fully adult development may be represented in *C. browni*." (Gilmore 1925, p. 392). It is this de-emphasis of morphology (however, see Rainger 1981, for an opposing view) and the recognition that a morphological species is not necessarily the same as a biological species that concerns many dinosaur paleontologists today. The First International Dinosaur Systematics Symposium was an attempt to gather as many dinosaur paleontologists as possible to unravel some of the problems surrounding the systematics of the dinosaurs. It was hoped that by examining specific groups, patterns might emerge to assist in the recognition of true species, sexual dimorphism, individual variation, and ontogeny.

It is difficult to imagine what it was like for those early paleontologists who had little or no comparative material and too few descriptive papers to rely upon. Consider, for example, what Joseph Leidy was faced with when F. V. Hayden presented him with a handful of teeth. It was clear to Leidy, an anatomist, that at least four distinct morphs were present to which the names *Palaeoscincus costatus*, *Trachodon mirabilis*, *Troodon formosus*, and *Deinodon horridus* were applied (Leidy 1856). Leidy seems to have considered them as biological entities, hence subject to variation, because the type material of *Trachodon mirabilis* also includes two teeth of a ceratopsian (Leidy 1860, pl. 9, figs 16–20). Leidy writes, "Two additional specimens, (figs. 16–20) found with the preceding, may perhaps belong to a different animal, but it is quite possible also that they belong to a different part of the jaws of the same animal" (Leidy 1860). But as Leidy began to acquire more dinosaur specimens, he seems to have made a subtle, but important, shift in the way he viewed the fossils. In 1865, he

illustrated and described *Hadrosaurus foulkii* in considerable detail. He also described and compared numerous other hadrosaur specimens to *Hadrosaurus foulkii*, but refused to give these specimens a name. As Leidy admitted, "When first examined and compared with the corresponding bone of *Hadrosaurus* the differences which were observable ... [were] not very remarkable" (Leidy 1865). Considering how similar the postcrania of hadrosaurs are, his caution in not referring these specimens to *Hadrosaurus foulkii* is surprising. He seems to have been influenced more by the differences this time than he was years earlier when he included ceratopsian teeth with *Trachodon*.

But it was Cope and Marsh who emphasized subtle morphological differences as grounds for naming new species. This was undoubtedly due, in part, to their intense rivalry. An example is Cope's naming five species of *Laelaps* based on teeth from a small area of the Judith River Formation, Montana. His descriptions (Cope 1876a,b) emphasized minor differences among the teeth. Others following in their footsteps maintained this methodology (e.g., Lambe 1902 for species of *Monoclonius* and Huene 1907–8 for *Plateosaurus*). It was inevitable that this strict adherence to morphological tradition, which resulted in a profusion of names, would be questioned. As early as 1898, Osborn wrote concerning sauropods, "It is a priori improbable that so many different genera of gigantic Saurians of similar size co-existed. It is against the principles of evolution that closely similar types of equal size should occupy the same territory at the same time. It appears moreover to the writer that the evidence which has been brought forward to demonstrate such an exceptional condition is inadequate ..." (Osborn 1898). Hatcher wrote, "it does not seem at all improbable that some of the remains which have been referred to *Pleurocoelus*, *Astrodon* or *Elosaurus* may in reality belong to the young of some of these genera of the large sauropoda [i.e., *Brontosaurus*, *Morosaurus*, and *Diplodocus*]" (Hatcher 1902). Gilmore was even more specific when he wrote concerning *Leptoceratops* from the Two Medicine Formation, "the much smaller size of the National Museum specimens is in all probability due to immaturity, as indicated by the open sutures of the skull and the noncoalescence of the vertebral processes" (Gilmore 1939).

Although it is now generally conceded that size is not an adequate criterion to establish a species of dinosaur, how much emphasis to place on morphological differences is still a problem, as may be illustrated by our own experience. In 1982, one of us (Carpenter) named *Pectinodon bakkeri* for small theropod teeth from the Lance Formation of Wyoming. Estes (1964) had earlier identified similar teeth as cf. *Saurornithoides*, but comparison with the holotype of *Saurornithoides mongoliensis* showed numerous differences making such an identification improbable. Nor could the teeth be matched to any other theropod. This presented a

quandary: the teeth were distinct from any known theropod, but was this grounds for a new name or should no name be attached to them? Because so many of the teeth were known, it was decided that a new name was justified. However, it was the discovery of a nearly complete dentary several years later that demonstrated *Pectinodon* was not a valid taxon. This dentary showed that the distinct morphology of *Pectinodon* teeth was due to their being from the posterior portion of the jaw (Currie 1987), a possibility which was not realized in 1982 from the available material.

Remarkably, individual variation does not appear to have been a factor considered by most dinosaur paleontologists. Certainly they were aware of this for Dollo wrote concerning *Iguanodon bernissartensis*, "[it] is represented by a considerable number of animals and among them they offer remarkable divergences" (translation in Rainger 1985). Rainger argues, "The need to identify a fossil organism and establish its taxonomic relation to other organisms was a principle objective of virtually all paleontological studies of the time ... To fulfill these objectives, Dollo had to concentrate on specific characters, the morphological features that distinguished each species [i.e., *Iguanodon mantelli* and *Iguanodon bernissartensis*], and as a result did not take into consideration variations within a species" (Rainger 1985). Marsh, Cope, von Huene, Osborn, and other early dinosaur paleontologists had much the same attitude.

Although morphological distinction played an important role historically in the naming of new species, this was not always the case. As Gilmore noted, "The occurrence of *Leptoceratops* in the Two Medicine formation would suggest, on geological position alone, that it probably represents a species distinct from these found in the Edmonton and St. Mary River formations" (Gilmore 1939). This idea that dinosaurs in different formations had to be different species was an outgrowth of the early stratigraphic work of William Smith. Smith had found that fossils of one formation differed from those in another, thus permitting him to make long-distance correlations. Although this work was done in marine beds, the concept was eventually carried over to non-marine formations, as seen by Marsh's reference to the *Atlantosaurus* beds or the *Triceratops* beds. Marine invertebrate paleontologists were the first to discover that a single formation may have a sequence of different species. Even mammalian paleontologists recognized that the same species could have broad geographical distribution, and thus be found in different formations (an early summary presented by Osborn 1910). But for some reason, dinosaur paleontologists have been slower to accept the presence of the same species in more than one formation.

Finally, one other factor that has influenced the naming of species had less to do with morphology or stratigraphy, than it did with politics. For example, Barnum Brown (1917) named *Monoclonius cutleri* for a

specimen having skin impressions found by William Cutler. Supposedly, one of the conditions Cutler imposed on Brown before giving it to him was that if the specimen proved to be a new species, it be named after him (Russell 1966).

Advanced prosauropods and primitive sauropods have long been known to resemble one another, leading von Huene (1932) to propose the term Sauropodomorpha for the two. It remains to be seen whether this is a natural group or not. Bonaparte (1986) noted several derived characters in the vertebrae of an unnamed advanced prosauropod from Argentina and those of the sauropod *Patagosaurus*. Sereno (1984) and Galton (1986), however, suggest that the Sauropodomorpha are not monophyletic.

The first prosauropod described was *Thecodontosaurus* (Riley and Stutchbury 1836) on the basis of isolated teeth. Since then, numerous genera and species have been named, especially by von Huene. Recent papers (see references in Galton 1984) have attempted to resolve some of the taxonomic problems associated with prosauropods, but there is much work yet to be done. In this volume (Chapter 3), Weishampel and Chapman use femora of *Plateosaurus* to illustrate the use of Principle Components Analysis in taxonomy. By using only a single monospecific assemblage, they have documented the degree of variation (possibly sexual and individual) in a population of prosauropods. In contrast with Galton (1984) who proposed to synonymize most *Plateosaurus* species into *P. engelhardti*, they tentatively conclude that there may be two species. They also document the presence of two morphs within a single population.

The first sauropod, *Cetiosaurus*, was described on the basis of vertebrae (Owen 1841). Since then, numerous sauropod species have been described from every continent except Antarctica. As with all other dinosaur groups, sauropod systematics has been confused by a proliferation of names. McIntosh (Chapter 4) does much to improve our understanding of all the families, genera, and species of sauropods, but especially those of the Morrison Formation. However, there are still many taxonomic problems that will have to be worked out (work in progress on Chinese sauropods by Dong and Russell).

Abundant material exists for studying the variability of many sauropods [juveniles being studied by Britt (1988) and Carpenter; massive numbers of individuals from single quarries in China including Zigong (Dong 1987a) and Xinjiang (Dong 1987b)], but these studies are hampered by the size of the material, and a lack of workers.

One of the first dinosaurs discovered and formally described was a carnivorous form (theropod) known as *Megalosaurus*, described by Buckland in 1824. Although it was the first to be discovered, it is still poorly known. Theropods tend to be rarer than her-

bivorous dinosaurs, and, as many of the species are small in size, their remains were often destroyed by scavengers and other natural processes. Nevertheless, good specimens are being recovered around the world, giving every indication of a remarkable range of diversity (Currie 1989a). Whereas we once assumed that all theropods could be assigned to only two lineages (Coelurosauria, Carnosauria), it is now realized that this approach was too simplistic and that many lineages developed over their long history (Gauthier and Padian 1989). New and remarkable species of theropods continue to be found (Bonaparte 1985; Chapter 9) that do not fit the mold. Although most species of theropods are known from only a few specimens, some forms – such as *Allosaurus* (Madsen 1976), *Coelophysus* (Colbert 1989; Chapter 6), and *Syntarsus* (Rowe 1989; Chapter 7) – are represented by numerous specimens from single localities, and can be used to evaluate the range of variation possible within single species of theropods. Other species (Chapter 10) may be represented by numerous specimens from wider geographic and stratigraphic ranges, which makes it more difficult to assess their relationships and variability. Finally, many theropods are only known from parts of their skeletons, although these may be diagnostic enough to provide some sense of variability in at least part of the animal (Chapter 8).

The Ornithopoda is a somewhat problematic group that at one time seemed to include all bipedal ornithischians. Accepted this way, the group is paraphyletic. Santa Luca (1980) attempted to redefine the Ornithopoda as those ornithischians having an obturator process, a condition that he considered derived. This was accepted by Maryańska and Osmólska (1985), but not as the sole criterion by Norman (1984) or Sereno (1984, 1986). There still is no agreement as to the composition of the Ornithopoda. Norman (1984) includes fabrosaur, hypsilophodonts, iguanodonts, hadrosaurs, and, surprisingly, ceratopsians. Sereno (1984, 1986) includes heterodontosaurs, hypsilophodonts, iguanodonts, and hadrosaurs in his concept of the Ornithopoda, whereas Maryańska and Osmólska (1985) include only the fabrosaur, iguanodonts, and hadrosaurs.

The first ornithopod named was *Iguanodon* (Mantell 1825) on the basis of several teeth. Ornithopods are one of the most abundant dinosaurs in Cretaceous strata, so it is not surprising that there is a surfeit of names. In Chapter 11, Norman continues his studies of iguanodontid systematics, and concludes that *Vectisaurus* is a juvenile *Iguanodon*. This gives Norman a basis for a cladistic analysis of the family Iguanodontidae.

Hadrosaurs were also first named for isolated teeth from the Judith River Formation of Montana (Leidy 1856). Morphometric analysis can be used to investigate the classification and phylogeny of hadrosaurs (Chapter 12), although even standard anatomical studies can produce some interesting results (Chapter

13). The greatest potential for the analysis of variation within single species of hadrosaurs remains with bone-bed material (such as the spectacular bone-bed near Choteau, Montana, being worked by the Museum of the Rockies, which may include the remains of more than 10,000 *Maiasaura* individuals) and nesting sites. Hatchlings of *Maiasaura* (Horner and Makela 1979) and embryos of *Hypacrosaurus* (Currie and Horner 1988) show variability even within a single nest.

Pachycephalosaurs, an intriguing group of dinosaurs, were among some of the first discoveries in western North America (Lambe 1902; Baird 1979), although it was a long time before there was enough skeletal material available to know what kind of animal they in fact represented (Gilmore 1924). Unfortunately, considerable confusion was introduced at the same time by the misconception that *Stegoceras* and *Troodon* were synonymous, when in fact the latter is a carnivorous dinosaur (Currie 1987). Over the years, a tremendous number of partial skulls have been recovered from around the world (Galton 1971; Maryańska and Osmólska 1974; Sues 1980; Sues and Galton 1987; Chapter 14), which have shown that pachycephalosaurs were successful in their diversity and numbers. Because of the number of skull caps recovered, it has been possible to look at the variation in pachycephalosaur species (Chapter 2; Chapman et al. 1981).

Stegosaurs are still poorly understood in spite of a good bone-bed known for *Kentrosaurus* (Hennig 1915; Janensch 1925; Galton 1982a), as much of the material has not been completely prepared or described. Juvenile specimens of *Stegosaurus* (Galton 1982b) and related forms (Galton 1981, 1983) provide ontogenetic information on this group of dinosaurs. With all of the new stegosaur material being recovered in China (Chapter 19), there is some hope for a better understanding of variability of at least mature specimens.

Hylaeosaurus armatus has the distinction of being the first ankylosaur named (Mantell 1833) and also of being the first dinosaur named from more than a few bones or teeth. This seemingly good start for ankylosaurs was upset by the naming of *Palaeoscincus costatus* (Leidy 1856) on the basis of a single tooth. This caused innumerable taxonomic problems when skulls and partial skeletons of ankylosaurs were discovered years later. The teeth associated with this new material were frequently compared to *P. costatus*, although the taxonomic validity of using ankylosaur teeth has never been demonstrated. Coombs (Chapter 20) examines this crucial problem and concludes that there is so much positional and individual variation that teeth cannot be used for ankylosaur taxonomy. This is an interesting contrast to the situation in theropods (Chapter 8), and shows that generalities ("all dinosaur teeth are taxonomically useful" or "no dinosaur teeth are taxonomically useful") should be avoided. Ankylosaur armor is commonly found in Cretaceous sediments, and

in Chapter 21 Carpenter demonstrates that it can be taxonomically useful to distinguish two sympatric species of ankylosaur. Ankylosaurs have generally always been relatively rare, isolated finds, making it difficult to sort out variability and taxonomy. The discovery of six sibling *Pinacosaurus* specimens in China (Currie 1989b) opens up the potential for studies on individual and ontogenetic variation, building on work already done by Maryańska (1971).

The first ceratopsian teeth figured were identified as *Trachodon mirabilis* by Leidy (1856), but were subsequently assigned to the Ceratopsia (on the basis of anatomy) and to *Monoclonius* (Hatcher et al. 1907) for stratigraphic reasons. This foreshadowed the taxonomic problems that developed as more genera and species were described, and much work is still needed to rectify the situation. Papers in this volume (Chapters 15, 16, 17, 18) independently show that many characters previously used to diagnose species are due to ontogeny or sexual dimorphism. Sereno (Chapter 15) concludes that an understanding of the ontogeny of a species is necessary before it can be properly diagnosed. Using this tool, he concludes that there are four species of *Psittacosaurus*, two of which have only recently been named (Sereno and Chao, 1988; Sereno et al. 1988).

The problem of distinguishing *Monoclonius* and *Centrosaurus* is discussed by Dodson (Chapter 17). Both were initially named for fragmentary material and, consequently, have been the source of much confusion when complete skulls were later found. In his analysis of the skulls, Dodson uses biometric analysis as in previous studies on lambeosaurine hadrosaurs (Dodson 1975a) and *Protoceratops* (Dodson 1975b). He concludes, in contrast with Lehman (Chapter 16), that *Brachyceratops* is a valid taxon.

Centrosaurine ceratopsians promise to give us some of the best information on individual, sexual, and ontogenetic variation for any group of dinosaurs because of the discovery of numerous monospecific bone-beds in Alberta and Montana. Work in progress on *Centrosaurus apertus* (Currie 1981; Currie and Dodson 1984; Ryan, M., pers. comm.), a new species of *Pachyrhinosaurus* (Tanke 1988; Langston, W., pers. comm.), and *Styracosaurus* (Rogers and Sampson 1989) is showing considerable differences between juveniles and adults, and a range of variation amongst mature specimens. Once these studies are further along, we should be able to better understand the systematic position of small centrosaurines like *Avaceratops* (Dodson 1986), *Brachyceratops* (Gilmore 1917), and *Monoclonius* (Dodson and Currie 1988).

Chasmosaurine ceratopsian variation (ontogenetic and sexual) is exemplified by work done on a monospecific *Chasmosaurus* bone-bed. Lehman (Chapter 16) uses his results to assess the status of other ceratopsian species, and reaches the same conclusion as Ostrom and Wellnhofer (Chapter 18) that all specimens

of *Triceratops* can be assigned to a single species. The latter study is restricted to specimens from Wyoming, and it remains to be seen whether the size gradient noted by Sloan (1976) indicates a distinct species in Canada.

The first dinosaur ichnofossils were named by Hitchcock in 1836. These were the species *giganteus*, *tuberosus*, *ingens*, *diversus*, *tetradactylus*, *palmatus*, and *minimus* [generic designations were not made until 1845 (Lull 1953)]. What was Hitchcock's intent in proposing these names? "When I speak of species here, I mean species in oryctology, not ornithology. And I doubt not, that in perhaps every instance, what I call a species in the former science, would be a genus in the latter; that is to say, these different tracks were made by birds that were generically different" (Hitchcock 1836). Although Hitchcock acknowledged that "these names, implying only a resemblance, leave the real nature of the tracks open to discussion ...," he advocated using the Linnaean system: "I propose the term Ichnolite ... to be the name of the Class [and] I would divide this Class into Orders ..." (Hitchcock 1841). He later modified his intent when he wrote four years later, "hitherto names have been given to the footmarks and not to the animals. But since all geologists now admit that these impressions are real tracks, this paper attempts to name the animals that made them, and to classify and describe them, so far as it can be done from the data hitherto obtained" (Hitchcock 1845). But as more and more footprints began to accumulate, it became clear that naming footprints was not necessarily naming the animal. As Lull noted, "It has been deemed wise ... to keep the ichnite genera and species apart in their nomenclature from that applied to the actual bones, for it is at once apparent ... that footprint genera and species do not necessarily correspond in limitations or numbers with those of the actual animals which made the impressions ..." (Lull 1953). Thus ichnology went the full circle, from names used to identify the footprints to names identifying the trackmakers, and back to names identifying the footprints.

The use of names in ichnology is not without problems as Lull observed, "names given in Ichnology must be kept in a separate series which, were the trackmakers actually known, might result in two names given to the same animal, regrettable but unavoidable ..." (Lull 1953). It is the problem of using Linnaean classification on footprints that Sarjeant examines in Chapter 22. He advocates treating them as sedimentary structures that should not be named using the Linnaean system despite the provisions of the International Code of Zoological Nomenclature [International Commission on Zoological Nomenclature, 1985, Art. 1a, 1d, 10d, 13b, 23g, 42b(i), 66 and 67m]. It remains to be seen, however, whether dinosaur ichnologists adopt Sarjeant's proposals. They will certainly spark debate, which is good for the field.

Anyone attempting a serious study of dinosaurs is

eventually faced with a plethora of names, many based upon material so fragmentary that it is doubtful the specimen(s) would be collected today (e.g., the teeth of the holotype of *Trachodon mirabilis* Leidy 1856). Nevertheless, many of these names are intimately linked with the early growth of dinosaur paleontology, both in North America and Europe (e.g., holotypes of *Hadrosaurus foulkii*, Leidy 1858, and *Iguanodon* Mantell 1825). But lest we be too critical of these early paleontologists, it should be realized that the plethora of names is the logical outcome of the morphological tradition of vertebrate paleontology. This tradition emphasizes differences among specimens, often at the expense of normal biological variation. Hence, Gilmore's (1909) recognition of four species of *Camptosaurus* (*C. dispar*, *C. browni*, *C. nanus*, and *C. medius*) from a single quarry in the Morrison Formation is understandable.

So where do we stand today? Dodson (1987) has pointed out that about 40% of the 265 genera of dinosaurs currently recognized have been described since 1969. That is the highest percentage of named taxa since the early days (pre-World War II) of dinosaur paleontology. This high percentage is certainly due to the maturity of the "baby boom" generation and the present renaissance of dinosaur paleontology. There are more dinosaur paleontologists alive today than there have been altogether in the past (about 110 since 1969 compared to 66 between 1824 and 1939). But the contributions made by the pioneers of the past are often not adequately appreciated by the present generation. It is all too easy to scoff because of the systematic "mess" we have inherited, forgetting that if we can see farther and clearer, it is because we stand on the shoulders of giants (Marsh, Cope, Sternberg, Brown, Osborn, von Huene, and Nopcsa to name a few).

As long as dinosaur paleontologists continue to collect and analyze new material, it seems unlikely that dinosaur taxonomy will ever have a final resolution. We will certainly not approach the accuracy of biologists working with living animals unless we have access to karyological or albumin immunological data. Nevertheless, it is hoped that the results of the First International Dinosaur Systematics Symposium presented in this volume will do much to improve our understanding of dinosaur species.

References

- Allen, G. 1969. T. H. Morgan and the emergence of a new American biology. *Quarterly Review of Biology* 44:168-188.
- Baird, D. 1979. The dome-headed dinosaur *Tylosteus ornatus* Leidy 1872 (Reptilia: Ornithischia: Pachycephalosauridae). *Notulae Naturae* 456:1-11.
- Bonaparte, J. 1985. A horned carnosaur from Patagonia. *National Geographic Research* 1:149-151.
1986. The early radiation and phylogenetic relationships of

- the Jurassic sauropod dinosaurs, based on vertebral anatomy. In Padian, K. (ed.), *The Beginning of the Age of Dinosaurs* (Cambridge: Cambridge University Press), pp. 247–258.
- Britt, B. 1988. A possible “hatchling” *Camarasaurus* from the upper Jurassic Morrison Formation (Dry Mesa Quarry, Colorado). *Journal of Vertebrate Paleontology* 8 (Supplement to no. 3):9A (Abstract).
- Brown, B. 1917. A complete skeleton of the horned dinosaur *Monoclonius*, and a description of a second skeleton showing skin impressions. *American Museum of Natural History Bulletin* 17:281–306.
- Brown, B. and Schlaikjer, E. M. 1940. The structure and relationships of *Protoceratops*. *New York Academy of Sciences, Annals* 40:133–266.
- Buckland, W. 1824. Notice on the *Megalosaurus*, or great fossil lizard of Stonesfield. *Geological Society of London, Transactions* 1:390–396.
- Carpenter, K. 1982. Baby dinosaurs from the Late Cretaceous Lance and Hell Creek formations and a description of a new species of theropod. *Contributions to Geology, University of Wyoming* 20:123–134.
- Chapman, R. E., Galton, P. M., Sepkoski, J. J. Jr. and Wall, W. P. 1981. A morphometric study of the cranium of the pachycephalosaurid dinosaur *Stegoceras*. *Journal of Paleontology* 55:608–618.
- Colbert, E. H. 1989. The Triassic dinosaur *Coelophysis*. *Museum of Northern Arizona Bulletin* 57:1–160.
- Cope, E. 1876a. Description of some vertebrate remains from the Fort Union beds of Montana. *Academy of Natural Sciences of Philadelphia, Proceedings* 1876:248–261.
- 1876b. On some extinct reptiles and Batrachia from the Judith River and Fox Hills beds of Montana. *Academy of Natural Sciences of Philadelphia, Proceedings* 1876:340–359.
- Currie, P. 1981. Hunting dinosaurs in Alberta’s great bone bed. *Canadian Geographic* 101(4):34–39.
1987. Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology* 7:72–81.
- 1989a. Theropod dinosaurs of the Cretaceous. In Padian, K. and Chure, D. J. (eds.), *The Age of Dinosaurs*, Paleontological Society, Short Course Notes in Paleontology, no. 2, pp. 113–120.
- 1989b. Long distance dinosaurs. *Natural History* 6/89:60–65.
- Currie, P. J. and Dodson, P. 1984. Mass death of a herd of ceratopsian dinosaurs. In Reif, W. E. and Westphal, F. (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems*, short papers (Tübingen: Attempto Verlag), pp. 61–66.
- Currie, P. J. and Horner, J. R. 1988. Lambeosaurine hadrosaur embryos (Reptilia: Ornithischia). *Journal of Vertebrate Paleontology* 8 (Supplement to no. 3):13A (Abstract).
- Dilkes, D. W. 1988. Relative growth of the hind limb in the hadrosaurian dinosaur *Maiasaura peeblesorum*. *Journal of Vertebrate Paleontology* 8 (Supplement to no. 3):13A (Abstract).
- Dodson, P. 1975a. Taxonomic implications of relative growth in lambeosaurine hadrosaurs. *Systematic Zoology* 24:37–54.
- 1975b. Quantitative aspects of relative growth and sexual dimorphism in *Protoceratops*. *Journal of Paleontology* 50:929–940.
1986. *Avaceratops lammersi*: a new ceratopsid from the Judith River Formation of Montana. *Academy of Natural Sciences of Philadelphia, Proceedings* 138:305–317.
1987. Dinosaur Systematics Symposium. *Journal of Vertebrate Paleontology* 7:106–108.
- Dodson, P. and Currie, P. J. 1988. The smallest ceratopsid skull – Judith River Formation of Alberta. *Canadian Journal of Earth Sciences* 25:926–930.
- Dong, Z. M. 1987a. *Dinosaurs from China* (Beijing: Ocean Press).
- 1987b. Untitled section on saurischian dinosaurs. In Zhao, X. J. et al. (eds.), *Stratigraphy and Vertebrate Fossils of Xinjiang* (Beijing: Institute of Vertebrate Paleontology and Paleoanthropology). [in Chinese]
- Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. *University of California Publications in Geological Sciences* 49:1–180.
- Galton, P. M. 1971. A primitive dome-headed dinosaur (Ornithischia: Pachycephalosauridae) from the Lower Cretaceous of England and the function of the dome of pachycephalosaurids. *Journal of Paleontology* 45:40–47.
1981. *Crateosaurus pottenensis* Seeley, a stegosaurian dinosaur from the Lower Cretaceous of England, and a review of Cretaceous stegosaurs. *Neues Jahrbuch für Geologie und Paläontologie* 161:28–46.
- 1982a. The postcranial anatomy of the stegosaurian dinosaur *Kentrosaurus* from the Upper Jurassic of Tanzania, East Africa. *Geologica et Palaeontologica* 15:139–160.
- 1982b. Juveniles of the stegosaurian dinosaur *Stegosaurus* from the Upper Jurassic of North America. *Journal of Vertebrate Paleontology* 2:47–62.
1983. A juvenile stegosaurian dinosaur, *Omosaurus phillipsi* Seeley, from the Oxfordian (middle Jurassic) of England. *Geobios* 16:95–101.
1984. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. 1. Two complete skulls from Trossingen/Württemberg with comments on diet. *Geologica et Palaeontologica* 18:139–171.
1986. Prosauropod dinosaur *Plateosaurus* (= *Gresslyosaurus*) (Saurischia: Sauropodomorpha) from the Upper Triassic of Switzerland. *Geologica et Palaeontologica* 20:167–183.
- Gauthier, J. and Padian, K. (eds.) 1989. *The Age of Dinosaurs*, Paleontological Society, Short Course Notes in Paleontology, no. 2, pp. 1–210.
- Gilmore, C. 1909. Osteology of the Jurassic reptile *Camptosaurus*, with a revision of the species of the genus, and description of two new species. *U.S. National Museum Proceedings* 36:197–302.
1917. *Brachyceratops*, a ceratopsian dinosaur from the Two Medicine Formation of Montana. *U.S. Geological Survey, Professional Paper* 103:1–45.
1924. On *Troodon validus*, an ornithomimid dinosaur from the Belly River Cretaceous of Alberta, Canada. *University of Alberta, Department of Geology Bulletin* 1:1–43.

1925. Osteology of ornithopodous dinosaurs from Dinosaur National Monument, Utah. *Carnegie Museum Memoir* 10:385–409.
1939. Ceratopsian dinosaurs from the Two Medicine Formation, Upper Cretaceous of Montana. *U.S. National Museum Proceedings* 87:1–18.
- Hatcher, J. 1902. Discovery of remains of *Astrodon* (*Pleurocoelus*) in the *Atlantosaurus* beds of Wyoming. *Annals of the Carnegie Museum* 2:9–14.
- Hatcher, J. B., Marsh, O. C. and Lull, R. S. 1907. The Ceratopsia. *U.S. Geological Survey Monograph* 49:1–300.
- Hennig, E. 1915. *Kentrosaurus aethiopicus* der Stegosauride des Tendaguru. *Sitzungsberichte der Gesellschaft Naturforschender Freunde, Berlin* 1915:219–247.
- Hitchcock, E. 1836. Ornithichnology. Description of the footmarks of (*Ornithichnites*), birds on New Red Sandstone in Massachusetts. *American Journal of Science* 29:307–340.
1841. *Final report on the geology of Massachusetts*, Pt. III (Amherst and Northampton), pp. 301–714.
1845. An attempt to name, classify and describe the animals that made the fossil footmarks of New England. *Proceedings, Annual Meeting, Association of American Geologists and Naturalists, New Haven, Connecticut*, 6:23–25.
- Horner, J. R. and Makela, R. 1979. Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* 282:297–298.
- Horner, J. R. and Weishampel, D. B. 1988. A comparative embryological study of two ornithischian dinosaurs. *Nature* 332:256–257.
- Huene, F. von. 1907–8. Die Dinosaurier der europäischen Triasformation mit Berücksichtigung der aussereuropäischen Vorkommnisse. *Geologische und paläontologische Abhandlungen*, Supplement 1:1–419.
1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographie zur Geologie und Paläontologie* 4:1–361.
- Janensch, W. 1925. Ein aufgestelltes Skelett des Stegosauriers *Kentrosaurus aethiopicus* E. Hennig aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica* Supplement 7:257–327.
- Kurzanov, S. M. 1972. Sexual dimorphism in protoceratopsians. *Paleontological Journal* 1972(1):91–97.
- Lambe, L. 1902. New genera and species from the Belly River series (mid-Cretaceous). *Contributions to Canadian Palaeontology* 3(2):25–81.
- Leidy, J. 1856. Notices of remains of extinct reptiles and fishes discovered by Dr. F. V. Hayden in the bad lands of the Judith River, Nebraska Territory. *Academy of Natural Sciences of Philadelphia, Proceedings* 8:72–73.
1858. Remarks concerning *Hadrosaurus*. *Academy of Natural Sciences, Proceedings* 1858:215–218.
1860. Extinct Vertebrata from the Judith River and Great Lignite formations of Nebraska. *American Philosophical Society, Transactions* 11:139–154.
1865. Cretaceous reptiles of the United States. *Smithsonian Contributions to Knowledge* 14, pp. 1–135.
- Lull, R. S. 1953. Triassic life of the Connecticut Valley. *Connecticut Geological and Natural History Survey, Bulletin* 81:1–336.
- Madsen, J. H. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineral Survey, Bulletin* 109:1–163.
- Mantell, G. 1825. Notice on the *Iguanodon*, a newly discovered fossil reptile, from the sandstone of Tilgate Forest, in Sussex. *Philosophical Transactions of the Royal Society* 115:179–186.
1833. *Memoir on the Hylaeosaurus, a newly discovered fossil reptile from the strata of the Tilgate Forest.* (Geology of South-east England, London).
- Maryńska, T. 1971. New data on the skull of *Pinacosaurus grangeri* (Ankylosauria). *Palaeontologia Polonica* 25:45–53.
- Maryńska, T. and Osmólska, H. 1974. Pachycephalosauria, a new suborder of ornithischian dinosaurs. *Palaeontologia Polonica* 30:45–102.
1975. Protoceratopsidae (Dinosauria) of Asia. *Palaeontologia Polonica* 33:133–181.
1985. On ornithischian phylogeny. *Acta Palaeontologica Polonica* 30:137–150.
- Norman, D. B. 1984. A systematic reappraisal of the reptile Order Ornithischia. In Reif, W. E. and Westphal, F. (eds.), *Third symposium on Mesozoic Terrestrial Ecosystems*, short papers (Tübingen: Attempto Verlag), pp. 157–162.
1987. A mass-accumulation of vertebrates from the Lower Cretaceous of Nehden (Sauerland), West Germany. *Royal Society of London, Proceedings, series B* 230:215–255.
- Osborn, H. 1898. Additional characters of the great herbivorous dinosaur *Camarasaurus*. *American Museum of Natural History, Bulletin* 10:219–233.
1910. The Age of Mammals in Europe, Asia and North America. (New York: Macmillan).
- Owen, R. 1841. Report on the British fossil reptiles. *Report of the eleventh meeting of the British Association of Science* 11:60–204.
- Rainger, R. 1981. The continuation of the morphological tradition: American paleontology, 1880–1910. *Journal of the History of Biology* 14:127–158.
1985. Paleontology and philosophy: a critique. *Journal of the History of Biology* 18:267–287.
- Riley, H. and Stutchbury, S. 1836. A description of various fossil remains of three distinct saurian animals discovered in the autumn of 1841, in the Magnesian Conglomerate on Durdham Down, near Bristol. *Geological Society of London, Proceedings* 2:397–399.
- Rogers, R. R. and Sampson, S. D. 1989. A drought-related mass death of ceratopsian dinosaurs (Reptilia: Ornithischia) from the Two Medicine Formation (Campanian) of Montana: behavioral implications. *Journal of Paleontology* (Supplement to no. 3), 9:36a.
- Rowe, T. 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology* 9:125–136.
- Russell, L.S. 1966. Dinosaur hunting in western Canada. *Royal Ontario Museum Life Sciences Contribution* 70:1–37.
- Santa Luca, A. 1980. The postcranial skeleton of *Heterodontosaurus tucki* (Reptilia, Ornithischia) from the Stormberg of South Africa. *South African Museum, Annals* 79:159–211.
- Sereno, P. C. 1984. The phylogeny of the Ornithischia: a reappraisal. In Reif, W. E. and Westphal, F. (eds.), *Third*

- Symposium on Mesozoic Terrestrial Ecosystems*, short papers (Tübingen: Attempto Verlag), pp. 219–226.
1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Research* 2:234–256.
- Sereno, P. C., and Chao, S. C. 1988. *Psittacosaurus xinjiangensis* (Ornithischia: Ceratopsia), a new psittacosaur from the Lower Cretaceous of northwestern China. *Journal of Vertebrate Paleontology* 8:353–365.
- Sereno, P. C., Chao, S. C., Cheng, Z. W., and Rao, C. G. 1988. *Psittacosaurus meileyingensis* (Ornithischia: Ceratopsia), a new psittacosaur from the Lower Cretaceous of northeastern China. *Journal of Vertebrate Paleontology* 8:366–377.
- Sloan, R. 1976. The ecology of dinosaur extinction. In Churcher, C. S. (ed.), *Essays on palaeontology in honor of Loris Shano Russell* (Royal Ontario Museum, Life Science Miscellaneous Publication), pp. 134–154.
- Sternberg, C. M. 1927. Horned dinosaur group in the National Museum of Canada. *Canadian Field-Naturalist* 51:67–73.
1951. Complete skeleton of *Leptoceratops gracilis* Brown from the Upper Edmonton member on Red Deer River, Alberta. *National Museum of Canada, Bulletin* 123:225–255.
- Sues, H. D. 1980. A pachycephalosaurid dinosaur from the Upper Cretaceous of Madagascar and its paleobiogeographical implications. *Journal of Paleontology* 54:954–962.
- Sues, H. D. and Galton, P. M. 1987. Anatomy and classification of the North American Pachycephalosauria (Dinosauria: Ornithischia). *Palaeontographica A* 198:1–40.
- Tanke, D. H. 1989. Centrosaurine (Ornithischia: Ceratopsidae) paleopathologies and behavioral implications. *Journal of Vertebrate Paleontology* (Supplement to no. 3), 9:41a.