

# Summary and prospectus

It became apparent over the course of the Dinosaur Systematics Symposium that significant advances have been made in recent years in the number of species known, in understanding the anatomy and interrelationships of those species, in narrowing the gap between morphological and biological species, and in recognizing the significance of associated geological and paleontological data. In a paper delivered at the Symposium, Peter Dodson (1987) noted that there are 265 genera of dinosaurs recognized, forty percent of which have been described since 1969. For many attending the conference, this was the first time that it became evident that dinosaur research had finally reached a level of activity comparable to the surge at the turn of the century.

Nevertheless, the data base is still small, dinosaurian studies are still in their infancy, and the field is wide open for further development. In comparison with the number of species of vertebrates known to be alive today (in 1969, Mayr estimated that there are 8,600 extant species of birds, 3,700 species of mammals, 6,300 species of reptiles, and 2,500 species of amphibians), the number of dinosaur species known for their 140 million year history is insignificant. Although most dinosaurs were relatively large animals that were probably long-lived, there could have been thousands of species alive at any one time throughout the world, and the discovery of new forms (Chapters 8, 9, 14, 15, 19) is inevitably going to continue.

## **Paleontological species**

It is critical that we gain a better understanding of what a paleontological species is (Chapter 5; Fox 1986). Species are the bricks of the foundation on which we build all of our theories of relationships. Refinement of the species concept will lead to refinement of our clas-

sifications. And it does not end there. The usefulness of dinosaurs in biostratigraphy is improved by correct identifications of species. Much of the evidence used to interpret dinosaur physiology is based on our understanding of species. Correct identification of species is critical as well in behavioral studies. Multidisciplinary research on paleoecology gives us the best understanding of how dinosaurs interacted with their world. Yet it makes a tremendous difference to our understanding of any ecosystem if taxa are oversplit or overlumped. A biological species (Chapter 5) is a population of interbreeding organisms that produce viable offspring, and this is the only level within our classification schemes that has a nonarbitrary definition. Even so, it is often difficult for neontologists to define extant species, because there are many gray areas (such as circular speciation). Paleontologists generally cannot apply the definition of biological species to fossils because evidence of breeding behavior and the viability of offspring cannot be observed in extinct animals. In some ways this simplifies the task of the paleontologist (Mayr 1969), but ultimately this is less satisfying because alternative, arbitrary definitions must be used at the species level. It is not surprising that the emphasis of many of the papers in this book is towards developing a better understanding of dinosaurs as biological species (but see Chapter 22 for an opposing viewpoint). With the imperfections of the fossil record, it is impossible to equate paleontological and biological species in most cases. But recent work on bone-beds and nesting sites suggest that the equation can be made for at least one species in each major group of dinosaurs. These species then can serve to show the range of variation expected in at least closely related forms.

With a large number of well preserved specimens, it is possible to define a fossil species. However, paleontologists rarely have complete specimens, and suites of specimens of the same species are even more uncommon. The concept of form species was an essential

aspect of the earliest dinosaur studies (i.e., Leidy 1856), and binomial names are still assigned to parts of skeletons without knowing what the rest of the animal may look like. If species were named only on the basis of complete specimens, less than 10% of the dinosaurs would be valid. Sometimes, form species are more useful than species based on more complete material. This is particularly true since the introduction of bulk sampling techniques at microvertebrate sites. Teeth tend to be more common and readily identifiable than other parts of the skeleton, and are therefore more useful in paleoecological studies than nearly complete skeletons that lack skulls or other diagnostic parts.

One of the dangers of working with form species is that different names (at the species or higher taxonomic levels) may be given to different skeletal parts of the same species (Chapters 8, 20), thereby creating a false impression of diversity. Unfortunately, the options are usually less desirable. Unnamed skeletons tend to be ignored, even if they are significantly different from other specimens. In faunal studies, apparent diversity will be low. Partial specimens are sometimes assigned on speculation to established species, but this can also be misleading [Berman and McIntosh (1978) give an excellent account of the problems created when Marsh added a *Camarasaurus*-like skull to a restoration of *Apatosaurus*].

There will always have to be some give and take in the application of names to form species. And if the biological significance of a form species is not overstated, and form species are eliminated as more complete specimens are found, then this concept is quite sound.

The concept of distinguishing species by name on the basis of geographic and/or temporal separation is common. Often, this cannot be backed up by anatomical evidence, either because of preservational differences, or because there are no significant differences. But species can have long periods of existence, and can span stratigraphic boundaries. Furthermore, stratigraphic differences cannot be equated strictly with temporal differences, when in fact they can represent a combination of environmental differences (resulting in different lithologies) and time. The more widespread a formation is, the less likely it is that the formation boundaries are synchronous throughout a given geographic range. Time lines that cross stratigraphic boundaries are recognized rarely.

One would intuitively expect that relating dinosaur species to time lines would have more validity than to stratigraphic boundaries within any given area. However, this is not always the case. For example, Dinosaur Provincial Park and Devil's Coulee in southern Alberta are separated by only 300 kilometers, but represent different ecosystems. Some species (large and small theropods) may be shared by the two sites, suggesting those species were capable of existing in a range of ecosystems. However, it would appear that the lambeosaurine hadrosaurs and centrosaurine ceratopsians are specifically distinct at the two sites, even though radiometric dating

(Eberth et al. in press) of associated volcanic ashes show that the sites are synchronous. Further analysis in progress of ash beds at productive dinosaur sites in Montana and southern Alberta will almost certainly show that some dinosaur species had narrow environmental preferences, while others inhabited a variety of ecosystems. As with form species, the designation of new species based on stratigraphic, lithologic (environmental), or temporal differences has to be carefully analyzed for it to be biologically meaningful.

Similarly, the geographic ranges of different species are highly variable, and are dependent on environmental preferences, size and mobility, behavior (including migration), and other species characteristics that are difficult to analyze. Often the assumption is that widely separated sites are going to produce different species, even if no morphological differences are apparent. In support of this approach, *Pachyrhinosaurus canadensis* from Scabby Butte in southern Alberta is distinct from a new species of *Pachyrhinosaurus* (Langston et al. in preparation) from Grande Prairie, 500 kilometers to the north. Yet the latter does not appear to be distinct from a new specimen of *Pachyrhinosaurus* found 1,500 kilometers farther north in Alaska (Clemens pers. comm. 1988). It is possible that there are temporal and/or environmental differences between Scabby Butte and Grande Prairie to account for the presence of distinct species of *Pachyrhinosaurus*, but it is also evident that the new species had a wide geographic range. Questions like these can only be resolved by additional fieldwork and analysis. And because of the imperfections of the fossil record, we must always recognize that some evidence will never be found.

The recognition of fossil species is based primarily on morphological differences. With few exceptions (Chapter 22), only the hard parts of dinosaurs are preserved, and we do not know what kind of variation there may have been in the soft anatomy or coloration. Skin impressions are now known from a variety of dinosaurs (Osborn 1912; Lessem 1989), but they are still not common enough to be useful for detailed comparisons between specimens.

Footprints, including those with skin impressions, provide some evidence on the anatomy of the foot. Unfortunately, the same basic foot structure can be shared by many species, and therefore more than one species can make footprints that are morphologically identical (Chapter 22). Ironically, a single species (and even a single individual) can also produce a wide range of footprint morphotypes, depending on the type of activity the animal is engaged in and the type of substrate in which footprints are left. For these reasons, it is unlikely that ichnospecies can ever be related to biological species concepts. That does not mean that biological information cannot be extracted from footprints, which have proven very useful in biomechanical, physiological, behavioral, and other studies.

There are modern species that are morphologically identical, but are genetically distinct because of behavioral or other differences. Such differences cannot be seen directly in the fossil record of dinosaurs. Nevertheless, dinosaur behavior can sometimes be deduced from the fossil record (Horner and Gorman 1988), which may eventually give us some information on speciation.

### Classification

Classification of organisms is an artificial, often arbitrary concept to help us sort and file the tremendous variety of living things, and to help us make some sense of the world. Understanding the interrelationships of – and developing classifications of – dinosaurs takes up a significant proportion of overall research effort (Chapters 9, 11, 13, 16, 17, 19, 21). Like filing systems, some classification systems are better than others. The best classification systems will reflect closely our understanding of the relationships of organisms. Within recent years, cladistics has had a major influence on the classification of dinosaurs (Chapters 1, 9, 11). The emphasis is on derived characters shared by animals. Because of the imperfect nature of the fossil record, the difficulties in recognizing character states produced by convergent and parallel evolution, and problems in quantifying genetic change, cladistic classifications are still subject to different interpretations by researchers. As a consequence of this, classifications proposed by different workers for the same groups of dinosaurs do not necessarily come to the same conclusions. As in all fields of science, differences in opinion indicate where additional research is needed.

Sereno (Chapter 1) compares and contrasts the clade and grade concepts. These might be considered the cladistic and traditional methods, as the former only recognizes monophyletic taxa, while the latter permits paraphyletic taxa. Unlike other fields of vertebrate paleontology, dinosaur systematists have been slow to use cladistic analysis (Chapters 1, 9). Ornithischian dinosaurs have received the most benefit from this approach (Milner and Norman 1984; Norman 1984a,b; Sereno 1984; Cooper 1985; Maryńska and Osmólska 1985; Sereno 1986), although some papers have appeared on saurischian cladistics (Paul 1984; Gauthier 1986). Brinkman and Sues (1987) used cladistic analysis to conclude that *Herrerasaurus* and *Staurikosaurus* do not fit into the Saurischia–Ornithischia dichotomy.

### Problems in assessing variation

Morphological differences remain the most important way of assessing variation. In most cases, there are limitations to what can be done because few specimens may exist for any species. In other cases, large numbers of specimens, often exhibiting considerable variation, are difficult to work with because of their size. There is an inverse correlation between the size of a dinosaur and the amount of detailed work done on it. Papers on small theropods (Chapters 6, 7, 8) are more numerous than those

on sauropods (Chapter 4), even though the material is less common.

Biases introduced by preservational differences, collection and preparation techniques, and researchers are frequently encountered problems in the study of morphological variation. Even when there is an overlap of skeletal parts, differential crushing can make specimens of the same species look very different. Preservational biases can favor the fossilization of some parts of the body (for example, the massive femur of a hadrosaur is more likely to be preserved than its fragile skull bones), or individuals of certain sizes. Collecting biases are more common than most people realize, and can range from differences in training and search image, to selective collection of dinosaurs by type, size, or even skeletal part. As pointed out by Sternberg (1970), it is essential for dinosaur paleontologists to get into the field to assess the potential for preservational and collection biases. Another type of bias is discussed by Brett-Surman and Chapman (Chapter 12), who show how an individual's philosophy about taxonomy can influence the outcome.

Dinosaur fossils have always been considered as prizes for museums to display. Many hours are invested in the preparation and mounting of dinosaurs, which are frequently damaged by poorly trained temporary staff or hasty preparation schedules. Because many are collected for display value rather than research potential, they can be restored and mounted in such a way as to obscure details of the real bone. Published drawings and photographs sometimes include reconstructed sections as if they were real. When only casts are available for study, it may be impossible to distinguish the parts based on real bone from the reconstructed regions.

Genetic variability is expressed to different degrees in different parts of the skeleton. Some bones, such as the vertebrae, can be indistinguishable over a wide range of species. At the other end of the scale, variation in the shape of footprints can be enormous even within a single trackway of a single species (Chapter 22). Consequently, paleontologists have to assess the variation of each bone differently. Bones associated with feeding and locomotion are usually more variable than bones of the axial skeleton, and tend to be more useful in understanding speciation. However, they also tend to be more variable within any given species.

### Analysis of variation

The emphasis of the majority of papers presented at the Dinosaur Systematics Conference was the variation (individual, ontogenetic, sexual) manifest in dinosaur species. As discussed above, there are many factors that must be considered when trying to determine if specimens belong to the same species or not. In reaching a conclusion, one has in fact set the parameters for individual variation within the species. The more specimens there are for any species, then the more sound are the conclusions related to analysis of variation.

Bivariate and multivariate analyses in morphological studies have been greatly sped up by computers, which have proven invaluable in sorting large fields of morphological data so that patterns can be seen (Chapter 17; Dodson 1975a,b,c,d). Similarly, shape analysis using computers (Chapters 2, 3, 12, 14) takes away some of the subjectivity in morphological comparisons. Morphometrics in general are useful in quantifying individual variation, sexual dimorphism, and ontogenetic change.

Variation has been recognized for a long time in protoceratopsian dinosaurs from central Asia (Brown and Schlaikjer 1940; Dodson 1975b; Maryńska and Osmólska 1975). The specimens were recovered from an environment that preserved eggs, hatchlings, juveniles, and all sizes of adults. Because there were so many specimens recovered from a single, relatively small locality (the Flaming Cliffs at Bayn Dzak), it was relatively easy to see the range of variation possible in a single population.

Most collecting sites for dinosaurs are not good for preserving juveniles (Jepsen 1964; Carpenter 1982). One of the richest collecting sites is Dinosaur Provincial Park in southern Alberta, where only a small percentage of thousands of specimens are juveniles. There was a bias in the depositional regime that strongly selected against the preservation of small animals, including juvenile dinosaurs (Currie 1987). Nevertheless, the skeletons of immature animals do exist, but are difficult to identify because of the amount of change that can take place during growth. In his monumental study on the lambeosaurine dinosaurs of the Park, Dodson (1975a) reviewed 12 species of crested hadrosaurs and concluded that they represented only three species assignable to two genera. All of the variation could be attributed to different forms of quantifiable variation.

Until recently, papers assessing ontogenetic change and sexual dimorphism in other dinosaurs (i.e., Casier 1960; Rozhdestvensky 1965; Russell 1970) have appeared infrequently. With the discovery of nesting sites and the analysis of bone-beds where whole herds of animals perished, the situation has improved dramatically. At this time, 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, 10), hypsilophodonts (Horner and Weishampel 1988), hadrosaurs (Horner and Makela 1979; Currie and Horner 1988; Dilkes 1988; Horner and Weishampel 1988), iguanodonts (Norman 1987), ceratopsians (Chapters 16, 18; Currie and Dodson 1984; Tanke 1988; Rogers and Sampson 1989), and ankylosaurs (Maryńska 1971; Currie 1989).

As time goes on and more fieldwork and analysis is done on isolated bones and skeletons, bone-beds, footprint sites, and nesting sites, we will get a better handle on ontogenetic, sexual, and individual variation. This will help us to evaluate our understanding of dinosaurs as biological species, and will certainly help us refine our

physiological, ecological, and other inferred levels of biological studies.

### Prospectus

By the end of the conference, an overwhelming amount of data had been presented, of which this volume represents only a fraction of the information. A feeling emerged that dinosaur systematics had taken several steps forward, and that problems that appeared impossible to resolve a decade or two ago now seemed to be within striking distance. That is not to say that these are resolved, but simply that for the first time there is some hope that they might be. At the current levels of funding, it is unlikely that this will be an overnight process.

The discovery and recognition of embryos and hatchlings associated with eggs and nests from India (Mohabey 1987), Mongolia (Sochava 1972), Montana (Dilkes 1988; Horner and Weishampel 1988), and Alberta (Currie and Horner 1988), has provided us with good growth ranges for sauropods, hypsilophodonts, hadrosaurs, and possibly protoceratopsians. The recognition of juveniles has similarly allowed us to look at longer ontogenetic series for psittacosaur (Chapter 15; Coombs 1982), several species of protoceratopsians (Maryńska and Osmólska 1975), ankylosaurs (Maryńska 1971), sauropods (Dong 1987), and ceratopsians (Dodson and Currie 1988).

The study of eggs and nestlings can also provide information on individual variation. One of the three hadrosaur embryos collected by the Tyrrell Museum of Palaeontology in 1987 was 10% smaller than the other two, even though it was taken from the same nest. However, the best hope for looking at individual and sexual variation comes from bone-beds, particularly those that appear to have been mass death events of single species.

Sites continue to be discovered where large numbers of articulated skeletons are found associated in single quarries. Continued preparation and study of this material will provide our greatest source of data on variability within a single species.

Articulated skeletons found in great numbers in a single area, especially if it represents rapid burial over a short interval, can provide almost as much information as the bone-beds. Good examples include *Protoceratops andrewsi* from the Djadokhta Formation of Mongolia and China, and the lambeosaurines of Dinosaur Provincial Park. As these are almost invariably attritional death assemblages, all ages can be represented, provided the animals were living in the area at all times of the year.

Bone-beds come in many forms. Monospecific bone-beds have already been discussed in detail. Multi-faunal bone-beds, usually resulting from long term accumulations of animal remains from wide geographic areas, can provide large samples for the study of variation. However, the identity of elements at a species level is usually prohibitively difficult.

Microvertebrate sites are a special type of bone-

bed where there are large concentrations of teeth and bones, each of which tend to be less than one centimeter in length. These can be good for providing information on juveniles of many of the dinosaurs (Chapter 8), which in turn can provide information on ontogenetic growth. Microvertebrate sites are usually formed by hydraulic sorting, but occasionally these are concentrates within coprolites. It is conceivable that scat analysis could provide information on particular prey preferences of a carnivore, and that because any single coprolite is produced over a very short period of time, this would give data on the instantaneous variation of a prey species.

Footprints are common elements of the fossil record in some areas (Gillette and Lockley 1989). Although much of the variation is caused by the interaction of the animal with the substrate, nevertheless real variation can also be seen in the footprints themselves. For example, Currie and Sarjeant (1979) recognized juveniles of the ornithomimid *Amblydactylus* in the Lower Cretaceous rocks of the Peace River Canyon, as did Bird (1944) in the sauropod tracks at Glen Rose, Texas. If the footprints are associated with herding behavior, then one can be reasonably confident that some of the variation may be biological.

And museum collections cannot be neglected as a source of new and valuable information, as reanalysis of existing material continues to produce new species, further examples of intraspecific variation, new evidence of relationships, and new information on the biology of dinosaurs.

The new sources of information are enhanced by the maturation of dinosaur studies themselves. The way we look at the resources is more sophisticated than ever before. Cladistics, for example, has greatly refined our understanding of the relationships of dinosaur taxa. The computer continues to speed up and simplify virtually all aspects of dinosaurian research, while new techniques and equipment (CT scans, SEM, geochemistry) are producing data and results that were undreamed of even a decade ago. And more people are involved in the study of dinosaurs than ever before. In a few more years, it may be desirable to run the Second International Dinosaur Systematics Symposium, which will document all of those exciting changes that are taking place now!

## References

- Berman, D. S. and McIntosh, J. S. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Carnegie Museum of Natural History, Bulletin* 8:1-35.
- Bird, R. T. 1944. Did *Brontosaurus* ever walk on land? *Natural History* 53:60-67.
- Brinkman, D., and Sues, H.-D. 1987. A staurikosaurid dinosaur from the Upper Triassic Ischigualasto Formation of Argentina and the relationships of the Staurikosauridae. *Palaeontology* 30:494-503.
- Brown, B. and Schlaikjer, E. M. 1940. The structure and relationships of *Protoceratops*. *New York Academy of Sciences, Annals* 40:133-266.
- Carpenter, K. 1982. Baby dinosaurs from the Late Cretaceous Lance and Hell Creek formations and a description of a new species of theropod. *University of Wyoming, Contributions to Geology* 20:123-134.
- Casier, E. 1960. *Les iguanodons de Bernissart* (Brussels: Institut Royal des Sciences naturelles de Belgique).
- Coombs, W. P., Jr. 1982. Juvenile specimens of the ornithomimid dinosaur *Psittacosaurus*. *Palaeontology* 25:89-107.
- Cooper, M. R. 1985. A revision of the ornithomimid dinosaur *Kangnasaurus coetzeei* Houghton, with a classification of the Ornithomimidae. *South African Museum, Annals* 95:281-317.
- Currie, P. J. 1987. Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology* 7:72-81.
1989. 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).
- Currie, P. J. and Sarjeant, W. A. S. 1979. Lower Cretaceous footprints from the Peace River Canyon, B.C., Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 28:103-115.
- 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.
- 1975c. Functional and ecological significance of relative growth in *Alligator*. *Journal of Zoology, London* 175:315-355.
- 1975d. Relative growth in two sympatric species of *Sceloporus*. *American Midland Naturalist* 94:421-450.
1987. Dinosaur Systematics Symposium, Tyrrell Museum of Palaeontology, Drumheller, Alberta, June 2-5, 1986. *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. 1987. 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]
- Eberth, D. A., Thomas, R. G., and Deino, A. In press. Preliminary K-Ar dates from bentonites in the Judith River and Bearpaw formations (Upper Cretaceous) of Dinosaur Provincial Park, southern Alberta, Canada. In Mather, N. J. and Chen, P. J. (eds.), *Aspects of Nonmarine Cretaceous Geology, Proceedings of the Conference on Nonmarine Cretaceous Correlations, Urumqi, China 1987* (Beijing: Ocean Press).
- Fox, R. 1986. Paleocene no. 1. Species in paleontology. *Geoscience in Canada* 13:73-84.

- Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *California Academy of Sciences, Memoirs* 8:1–47.
- Gillette, D. D. and Lockley, M. G. (eds.), 1989. *Dinosaur Tracks and Traces* (New York: Cambridge University Press).
- Horner, J. R. and Gorman, J. 1988. *Digging Dinosaurs* (New York: Workman Publishing).
- 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.
- Jepsen, G. L. 1964. Riddles of the terrible lizards. *American Scientist* 52:227–246.
- Leidy, J. 1856. Notices of remains of extinct reptiles and fishes, discovered by Dr. F. V. Hayden in the bad lands of Judith River, Nebraska Territory. *Academy of Natural Sciences of Philadelphia, Proceedings* 8:72–73.
- Lessem, D. 1989. Skinning the dinosaur. *Discover* 10(3):38–44.
- Maryańska, T. 1971. New data on the skull of *Pinacosaurus grangeri* (Ankylosauria). *Palaeontologia Polonica* 25:45–53.
- Maryańska, T. and Osmólska, H. 1975. Protoceratopsidae (Dinosauria) of Asia. *Palaeontologia Polonica* 33:133–181.
1985. On ornithischian phylogeny. *Acta Palaeontologica Polonica* 30:137–150.
- Mayr, E. 1969. *Principles of Systematic Zoology* (New York: McGraw-Hill).
- Milner, A. and Norman, D. 1984. The biogeography of advanced ornithomimid dinosaurs (Archosauria: Ornithischia) – a cladistic-variance model. In Reif, W. E. and Westphal, F. (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems*, short papers (Tübingen: Attempto Verlag), pp. 145–150.
- Mohabey, D. M. 1987. Juvenile sauropod dinosaur from Upper Cretaceous Lameta Formation of Panchmahals District, Gujarat, India. *Journal of the Geological Society of India* 30:210–216.
- Norman, D. B. 1984a. 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.
- 1984b. On the cranial morphology and evolution of ornithomimid dinosaurs. *Zoological Society of London Symposium* 52:521–547.
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. F. 1912. Integument of the iguanodont dinosaur *Trachodon*. *American Museum of Natural History, Memoirs* 1:33–54.
- Paul, G. 1984. The archosaurs: a phylogenetic study. In Reif, W. E. and Westphal, F. (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems*, short papers (Tübingen: Attempto Verlag), pp. 175–180.
- 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 Vertebrate Paleontology* 9 (Supplement to no. 3):36A.
- Rozhdestvensky, A. K. 1965. Growth variability and some aspects of dinosaur systematics in Asia. *Paleontologicheskij Zhurnal* 1965:95–103.
- Russell, D. A. 1970. Tyrannosaurs from the Late Cretaceous of western Canada. *National Museum of Canada, Publications in Palaeontology* 1:1–34.
- 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.
- Sochava, A. V. 1972. The skeleton of an embryo in a dinosaur egg. *Paleontological Journal* 6:527–531.
- Sternberg, C. M. 1970. Comments on dinosaurian preservation in the Cretaceous of Alberta and Wyoming. *National Museums of Canada, Publications in Palaeontology* 4:1–9.
- Tanke, D. 1988. Ontogeny and dimorphism in *Pachyrhinosaurus* (Reptilia, Ceratopsidae), Pipestone Creek, N.W. Alberta, Canada. *Journal of Vertebrate Paleontology* (Supplement to no. 3)7:27A.