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THEROPOD PALEOBIOLOGY, MORE THAN JUST BIRD ORIGINS

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BUCKLAND's 1824 description of *Megalosaurus* initiated the study of the paleobiology of theropod dinosaurs. Given the limited material upon which he based his taxon, Buckland misconceived of the "Great Fossil Lizard of Stonesfield" as an enormous Jurassic varanid. The subsequent description of *Dryptosaurus* by COPE (1866) revealed the bipedal posture and reduced forelimbs of theropod dinosaurs, and the discovery of relatively complete skeletons of *Compsognathus longipes* WAGNER, 1859 (not initially recognized as a dinosaur) and of *Ceratosaurus nasicornis* MARSH, 1884 revealed much of the basic anatomy of the carnivorous dinosaurs. Theropod ichnology can be traced to the classic work of HITCHCOCK (1858).

The early 1900s brought to light the highly specialized anatomy of some of the Cretaceous theropods, such as the gigantic tyrannosaurids (OSBORN, 1905, 1906, 1916), ostrich-like ornithomimosaurs (OSBORN, 1916), sail-backed conical toothed spinosaurids (STROMER, 1915), and the various small-bodied derived coelurosaurs of Mongolia (OSBORN, 1924). The discovery of *Deinonychus* by OSTROM in the mid-1960s (1969a, b) revolutionized various concepts of dinosaur biology, reviving late 19th Century hypotheses of the possibility of dinosaurian endothermy and of the dinosaurian origin of birds. The latter concept was further expanded by phylogenetic analyses (e.g., GAUTHIER, 1986) that demonstrated that Aves lies within the coelurosaurian theropods, and thus that birds are the surviving part of the theropod dinosaur radiation; bolstering this hypothesis is the discovery of feathers in non-avian theropod taxa (CHEN, DONG & ZHEN, 1998; JI *et al.* 1998). Discoveries of extremely primitive theropods (SERENO & NOVAS, 1992; SERENO *et al.* 1993) from Argentina reveal the ancestral conditions of the carnivorous dinosaurs. Bizarre new theropod taxa, such as the therizinosauroids of Asia (PERLE, 1979) and the abelisaurids of Gondwana (BONAPARTE & NOVAS, 1985), continued to be discovered around the world in the latter part of the 20th Century: with the discovery of *Cryolophosaurus* HAMMER & HICKERSON, 1994, non-avian theropods have now been found on every continent. New analyses in the field of theropod ichnology (e.g., FARLOW, 1981; THULBORN, 1990; LOCKLEY, 1991) help to reconstruct the locomotory ability and diversity within the carnivorous dinosaurs, while functional morphological studies have examined theropod mastication (ERICKSON *et al*. 1996), grasping ability (GALTON, 1971), and cursoriality (HOLTZ, 1995).

In this volume we examine new advances in the study of the anatomy, taxonomy, systematics, ichnology, functional morphology, and distribution of theropod dinosaurs, with emphasis on the non-avian members of this clade. We have organized the twenty-nine papers in this volume around these major themes in research on Theropoda.

The understanding of the phylogenetic relationships and global distribution of theropod dinosaurs has increased greatly in recent years. A new phylogeny of theropods, incorporating these recent discoveries, is presented by Holtz provides a new comprehensive analysis of the phylogeny of theropod dinosaurs. Heckert & Lucas and Rauhut & Hungerbühler examine aspects of Triassic theropod diversity. Coria & Salgado describe for the first time a new theropod taxon from the Cretaceous of Argentina, which appears to represent a basal member of the abelisaur radiation. Jones & Chure report on the use of systematic radiological surveying techniques (a promising technology for future paleontological exploration), which resulted in the recovery of the skull of a new allosaurid species from the Upper Jurassic Morrison Formation. Additional new discoveries are also reported here, including new forms from the mid-Cretaceous of Argentina (Rich *et al*.; Calvo & Coria), and an unusual association of troodontid teeth with baby hadrosaurids (Ryan *et al*.).

The majority of the contributions concern the functional anatomy and possible behaviors of various theropod dinosaurs. Carpenter describes two key specimens indicating active predation attempts by theropod dinosaurs: the famous "fighting dinosaur" pair of the dromaeosaurid *Velociraptor* and the ceratopsian *Protoceratops*, and evidence of a failed attack by a large theropod (almost certainly *Tyran-*

nosaurus) on a hadrosaurid. The trophic apparatus (jaws and teeth) of theropods has received considerable attention: studies included herein examine the function of the jaws of allosaurids (Bakker), the dentition of *Troodon* (Holtz, Brinkman & Chandler), the jaws (and hindlimbs) of *Carnotaurus* (Mazzetta, Fariña & Vizcaíno), and the skull of *Tyrannosaurus* (Molnar). Tanke & Currie review the abundant but larger unreported evidence of head-biting behavior in a number of large theropod dinosaurs. Henderson compares the skulls of various forms of the Morrison Formation in terms of trophic and display apparatus, while Chure, Fiorillo & Jacobsen report on new examples of the prey bone utilization by theropods in the same stratigraphic unit. Moving posteriorly from the jaws, Chure discusses the diversity of form of the orbit between different theropod taxa. The hindlimb anatomy of theropods, and the implications of these in terms of the possible cursorial ability in some of these taxa, is the subject of papers by Christiansen and Paul. Concluding the section on functional anatomy and behavior, Currie presents a significant report of multiple individuals of tyrannosaurids form the same site in the Upper Cretaceous Horseshoe Canyon Formation of Alberta, and its implication for possible gregarious behavior between adult and juvenile individuals within this group.

The section on theropod ichnology begins with a personal philosophical examination of track morphology studies by Lockley. Reports of tracks of carnivorous dinosaurs from the Upper Triassic of Queensland, Australia (Thulborn), the Middle and Upper Jurassic of Portugal, Germany, and Uzbekistan (Lockley, Meyer & Santos), the Upper Jurassic and Lower Cretaceous of North America, Asia, and Europe (Lockley, Meyer & Moratalla), the Lower and lowermost Upper Cretaceous of Italy and Croatia (Dalla Vecchia), and the Upper Cretaceous of Brazil (Carvalho & Pedrão). Additionally, Loyal *et al*. present new information of the eggs probably referable to carnivorous dinosaurs from India.

Finally, two papers speculate on soft tissue structures of the non-avian theropods: the reproductive system (LARSON) and the earliest stages of feather evolution (GRIFFITHS).

Even as this volume went to press, significant new theropod specimens have been brought to light, among the most dramatic of which are the first documented feathered specimens of therizinosauroids (XU, TANG & WANG, 1999) and dromaeosaurids (XU, WANG & WU, 1999). The Theropoda remain a great source of study for current and future paleontologists: we hope this volume serves as a useful source in these explorations.

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