PERSPECTIVES: PALEONTOLOGY

Spinosaurs as Crocodile Mimics

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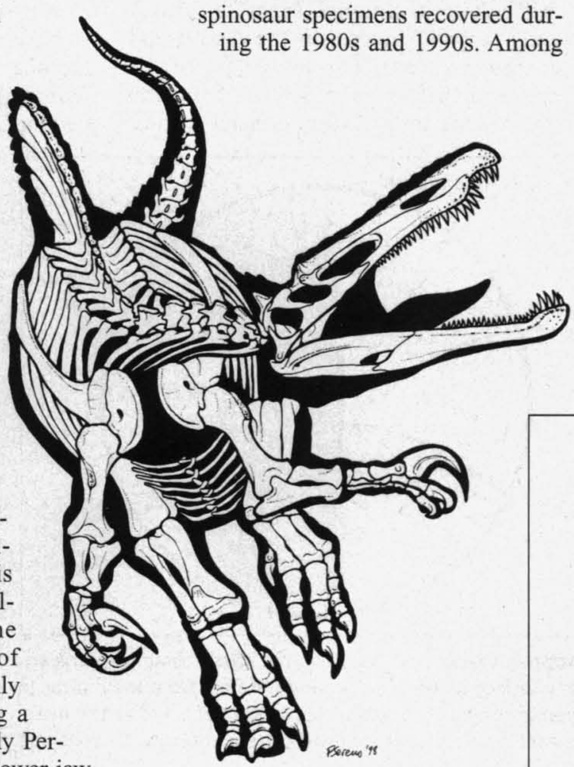
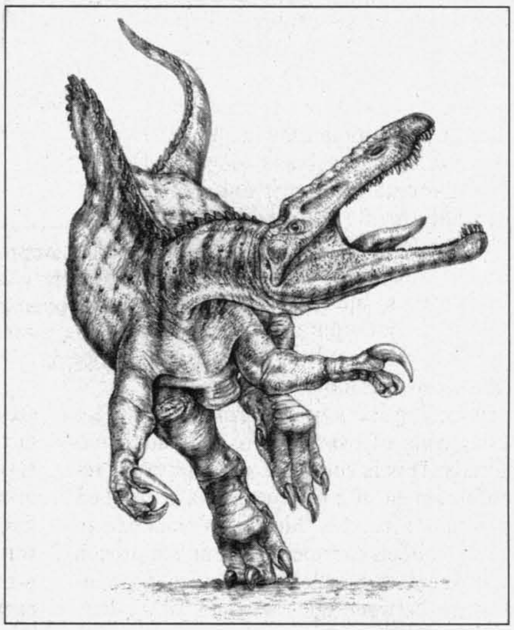
Theropod dinosaurs (bipedal, primarily carnivorous forms) have received widespread attention in recent years owing to their importance in understanding the origin of birds (*1*). However, the evolution of theropods was more than a "bird factory": Indeed, these dinosaurs represent one of the most successful radiations of terrestrial predators in Earth history. On page 1298 of this issue, Sereno *et al.* report (*2*) the discovery of a new theropod belonging to the specialized lineage known as spinosaurs, which provides important new insights on the evolution and adaptation of this group and their place in Mesozoic ecosystems.

One of the most mysterious theropods ever discovered is *Spinosaurus aegyptiacus*, first described by Ernst Stromer in 1915 on the basis of skeletal material from the lowermost Upper Cretaceous Baharîya Formation (about 95 million years old) (*3*). Its mystery is in part due to the highly specialized nature of its anatomy. The neural spines of the vertebrae of the trunk of the body were highly elongate (up to 1.69 m), forming a tall "sail" reminiscent of the Early Permian synapsid *Dimetrodon*. The lower jaw was quite long and slender for a large theropod, and the teeth were conical, rather than the bladelike serrated teeth found in most theropods (such as *Allosaurus* or *Velociraptor*).

However, part of the mystery of *Spinosaurus* lies in the fact that it was twice lost: once because of extinction sometime in the Cretaceous Period and again because of the destruction of Stromer's collection during the bombing of Munich in World War II. For many decades, paleontology's sole knowledge of spinosaurs came from Stromer's monographs (*3*).

In recent decades, new specimens of *Spinosaurus* and those of related dinosaurs have been discovered in Lower Cretaceous and lowermost Upper Cretaceous formations of Africa (*4*), Europe (*5*, *6*), and South America (*7*). Together, these fossils make up our knowledge of Spinosauridae, a radiation of unusual theropods known from the Barremian to the Cenomanian stages of the Cretaceous (about 125 to 95 million years ago). Although most of these fossils are only isolated teeth and bones, there have been some notable spinosaur specimens recovered during the 1980s and 1990s. Among these are *Baryonyx walkeri*, known from one of the most complete dinosaur specimens ever recovered in England (*5*, *6*) and *Irritator challengeri* and *Angaturama limai*, known from the main section of a skull and an isolated snout (possibly of the same species, or even the same individual, and published only a month apart) from Brazil (*7*). Sereno and colleagues report on the newest spinosaur fossil and one of the most complete ever discovered (*2*). Sereno *et al.* have named this new species from the late Early Cretaceous of Niger *Suchomimus tenerensis*, the crocodile mimic of Ténéré Desert (see figure).





Going fishing? Skeletal restoration of *Suchomimus tenerensis*, showing elongated crocodile-like snout and conical teeth. These adaptations may have been the result of changing from a diet of meat to one of fish.

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The relatively complete material of *Suchomimus*, combined with the discoveries of the 1980s and 1990s, increases our resolution of spinosaur anatomy, phylogeny, and functional morphology. By comparing this new discovery with previous specimens, Sereno *et al.* have determined which features of *Spinosaurus* are characteristic of the whole family (among them, the morphology of the lower jaws and teeth) and which are unique to that genus (including the eponymous elongated neural spines). Sereno *et al.* have combined knowledge of the skulls of *Baryonyx* and *Suchomimus* to discover that the heads of spinosaurs were even more narrow, slender, and crocodile-like than previously reconstructed (*5*). (Additional information from the relatively complete cranial material of *Irritator*, still under study, will help to fill in the elements missing in both *Baryonyx* and *Suchomimus*.)

The jaw and tooth morphology of spinosaurs is considerably different from that of typical theropod dinosaurs (for example, *Ceratosaurus* or *Allosaurus*). In the primitive condition for theropods, the snout is relatively tall and narrow ("hatchet-shaped"), and the teeth are bladelike, with a lenticular cross section at the base and a serrated ridge running up the front and back of each tooth. Such a skull shape is resistant to vertical compressive loads and functions most effectively as a slicer or slasher (*8*). Typical theropod skulls lack a well-developed ossified secondary palate; that is, they lack a hard bony surface on the roof of the mouth. As a consequence, they would be less resistant to torsional

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forces exerted on the skull during predation and feeding (*8*). The skulls of *Suchomimus*, *Baryonyx*, and their kin are long and narrow, and their teeth are subcircular in basal cross section, with either very fine serrations or none at all. The anterior end of a spinosaur snout is expanded into a pincerlike "terminal rosette," containing the largest teeth in the skull. As demonstrated by *Suchomimus* and other new discoveries, spinosaur skulls had a substantial secondary palate (formed by medial extensions of the maxillae).

The cranial adaptations in spinosaurs parallel those of crocodilians. Early crocodylomorphs had skulls similar to those of typical theropods and bladelike teeth with serrations running along the front and back margin (*9*). With the assumption of an aquatic habit, the snout of crocodilians became elongate, the bones of the palate joined to form a solid roof of the mouth with rearward-placed internal nostrils, and the teeth became conical (*10*). These changes have been considered adaptations toward a piscivorous (fish-eating) diet from one based primarily on the meat of terrestrial animals. A narrow snout may allow more rapid passage through the water, and teeth with a rounded cross section function better as piercers and graspers rather than as slicers and slashers (that is, as meat hooks rather than steak knives). The solid secondary palate of crocodilians allows them to absorb the torsional loads generated by struggling fish (and, in some species, by their habit of rolling in the water to disarticulate limbs from their prey) (*8*).

Might spinosaurs have been specialized fish eaters? This hypothesis has been suggested before by Charig and Milner (*5*) for *Baryonyx* on the basis of both the anatomical similarity with crocodilians and the presence of digestive acid-etched fish scales within the rib cage of the type specimen. Large fish are known from the faunas containing other spinosaurids, including the 3.5-m coelacanth *Mawsonia* in the mid-Cretaceous of northern Africa and Brazil (*11*), and the highly diverse fish community co-occurring with *Irritator* and *Angaturama* (*12*). Charig and Milner (*5*) indicate the presence of the acid-etched remains of a young specimen of the plant-eating ornithopod dinosaur *Iguanodon* in the body cavity of *Baryonyx*, so it almost certainly fed on the meat of terrestrial animals as well as fish.

The anatomical differences in the feeding apparatus of spinosaurs, regardless of the proportion of fish in their diet, may go some way in explaining the high diversity of extremely large theropods in North Africa in the mid-Cretaceous. *Spinosaurus* co-occurs with at least two other multiton theropods: the allosaur *Carcharodontosaurus* and *Deltadromeus*, a coelurosaur more closely related to advanced forms such as dromaeosaurid "raptors" and tyrannosaurs than to either allosaurs or spinosaurs (*13*), with possible evidence for an abelisaurid ceratosaur in the same region (*4*). Perhaps these different enormous carnivores were capable of coexisting by exploiting different parts of the potential food supply and in particular because spinosaurs had more immediate access to the freshwater part of the food web than theropods of more typical morphology.

Clearly the crocodile analogy does not extend beyond the skull of spinosaurs. The postcranial skeleton of *Suchomimus*, *Baryonyx*, and related forms lacks any particular specializations for aquatic life. Nevertheless, the remarkable skulls of spinosaurid dinosaurs represent an intriguing case of convergence between distantly related reptilian forms. Additionally, the skeletal specializations of *Suchomimus* helps to reinforce the idea that there is much more to theropod history than the beginnings of avian flight.

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PERSPECTIVES: NEUROSCIENCE

Gathering Glycine Receptors at Synapses

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Synapse formation in the central nervous system is exceptionally complex. A single neuron may receive input from thousands of synaptic connections on its cell body and dendrites—some inhibitory, some excitatory. To integrate these signals rapidly and specifically, the neuron anchors high concentrations of receptors at postsynaptic sites, matching the correct receptor with the neurotransmitter released from the presynaptic terminal. Receptor-associated proteins are thought to be involved in forming these postsynaptic specializations, possibly by linking the receptor to the postsynaptic cytoskeleton (*1*). This idea has been most thoroughly studied at the neuromuscular junction, where nicotinic receptors are associated with the clustering protein rapsyn (*2, 3*). Now, the laboratories of J. R. Sanes and H. Betz have tested this theory on neurons in the central nervous system. In a report on page 1321 of this issue, they show by targeted gene disruption that gephyrin, a protein associated with the glycine receptors, is required for the formation of inhibitory synapses in the spinal cord and brain (*4*). Their results also reveal an intriguing link between gephyrin and neurological diseases related to molybdenum deficiency.

Glycine receptors are members of the pentameric family of ligand-gated ion channels, which also includes nicotinic acetylcholine receptors, γ-aminobutyric acid (GABA) receptors (another type of inhibitory receptor), and, more distantly, NMDA- and AMPA-type glutamate receptors. In earlier experiments, Betz and colleagues found that a 93-kilodalton peripheral membrane protein, now called gephyrin, was localized at inhibitory synapses on motor neurons in a complex with the glycine receptor (*5*). A clue to gephyrin's function came from experiments in which depletion of gephyrin with antisense oligonucleotides

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