A Triassic Aquatic Protorosaur with an Extremely Long Neck

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By the Middle Triassic, a number of reptile lineages had diversified in shallow epicontinental seas and intraplatform basins along the margins of Pangea, including the giraffe-necked protorosaurid reptile *Tanystropheus* from the Western Tethys (modern Europe and the Middle East). Here we report another long-necked fossil, *Dinocephalosaurus orientalis*, a protorosaur earlier named (on the basis of an isolated skull) for its appearance (*1*). Unlike some other protorosaurs, this taxon represents a fully aquatic species.

The new specimen preserves much of the postcranial skeleton. The neck is ~1.7 m long, but the trunk is less than 1 m (the tail was not preserved) (Fig. 1). Together with ichthyosaurs and fishes, *Dinocephalosaurus* was found in Middle Triassic (Anisian stage, 230 million years ago) marine limestone in southern China (the Guanling Formation near Xinmin, Guizhou Province).

Neck elongation is a derived character of protorosaurs, a group that originated in the Permian and diversified in the Triassic. *Dinocephalosaurus* shares additional diagnostic characters with protorosaurs, such as elongated cervical ribs and very low neural spines on the neck vertebrae. The limbs of *Dinocephalosaurus* indicate fully aquatic (marine) habits, and they differ from all other protorosaurs in that they retain juvenile characteristics in the adult stage, as in many other aquatic tetrapods. The limbs are relatively short and broad; the distal carpal and tarsal elements remain unossified (except for one). The astragalus and calcaneum of the tarsus form simple rounded ossifications without any complex contact between them. The fifth metatarsal is a simple straight ossification. Unlike *Dinocephalosaurus*, *Tanystropheus* and its closest allies show a combination of a short fifth metatarsal with a much-elongated first phalanx in the fifth toe that mimics a metatarsal in its structure.

The neck of *Dinocephalosaurus* incorporates 25 elongated vertebrae (*Tanystropheus* has 12). The longest neck vertebra is 2.75 times longer than an anterior dorsal vertebra (in adult *T. longobardicus*, this ratio is 7 to 8). As in *Tanystropheus*, the cervical ribs are long and slender, running parallel to the ventrolateral edges of the neck. As the cervical rib length increases from front to back and the vertebrae become shorter posteriorly, the number of intervertebral joints bridged by the ribs increases.

Cladistic analysis based on published data (*2*) shows that *Dinocephalosaurus* nests within the Protorosauria but outside the most derived members of the group, which include *Tanystropheus* (supporting online text). The elongation of the neck is convergent in *Dinocephalosaurus* and *Tanystropheus*, as is also indicated by the anatomy. *Tanystropheus* adopted an extreme "giraffe-neck" developmental program (*3*) with only a moderate increase in the number of cervical vertebrae, whereas *Dinocephalosaurus* shows a lesser elongation of individual neck vertebrae but an increase in their number, as is also known in plesiosaurs. The adaptive significance of neck elongation in *Tanystropheus* has generated much speculation (*4*, *5*), but in *Dinocephalosaurus*, it presumably served a functional role. Extending the head vertically in order to gulp air at the surface would have been impossible; hydrostatic pressure would have prevented lung inflation. To breathe, the animal would have had to move with the neck held nearly horizontal at the air-water interface, the head emerging from the water. Such a posture increases the "hull length" of the animal, reducing wave-induced resistance to locomotion.

The slender neck also positions the head well in front of the sturdy body, such that *Dinocephalosaurus* could have closely approached potential prey before the profile of the predator would have become apparent in dimly lit water. Given the length and slenderness of the cervical ribs, moderate lateral flexion of the neck must have been possible. Contraction of muscles [originating from cervical ribs and bridging the intervertebral joints (*6*)] would have rapidly straightened the neck while the ribs would have simultaneously splayed outward. The consequent increase of the esophageal volume would have created suction such that the animal would have essentially swallowed the pressure wave created as its head lunged forward. This would have resulted in an almost perfect strike at a prey item in water. Unlike other protorosaurs, but similar to extant crocodiles, *Dinocephalosaurus* shows concave-convex dental margins with fanglike teeth on both upper and lower jaws. This tooth arrangement would have helped the animal to secure its prey once caught.

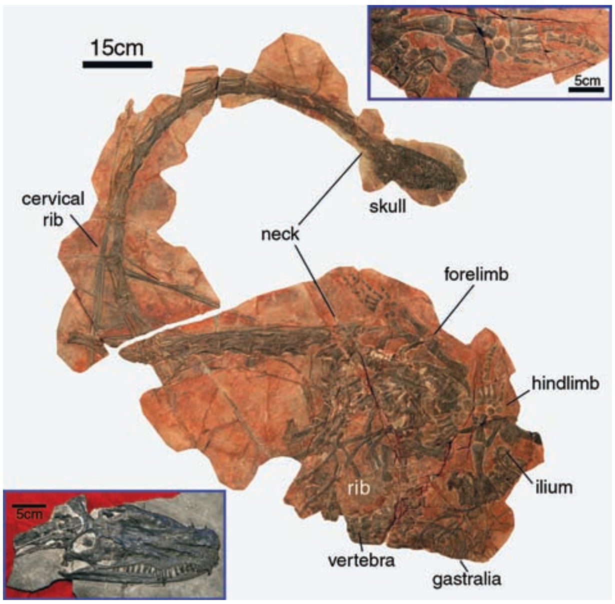

Fig. 1. The Middle Triassic marine protorosaur *D. orientalis* is known from a skull [(**bottom inset**) IVPP fossil no. V13767] and a nearly complete skeleton (IVPP V13898). The structure of its hindlimb (**top inset**) documents fully aquatic habits.

References and Notes

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