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Predation in the meat eating dinosaurs. G.S. Paul (Baltimore, Maryland).

Predaceous dinosaurs were the dominant big land predators for 170 million years. Yet the specific ways in which they hunted has received relatively little attention. In the popular media dinosaurs usually meet, roar at each other and then engage in protracted wrestling matches. Real dinosaurian combat must have been a sudden, swift and sophisticated hit-and-run attack by the predator, followed by a lingering death watch.

The following notes are results from the preparation of a volume on predatory dinosaurs (Paul in pressb). These are here considered to include the "protodinosaur" lagosuchians, lewisuchians and lagerpetons, the more derived staurikosaurs and herrerasaurs, and the theropods proper (Paul 1984a, in pressb). All four toed predatory dinosaurs will be placed in a new group, the paleodinosaurs. Theropods include only those species with a tridactyl bird foot in which the first metatarsal does not reach the ankle, and segnosaurs are not theropods (Paul 1984a,b). In its morphology Archaeopteryx is a flying theropod. With few exceptions predatory dinosaurs were fairly uniform in design, most being obligatory, striding bipeds with blade-toothed jaws, large eyes, well developed and sensitive auditory and olfactory organs, long S-curved necks, short trunks, grasping hands, and long, flexed kneed, fully erect, digitigrade hindlimbs. Their overall form was bird-like, and it is assumed that all taxa were avian-mammalian endothermic homeotherms (Bakker 1971, 1986, Paul in pressb). The protodinosaurs differ in being longer trunked, partly quadrupedal gallopers. Along with these shared adaptations, the various taxa exhibit differing adaptations for hunting. Not discussed here are the toothless, non-hooked beaked oviraptors, ornithomimids (including Deinocheirus?) and avimimids, which most likely were largely herbivorous.

Recent studies show that a number of living and extinct predators use hit-and-run tactics to kill their prey (Diamond 1986, Bryant & Churcher 1987). Carcharodont sharks, sabre-toothed cats and marsupials, hyaenas and human killers either bite out chunks of flesh from their victims, or slash them, and then retire to let shock and hemorrhaging weaken the victim enough for it to be safely dispatched. Various sabre-toothed therapsids probably used similar tactics. This is quite different from the more familiar, rough-and-tumble tactics of the big canids and cats, which usually hang onto their victims until they are dead.

Most predatory dinosaurs probably practiced the stand-offish method of big game killing. Being relatively lightly built, stiff limbed, bird-like forms, they probably could not afford to grapple with their prey the way supple bodied big cats do. The risk of serious injury was too great, especially for the gigantic forms which massed up to ten or more tons. A simple fall could have been fatal for them.

Predatory dinosaurs descended from semi-erect gaited, blade-toothed thecodonts rather like Euparkeria. These low slung predators probably struck prey with a lizard-like sideways throw of the head. The S-curved necks and taller stature of dinosaurs show that they struck with an avian-like, down and forwards head action. Their long, irregular rows of serrated teeth were powered by muscles that filled up much of the skull's internal volume, including the snout (Walker 1964, Bakker 1986). These jaws were not well suited for precision bites, nor for holding onto struggling prey. Instead, the teeth were flesh slicers. In many theropods, such as allosaurs, the premaxillary teeth were partly D shaped in cross section and tended to scoop out flesh (Fig. 1). The smaller, more conical lower teeth pinched out a fold of flesh that the larger, more bladed upper teeth cut with a backwards motion (Bakker 1986).

Running a is normal tetrapodian adaptation, only bizarre creatures with highly modified limbs and inflexible ankles, such as tortoises and elephants, cannot achieve a true run. The predatory dinosaur's consistently bird-like limbs indicate that they were all fast runners (Bakker 1971, Paul in pressb). A trackway of a 10 kg bipedal dinosaur, perhaps a theropod (Welles 1971), shows it running at about 70 km/h, about as fast as gracile ground birds, carnivores, and ungulates. This may be the top speed for large theropods too. Fairly large theropod trackways show 20-40 km/h speeds, but there is no reason to believe these were their fastest gaits (Farlow 1981). High speed trackways will make up only a tiny fraction of a typical footprint population, and giant theropod spoor are too scarce for fast trackways to have a good chance of being found. A stress, structural, and scaling study proving that large to giant animals cannot run fast has never been published, but modern biomechanics does predict that great size should not impair speed (see McMahon 1984). Indeed, 3.5 ton white rhinos achieve full gallops. Even T. rex had bird-like limbs, ones far different from those of slow humans and elephants, and a scaling analysis in preparation confirms that giant theropod limbs were allometrically scaled to maintain a high locomotary performance.

Most predaceous dinosaurs probably used their speed and jaws to dash in and deliver long raking wounds to the flanks, necks and limbs of victims (Bakker 1986). The former could result in slow death, if enough limb muscle fibers were cut the victim could be crippled immediately.

A variation on this theme was employed by modest sized Aublysodon (= Shanshanosaurus) and its bigger tyrannosaur relatives, which descended from derived allosaurs (Paul in pressb). In these the skull was more massive and powerfully muscled, especially in Tyrannosaurus (= Tarbosaurus, Daspletosaurus, Paul in pressa,b), and the premaxillary teeth were fully D-shaped in cross section. These teeth were themselves arrayed in a much larger, broad, D-shaped arc, forming a large scoop shaped flesh cutter (Fig. 1). The upper mid row teeth were larger and more bladed, increasing the length of the cutting "scoop". In tyrannosaurs, especially *Tyrannosaurus*, the eyes faced more forwards than in most theropods and allowed substantial binocular vision. Aublysodonts and tyrannosaurs, including *T. rex*, also had the best speed adapted limbs among predaceous theropods, ones very like the swift ostrich-mimic dinosaurs. So they must have run in to accurately aim and bite out a long, deep cup shaped wound from their prey, a cut rather like those made by sharks. Such firepower and speed allowed *T. rex* to regularly prey upon elephant sized, rhino-limbed, and horned *Triceratops*.

A further variation in theropodian hit-and-run predation was followed by the coyote to wolf sized, big brained, binocular visioned, sickle-clawed dromaeosaurs. Of these, *Velociraptor* (= *Deinonychus* and *Saurornitholestes*, Paul 1984a, in pressa,b) had a large but lightly built head, and it bore a greatly enlarged killing claw on a hyperextendable second toe. The arms were long, powerful and bore an array of hook claws. The posterior ilium and cnemial crest were shorter than most theropod's, giving it low-

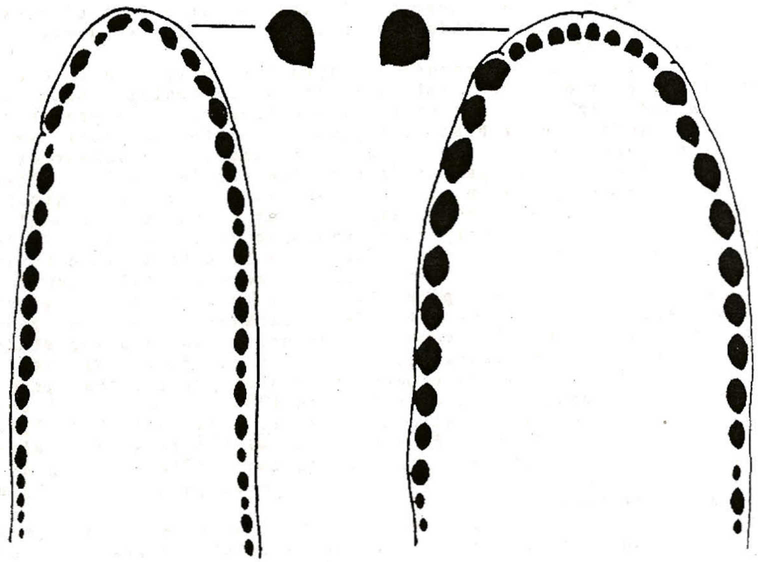

Fig. 1. The upper tooth rows in ventral view of (left) *Allosaurus atrox* UUVP 6000, and (right) *Tyrannosaurus rex* AMNH 5027. Tooth crossections at about midcrowns, examples of premaxillary teeth are shown. After Madsen (1976) and Osborn (1912). Not to scale.

er leverage limbs rather like those of leaping primates and tree frogs. The tail had a highly mobile base, and was distally stiffened into a dynamic balance by ossified rods. *Velociraptor* probably leaped upon its victim's backs, held on with the hand claws, raked the victim's flanks with paired strokes of its sickle claws, and then leapt off to safety. In contrast, the head of *Dromaeosaurus* was much more strongly built, much broader posteriorly, and more powerfully muscled, like tyrannosaur's. Its teeth were large and well serrated. Like *Adasaurus*, its robust second toe may have borne a relatively small, stout sickle claw (Barsbold 1983, the large, gracile Judith River sickled claws refered to *Dromaeosaurus* probably belongs to more common *Velociraptor*). Instead of clawing, *Dromaeosaurus* probably bit the prey before leaping off its back. The detailed morphology of skull and toe bones show that *Velociraptor* and *Dromaeosaurus* were close relatives that developed significantly different methods for wounding their prey.

Troodon (= *Saurornithoides*, *Stenonychosaurus*, Paul 1984a, in pressa,b, Currie 1985) was a more distantly related sickle claw of jackal to wolf size. The claw was much smaller than in *Velociraptor*, the skull and body more gracile, the forelimbs shorter, and the teeth smaller, more numerous and with very large serrations. Russell (1969) suggested that *Troodon*'s large brain, large, binocular vision eyes, grasping hands and speed indicate it was a specialized nocturnal hunter of small mammals. Certainly this is possible, as are fishing habits, but both day and night living animals have very large eyes and brains. The teeth were good rippers, and the sickle claw was a powerful weapon. So, *Troodon* probably hunted fairly large game also, but without leaping on their backs.

Intriguingly, *Archaeopteryx* shows evidence of a shortened hyperextendable second toe, and has low leverage leaping limbs (Paul in pressb, Paul & Carpenter in prep.). This protobird also shares many morphological details with dromaeosaurs, and the latter and troodonts possess what appear to be inherited, reduced flight adaptations. The modified second toe and leaping limbs may have evolved as climbing aids in flying protobirds, and been modified for hunting in secondarily flightless dromaeosaurs and troodonts (see Paul 1984a).

Small *Noasaurus* (Bonaparte & Powell 1980) developed its sickle claw completely seperately from dromaeosaurs and troodonts. Skull and vertebral morphology indicate that it was a dwarfed relative of *Abelisaurus* and *Carnotaurus*, and that these were all South American relatives of *Megalosaurus* (=*Poekilopleuron*, *Torvosaurus*, Paul 1984a, in pressb).

Velociraptor, *Troodon* and *Noasaurus* were probably unusual in using claws as primary killing weapons, for in most theropods the tooth rows were the much larger and more lethal weapons. Likewise, their arms were manipulative organs rather than killing ones. Welles (1984) suggests that the premaxillary-maxillary articulation in *Dilophosaurus* was too weak for predation, but the vomers braced and strengthened the snout internally (also see below). In allosaurs and tyrannosaurs the toe claws were becoming blunter and more hoof-like, a running adaptation.

Hit-and-run hunting tactics are enhanced if the prey can be surprised. Great white sharks attack larger and more agile elephant seals via a high speed, climbing strike from below (Diamond

1986). When possible, theropods probably used floral cover to approach their prey without being seen. Such stalking theropods may have reduced their height by adopting a slow speed, plantigrade walk. Plantigrade theropod trackways are known (Hastings 1986). In more open habitats the need would be to panic the herbivores into a run that would expose their vulnerable rears. The large ribcages of theropods indicate they possessed large, high endurance respiro-circulatory systems which, along with high metabolic rates, were suitable for extended chases.

Some species of big game hunting theropods may have led solitary lives, like most big cats. Others may have organized themselves into packs. Gregarious trackways and death assemblages suggest predatory dinosaurs, from small ones to tyrannosaurs, did so (Ostrom 1972, Farlow 1976, Paul in pressb). Considering the increasing body of evidence that dinosaurs, including predatory ones, nested and raised their young until they were well grown (Horner 1984) reduces, and may eliminate, the potential for competition between the young of large species and the adults of small species (contra Farlow 1976). Trackways and bonebeds show that many herbivorous dinosaurs organized themselves in defensive groups (Ostrom 1972, Bird 1985). A theropod pack attack upon an ornithopod flock may be recorded by the trackways described by Thulborn and Wade (1984, predators tend to drive herbivores away from water sites instead of mingling with them, and the big "theropod" trackway supposedly responsible for the stampede is really an iguanodont).

Hit-and-run tactics and group predation not only improve the predator's safety, they increase the relative size of prey they can bring down. Packs of blade toothed coyote-sized Coelophysis could probably bring down cow-sized prosauropods, allosaur packs the occasional sauropod.

Most theropods probably picked up small game on occasion, some specialized in it. Little Compsognathus and Ornitholestes had rather conical teeth suitable for small game and fishing. The island-lagoonal habitat and rather Hesperornis like teeth of Archaeopteryx suggest it was a fisher (also see Bakker 1986, Thulborn & Hamley 1984). One rather like a small cat, which used its long limbs to climb its arid habitat's scrub flora (Viohl 1984). Protodinosaur teeth are too poorly described to interpret their use, but Lewisuchus seems unusually big headed. Coelophysians and medium sized dilophosaurs had conical teeth on a mobile snout tip to pick up small items with, and big blades further back for slashing large game. The dilophosaur's possible relatives, the large baryonyxians (Charig & Milner 1986) and four ton spinosaurs (Stromer 1915, Paul in pressb), had even more mobile snouts, more conical teeth and crocodile-like jaws. Fish seem to have been a key dietary item (Charig & Milner 1986, Reid 1987, Kitchener 1987). However, no large modern land animals fish full time. Even brown bears do so mainly during brief, intense salmon runs in narrow streams. The dinosaurs are known from low lying floodplains where streams were broader and fish usually less abundant. Crocodilians can take large animals, so medium sized game must have been important to terrestrial spinosaurs.

Especially difficult to understand are the predatory habits of bizarre Carnotaurus (Bonaparte 1985). The skull is very deep, but the teeth are slender and the mandible is very shallow and weak.

Although predatory dinosaurs certainly scavenged, this role should not be emphasized to the degree Halstead & Halstead (1981) and Kitchener (1987) do. The only true scavengers are vultures and condors, whose relatively small weak beaks and feet are quite different from the big heads and teeth of most theropods. Large land predators do not and cannot make a living from randomly found carcasses alone, only fast, energy efficient, high soaring birds can do so (Houstan 1979).

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BAKKER, R.T. 1971. Evolution, 25, 636-658.
BAKKER, R.T. 1986. The Dinosaur Heresies. William Morrow & Co., New York.
BARSBOLD, R. 1983. Joint Soviet-Mongol. Palaeont. Exp., Trans., 19, 96-103.
BIRD, R.T. 1985. Bones for Barnum Brown. Texas Christan University Press, Fort Worth.
BONAPARTE, J.F. 1985. Natl. Geog. Res., 149-151.
BONAPARTE, J.F. & POWELL, J.E. 1980. Mem. Soc. geol. Fr., 139, 19-28.
BRYANT, H.N. & CHURCHER, C.S. 1987. Nature, 325, 488.
CHARIG, A.J. & MILNER, A.C. 1986. Nature, 324, 359-361.
CURRIE, P.J. 1985. Canadian J. Earth Sci., 22, 1643-1658.
DIAMOND, J.M. 1986. Nature, 322, 773-774.
FARLOW, J.O. 1976. Amer. Midl. Nat., 95, 186-191.
FARLOW, J.O. 1981. Nature, 294, 747-748.
HALSTEAD, L.B. & HALSTEAD, J. 1981. Dinosaurs, Blanford Press, Dorset.
HASTINGS, R.J. 1987. J. Geol. Educ., 35, 4-15.
HORNER, J.R. 1984. Sci. Amer., 250(4), 130-137.
HOUSTAN, D.C. 1979. In Serengeti; Dynamics of an Ecosystem. Univ. Chicago Press, Chicago, 263-286.
KITCHENER, A. 1987 Nature 325, 114.
McMAHON, T.A. 1984. Muscles, Reflexes and Locomotion. Princeton Univ. Press, Princeton.
MADSEN, J.H. 1976. Bull. Utah Geol. Min. Surv., 109, 1-51.
OSBORN, H.F. 1912. Amer. Mus. Nat. Hist. Mem. (n.s.), 1, 1-30.
OSTROM, J.H. 1972. Palaeogeog., Palaeoclimat., Palaeoecol., 11, 287-301.
PAUL, G.S. 1984a. In Third Symposium on Mesozoic Terrestrial Ecosystems. ATTEMPTO-Verlag, Tubingen, 175-180.
PAUL, G.S. 1984b. J. Vert. Paleont., 4, 507-515.
PAUL, G.S. in pressa. In Proc. 4th N. Amer. Paleont. Conf., NAPC, Boulder.
PAUL, G.S. in pressb. Predatory Dinosaurs of the World. Simon & Schuster, New York.
REID, R.E.H. 1987. Nature., 325, 487.
RUSSELL, D.A. 1969. Canadian J. Earth Sci., 6, 595-612.
STROMER, E. 1915. Abh. bayer. Akad. Wiss., 28, 1-32.
THULBORN, R.A. & HAMLEY, T.L. 1984. In The Beginnings of Birds. Fruende Jura-Museums, Eichstatt, 81-90.
THULBORN, R.A. & WADE, M. 1984. Mem. Queensl. Mus., 21, 413-517.
VIOHL, G. 1984. In The Beginnings of Birds. Fruende Jura-Museums, Eichstatt, 31-44.
WALKER, A.D. 1964. Phil. Trans. R. Soc. Lond. (B), 248, 53-134.
WELLES, S.P. 1971. Plateau, 44, 27-38.
WELLES, S.P. 1984. Palaeontographica A, 185, 85-180.