BRONTOSAUR KILLERS: LATE JURASSIC ALLOSAURIDS AS SABRE-TOOTH CAT ANALOGUES

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ABSTRACT: According to Kowalevskian logic, sabre-tooth top predators evolve to harvest giant, slow-moving prey. Late Jurassic sauropods, who dwarfed the largest contemporaneous predators, may be ecological equivalents of proboscideans and ground sloths. Allosaurid theropods evolved unusual jaw joints that permitted exceptional gapes, special neck muscle attachments that increased the ventral-flexing leverage, reduced temporal muscles, and tiny teeth that could have functioned as mega-serrations for an upper jaw war club. This suite of modifications could have allowed allosaurids to attack prey very much bigger than themselves.

"If a student to-day asks, 'how shall I study palaeontology?', we can do no better than direct him to Kowalevsky..." H. F. OSBORN, 1910.

INTRODUCTION

KOWALEVSKIAN CO-EVOLUTION OF PREDATOR AND PREY

OSBORN (1910) praised Vladimir Onufrievich Kowalevsky for the invention of the theory-testing protocol in vertebrate paleontology. Kowalevsky was the first to use a two-stage analysis: define an apparent adaptive need, caused by a shift in environmental resources, and then search the fossil record for the morphological response predicted. Kowalevsky predicted changes that should take place in the limbs and teeth of mammalian herbivores as soil conditions shifted from moist and tropical to hard and and temperate (KOWALEVSKY, 1873). Taken in a Kowalevskian context, the evolution of large, slow herbivorous mammals in Holarctica and South America presented an ecological opportunity that solicited new adaptations among top predators; killing such giant prey requires different tactics than killing swifter medium-size herbivores. The mammalian predators who adapted to giant prey did not increase body size. Instead, sabre-tooth mechanics developed a half dozen times independently among medium-size predators. In each case, changes in head-neck joints increased the usefulness of the neck for swinging the head down like a war-club; modification of the jaw joint increased the gape so the lower jaw could be swung out of the way of the enlarged upper teeth (Fig. 1). Sabretooth "cats" evolved independently among the neofelids and nimravids, as well as in one family of South Ameri-

can marsupial (thylacosmilids), and one subfamily of primitive placental creodont (machaeroidines). In all four cases, the details of jaw joint, occiput, canine teeth and jaw muscle attachments were modified in nearly exactly the same way (TURNBULL, 1978; EMERSON & RADINSKY, 1980; TURNER & ANTON, 1997). Such precison in homoplasy shows that there is only one mammalian solution to the problem of killing large, slow prey by slashing with the upper teeth.

Here I will describe the head-neck mechanics in the Late Jurassic allosaurid theropods, adaptations that mimic those of sabre-tooth mammals in allowing the upper jaw to act as a saw-edged weapon for inflicting wounds on gigantic sauropod dinosaurs, a mode of predation that could be termed "brontophagy"

GIANT POTENTIAL PREY OF THE LATE JURASSIC

The mid to latest Jurassic interval records an episode in the co-evolution of carnivores and herbivores when the potential prey became exceptionally huge compared to the top predators. The earliest well-documented samples with dinosaurs as top predators are the prosauropod faunas, best represented by the early Jurassic Chinese collections, which show theropods almost equal in body bulk to the largest herbivores: the largest predator is a dilophosaur-like theropod with a femur length of about 800mm, about equal to that of the commonest large herbivores *Lufengosaurus* YOUNG and *Yunnanosaurus* YOUNG (YOUNG, 1951; SUN & CUI, 1986; DONG, 1992). However, in the mid to Late Ju-
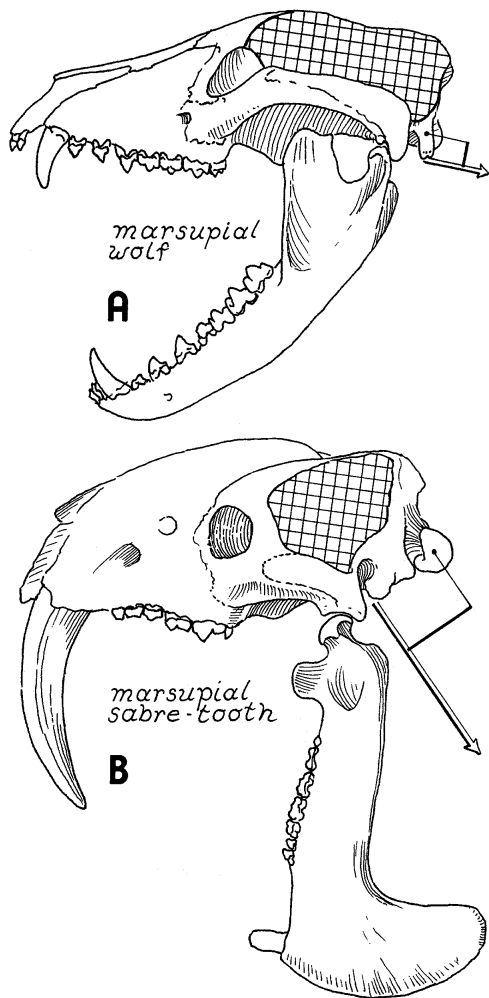
Fig. 1 - How a biting predator can be transformed into a sabre-tooth. **A** - Marsupial Wolf, *Thylacinus* TEMMNICK, drawn from a cast, length 245 mm. **B** - Marsupial sabre-tooth, *Thylacosmilus atrox* RIGGS, redrawn from TURNBULL (1978), length 245 mm. Arrow shows line of pull of neck ventral-flexors on the mastoid at maximum leverage; dot indicates center of rotation at occipital condyle; short line perpendicular to line of pull shows leverage; grid pattern shows area of temporal fenestra. Note re-orientation of jaw joint in the sabre-tooth.

ing of the forearm, as in CURRIE & ZHAO, 1993); the average adult femur length we have found in the latest Jurassic at Como Bluff Morrison is 890 mm (BAKKER, 1997). Not only were sauropods huge, they were slow, with the femur length always greater than the combined tibia and foot length. Thus the explosion of sauropods in the Late Jurassic is comparable to the effusive radiation of Late Cenozoic proboscideans and ground sloths. Both events presented top predators with potential prey who were ten times heavier than the predators themselves. If a Kowalevskian view of evolution is correct, and predator-prey co-evolution is regular and predictable, then we should expect to see Late Jurassic predatory dinosaurs evolving mechanical adaptations that are analogous to those of sabre-toothed mammals.

The Latest Jurassic faunas of the Morrison Formation record two predator families - megalosaurids, and ceratosaurids - with morphology that is little changed from a Mid Jurassic condition (DESLONGCHAMPS, 1838; PHILLIPS, 1871; GILMORE, 1920; TAQUET & WELLES, 1977; GALTON & JENSEN, 1977; WALDMAN, 1974; BRITT, 1991). In addition, there is one family - the allosaurids - that is distinguished by many unusual features of skull and dentition (GILMORE, 1920; MADSEN, 1976). The allosaurids outnumber all other top predators by about ten to one in Morrison samples (MADSEN, 1976; BAKKER, 1996), and shed teeth show that allosaurids were, indeed, sauropod predators. At Como Bluff, WDIS Museum parties have found shed allosaurid teeth with all large sauropod carcasses, but shed megalosaurid and ceratosaurid teeth are rare and concentrated in unusual environments (BAKKER, 1997). I would predict that the allosaurids would show sabre-toothed features missing in ceratosaurids and megalosaurids.

In the following discussion, I distinguish between two types of Morrison allosaurid (Fig. 2-3):

1) True *Allosaurus* MARSH: specimens from the type locality of *Allosaurus fragilis* MARSH - the skeleton United States National Museum USNM 4734 and dentary USNM 2315 (this dentary fits well into the anterior end of the post-dentary bones of USNM 4734 and certainly belongs to the same species if not the same individual); Bone Cabin Quarry skull American Museum of Natural History AMNH 600; Wyoming Dinamation Society (WDIS) from Como Bluff 091.

2) The creosaur-type allosaurid (unfortunately, the type of *Creosaurus* MARSH is, by itself, indeterminate): Dinosaur National Monument skeleton University of Utah UUVP 6000, Bone Cabin skeleton AMNH 666, Como Bluff skeleton AMNH 5357, Como Bluff skeleton skeleton WDIS 011. These two types of skulls are easy to tell apart from the quad-

rassic, the large herbivores pull away in body size from the large carnivores. Herbivore faunas become dominated by sauropod dinosaurs who become larger and larger through evolutionary time. Sauropods with a femur length of 1.4 m are found in the mid Jurassic of England (PHILLIPS, 1871). At Como Bluff, in the latest Jurassic Morrison Formation, adult sauropod femur lengths vary from 1.3 m for camarasaurids, to 1.8 m for apatosaurs, to 2.1 m for brachiosaurs (BAKKER, 1996). The predatory dinosaurs do not experience a commensurate increase in size. Megalosaurids in the Middle Jurassic reached a femur length of 900 mm (PHILLIPS, 1871) (I define the Megalosauridae by the derived shorten-

rate, lower temporal fenestra, and depth of the mandible; however, I find it impossible to separate the two taxa from isolated snout bones or post-crania.

As background for reconstructing theropod myology (Fig. 4, 6), I have carried out dissections of the head, neck and forelimb of *Paleosuchus trigonatus* SCHNEIDER and *Alligator mississippiensis* CUVIER.

ADAPTATIONS FOR KILLING LARGE PREY

RECRUITMENT OF NECK INTO KILLING STROKE

The throttling hold of cats, or the neck bite practiced by many mammal predators, or the grab-and-shake bite of crocodilians, monitor lizards, and long-snouted mammalian Carnivora, have inherent limitations: the maximum bite force is limited by the size of the jaw adductor muscles, which constitute a small fraction of the total body musculature. Moreover, biting and holding on may be dangerous when the prey is ten times stronger than the predator. The key adaptive shift in sabre-tooth mammals is the recruitment of another muscle group, the long head-neck ventral-flexors, into the function of killing prey by swinging the snout and upper teeth downwards (Fig. 1). The head-neck ventral-flexors, muscles running from the sternum and shoulder region to the head, are capable of evolutionary enlargement to a greater extent than that possible in the jaw adductors, a muscle system that is constrained because it must be housed within the skull.

In primitive carnivorous mammals there are long muscles running from shoulder to the astoid-paroccipital region of the skull located just behind the ear. These muscles turn the head sideways and twist it about its long axis. In sabre-tooths the paroccipital process and mastoid process are shifted downward, far below the center of rotation of the head-neck joint at the occipital condyle (Fig. 1). As a result, the line of action of the long ventral-flexing muscles is displaced downward, and so the leverage of the muscles for swinging the head down is increased.

Primitive archosaurs also have long head-neck muscles attaching to the paroccipital process, though the lines of action differ from those of mammals (Fig. 2, 4, 6). In primitive archosaurs and their close kin, the neck ribs carry long shafts which are directed posteriorly and overlap one another, so that, in the mid-neck region, three or more shafts constitute a composite bundle surrounded by connective tissue (Fig. 4). Within the bundle the shafts are free to slide over one another. Several large muscles run from the shoulder to the shaft-bundle. (Fig. 4, 6: lev scap; sterno mastoideus; scal.). Another muscle group takes origin from the shaft bundle and runs to the paraoccipital process (Fig. 4, 6:
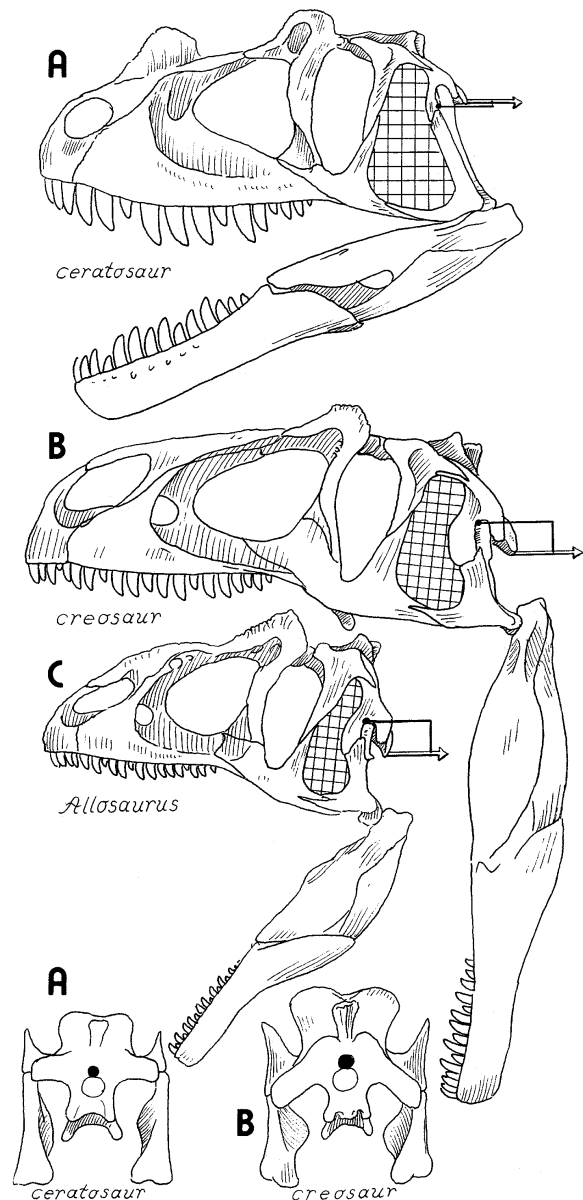

Fig. 2 - How a primitive, ceratosaurid-grade theropod may be converted into a slashing allosaurid. Skulls drawn to the same height. **A** - *Ceratosaurus* MARSH: USNM 4735 (antorbital fenestra drawn from undamaged right side); lateral and occipital views. **B** - Creosaur-style allosaurid: AMNH 666 with missing parts restored from AMNH 5357; lateral and occipital views. **C** - True *Allosaurus* MARSH: USNM 4734, lateral view. Muscle parameters indicated as in Figure 2. Paroccipital process in ceratosaurs is so high that most neck muscles attaching here elevate the head when line of action is horizontal.

trans). The rib-shaft-bundle is a key character defining the archosauromorph clade. Well developed rib-shaft-bundles are present in all large theropod dinosaurs but are lost among ostrich dinosaurs, many sauropods, many ornithischians, and all modern birds.
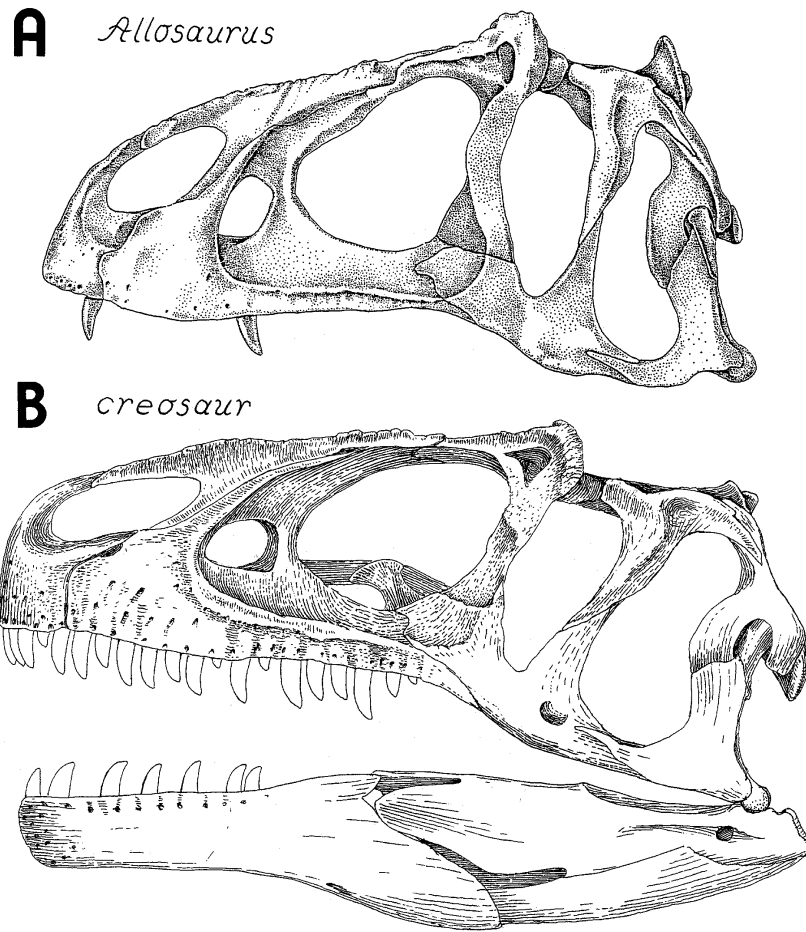
Fig. 3 - Lateral view of two kinds of allosaurid skull. **A** - True *Allosaurus* MARSH: AMNH 600, Bone Cabin Quarry. Note the near closure of the lower temporal fenestra by the forward bending of the squamosal. **B** - Creosaur-style: UUVP 6000, Dinosaur National Monument. Note the backward bending of the lower end of the quadrate.

In the more conservative large predators of the Late Jurassic, the megalosaurids and ceratosaurids, the paroccipital process extends horizontally outward, and the outer end is almost at the same level as the occipital condyle, as seen in lateral view (Fig. 2, 4). Therefore the long ventral head-neck muscles have little or no leverage for flexing the head downwards. This condition is the rule for Triassic predatory archosaurs as well. Allosaurids show a dramatic departure. The paroccipital processes are bent downwards at their outer ends, so that the leverage for ventral-flexion is augmented (Fig. 2-4, 6). Allosaurids are the only large theropods with strongly deflected paroccipital wings.

The geometry of the allosaurid long head-neck flexors differs from that of mammals: In sabre-toothed mammals, the attachment site on the skull is below and anterior to the occipital condyle, and therefore the greatest leverage for head ventral-flexion occurs when the long flexors are pulling down and backward (Fig. 1). In allosaurids, the attachment on the skull is below and behind the condyle; the greatest leverage occurs when the transversarius muscle is pulling posteriorly and slightly upward (Fig. 2). This arrangement suggests that allosaurids struck with the snout tilted upwards more than the condition in mammals. Modern crocodilians do, in fact, tilt the snout upwards strongly before making a strike.

REDUCTION OF BITING MUSCLES

The increase in ventral-flexion leverage in sabre-tooth mammals is accompanied by a decrease in the anterior-posterior width of the attachment of the jaw closing muscles on the skull. As seen in side view, the area of the temporal fenestra is smaller in the sabre-tooths than in a normal, biting mammal (Fig. 1). Muscle fiber-tract length is not reduced, and may be increased by a deepening of the fenestra to allow greater gape (TURNBULL, 1978). In the more conservative theropods of the Late Jurassic, the area of the lower temporal fenestra is large, because the lower border of the fenestra, the bar of bone composed of quadratojugal and jugal, is long; this condition is the

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rule among Triassic predatory archosaurs (Fig. 2, 4). Allosaurids demonstrate a marked reduction in temporal area. In the creosaur-style allosaurid, the lower temporal bar is shorter than that of ceratosaurids. In *Allosaurus* MARSH the lower temporal fenestra is sharply reduced in area by the shortening of the lower bar and by the near closure of the upper part of the fenestra by a forward bending of the squamosal (Fig. 3). True *Allosaurus* MARSH has a fenestra more restricted anterior-posteriorly than that of any other large theropod of any age; however, muscle fiber tract length is augmented by a deepening of the lower jaw where dentary meets postdentary elements (Fig. 2).

These two changes in muscle attachment, increased ventral-flexing leverage and reduced temporal area, are precisely what would be expected if allosaurids were evolving stronger participation of the neck muscles in the killing stroke and weaker participation of the biting muscles.

JAW JOINTS FOR WIDE GAPES

Sabre-tooth cat jaw joints are rearranged to prevent dislocation when the mandible is opened to extreme gapes (Fig. 1). The joint surface in the skull for the jaw - the glenoid - is a cylindrical notch that faces forward in normal mammalian predators. In sabretooths, the glenoid is shallower, wraps around the lower jaw to a smaller degree, and faces downward. The joint surface on the mandible - the dentary condyle - is redirected to face more posteriorly. In primitive theropod dinosaurs, as in primitive archosaurs generally, the joint surface on the skull, carried by the lower end of the quadrate, is in the form of inner and outer spindles with a spiral groove in between (Fig. 5). The spiral groove fits against a spiral ridge in
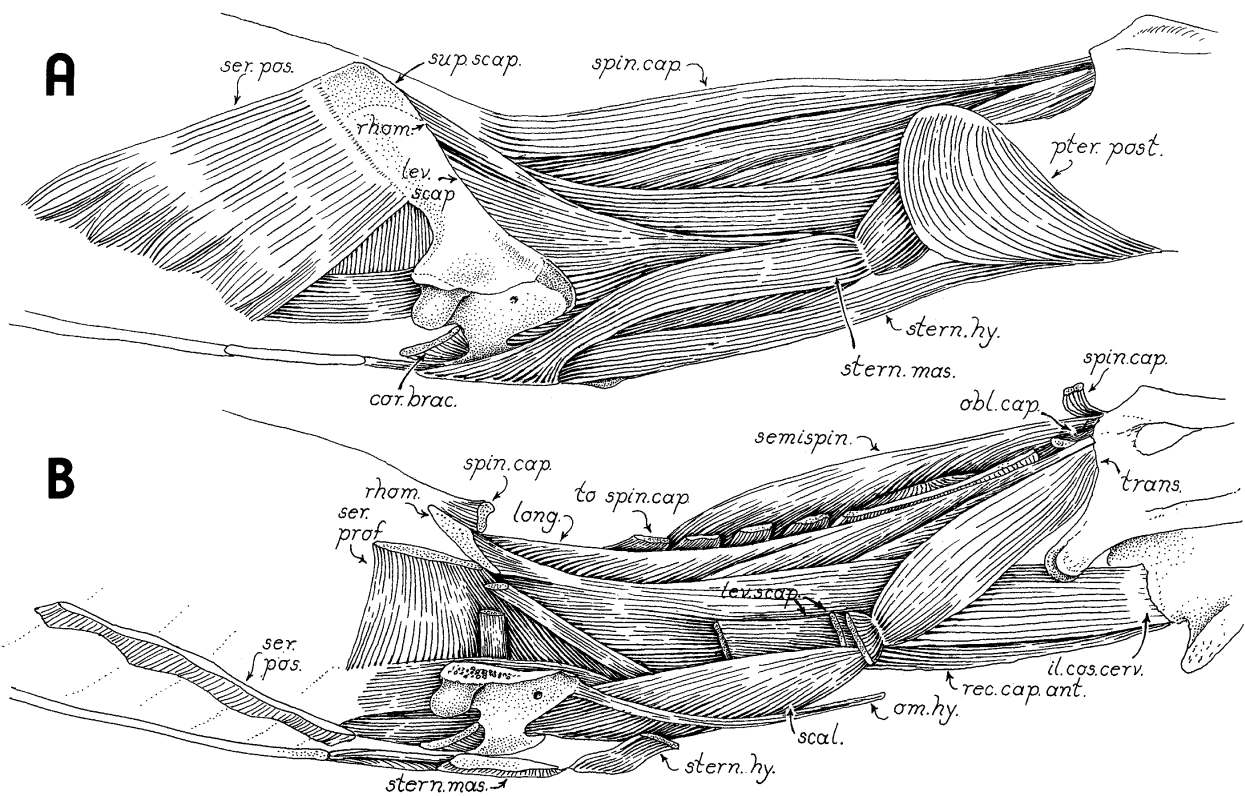

Fig. 4 - Head-neck muscles. Dissection of right neck region in *Paleosuchus trigonatus* SCHNEIDER: **A** - skin and trapezius removed. **B** - deeper dissection. Terminology as in EVANS (1939) and OLSON (1936). Abbreviations: baspt, bstp - basipterygoid process; bastb, bstb - basituberal process; cerv - cervical division; crsp - crista prootica; dep - m. depressor mandibulae; epot - epiotic; fen - fenestra; il cos - m. iliocostalis; il cos cerv - m. iliocostalis cervicis-capitis; lev scap - m. levator scapulae; long - m. longissimus; obl cap - m. obliquus capitis; om hy - m. omohyoideus; para - parasphenoid rostrum; paroc - paroccipital process; pneu - pneumatic space; pter post - m. pterygoideus posterior; pter shlf - pterygoid shelf; qj - quadratojugal; q.ram.pter - quadrate ramus of pterygoid; rec cap ant - m. rectus capitis anterior (=m. longus colli et capitis); rhom - m. rhomboideus; scal - m. scalenus; semi spin - m. semispinalis; ser pos - m. serratus posterior; spin cap - m. spinalis capitis (= m. biventer of avian terminology); sq - squamosal; stap lig - stapedial ligament; stern hy - m. sternohyoideus; stern mas - sternomastoideus; sup scap - suprascapular cartilage; trans - m. transversarius; tymp cav - tympanic cavity. (**Continued**)
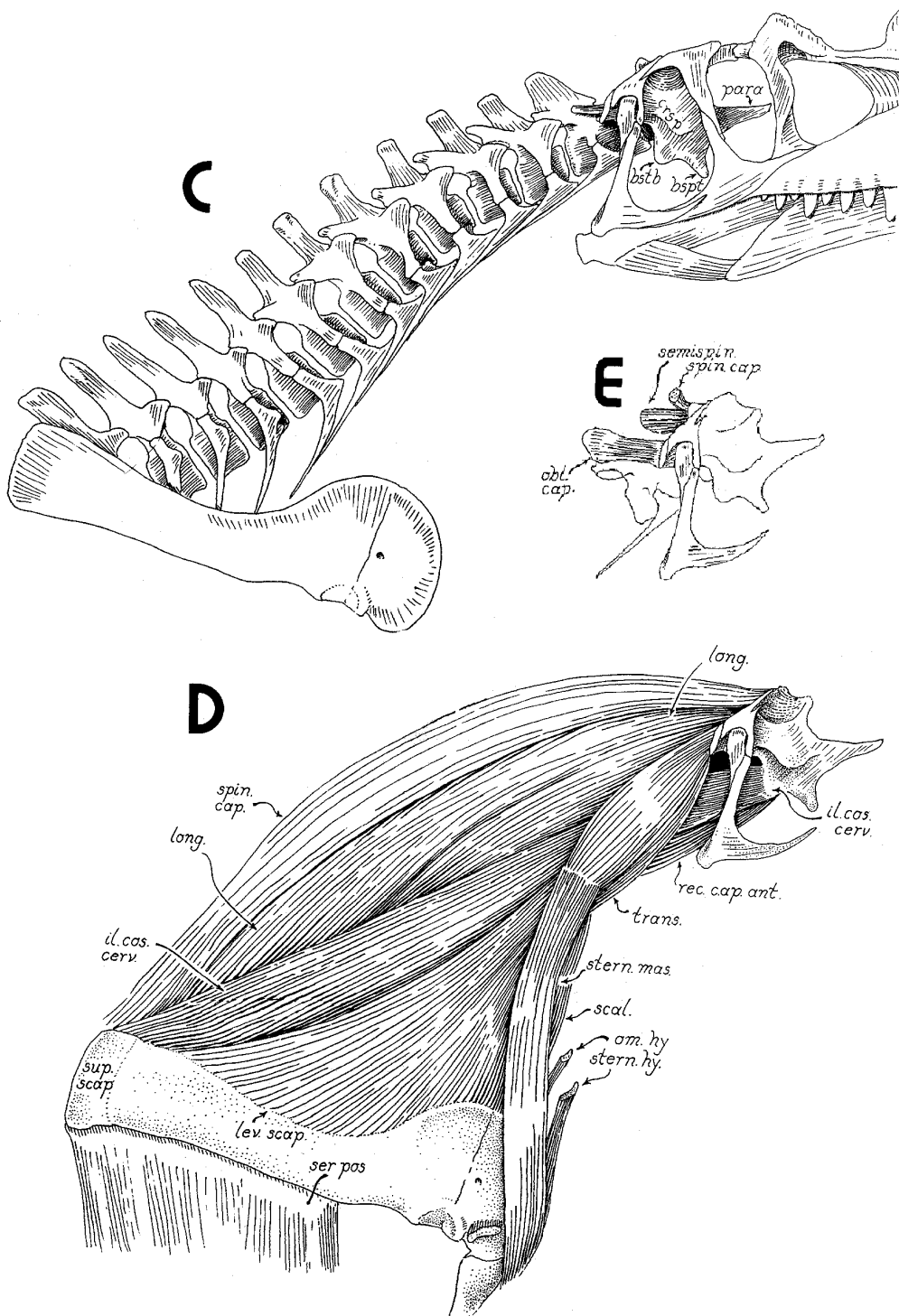
Fig. 4 (**continued**) - Muscles in *Ceratosaurus* MARSH: **C** - right shoulder, neck and skull. **D** - Muscles with skin, rhomboideus and trapezius removed. **E** - Lateral view of braincase with short muscles. Terminology as in EVANS (1939) and OLSON (1936). Abbreviations: baspt, bstp - basipterygoid process; bastb, bstb - basituberal process; cerv - cervical division; crsp - crista prootica; dep - m. depressor mandibulae; epot - epiotic; fen - fenestra; il cos - m. iliocostalis; il cos cerv - m. iliocostalis cervicis-capitis; lev scap - m. levator scapulae; long - m. longissimus; obl cap - m. obliquus capitis; om hy - m. omohyoideus; para - parasphenoid rostrum; paroc - paroccipital process; pneu - pneumatic space; pter post - m. pterygoideus posterior; pter shlf - pterygoid shelf; qj - quadratojugal; q.ram.pter - quadrate ramus of pterygoid; rec cap ant - m. rectus capitis anterior (=m. longus colli et capitis); rhom - m. rhomboideus; scal - m. scalenus; semi spin - m. semispinalis; ser pos - m. serratus posterior; spin cap - m. spinalis capitis (= m. biventer of avian terminology); sq - squamosal; stap lig - stapedial ligament; stern hy - m. sternohyoideus; stern mas - sternomastoideus; sup scap - suprascapular cartilage; trans - m. transversarius; tymp cav - tympanic cavity. (**Continued**)

the lower jaw; as the jaw closes, the spiral forces the lower jaw inwards on the quadrate. In ceratosaurids and megalosaurids, as well as in primitive theropods generally, the quadrate joint surface is small in area as viewed from below, there is little constriction between inner and outer condylar spindles, and the joints are not expanded anteriorly or posteriorly. In all allosaurids, the inner and outer condyles bulge to the front and to the rear and take on the appearance of a knee joint; there is a marked constriction in the center. The enlargement is especially well expressed in the creosaur-style allosaurids, where the quadrate condyle is larger relative to the skull than in any other theropod. Not only is the anterior and posterior bulge of the joint increased, but the condyle is twisted, with the outer condyle rotated forwards, the inner condyle backwards. The twist further increases the area of the condyle relative to the skull breadth between the two quadrates. This enlargement of the articulating surfaces improves the stability of the joint when the mouth is opened very widely.

A second form of joint-stabilization comes about with the development of ligaments in the center of the spiral groove on the quadrate, between inner and outer condylar spindles (Fig. 5). In all allosaurids, there is a pit in the rear of the spiral groove near the posterior edge of the joint surface as seen from below; the pit is especially well developed in creosaur-style animals. Behind the pit on both sides the joint surfaces bulge posteriorly. The pit strongly resembles the depression for attachment of the cruciate ligaments in the knee joints of birds and crocodiles, and so I conclude that part of the joint capsule in allosaurids was elaborated into one or more ligaments within the quadrate-mandibular articulation. The pit is absent or poorly developed in all other Jurassic theropods.

A third form of gape-increasing device is seen in the backward bend of the lower end of the quadrate in allosaurs (Fig. 2-3, 5). In megalosaurids and ceratosaurids the quadrate, as viewed from the side, is almost straight-shafted from the upper joint with the squamosal to the lower joint for the mandible. In creosaur-style allosaurids, a backward tilt is immensely exaggerated, more so than in any other large theropod. Manipulation of creosaur-style
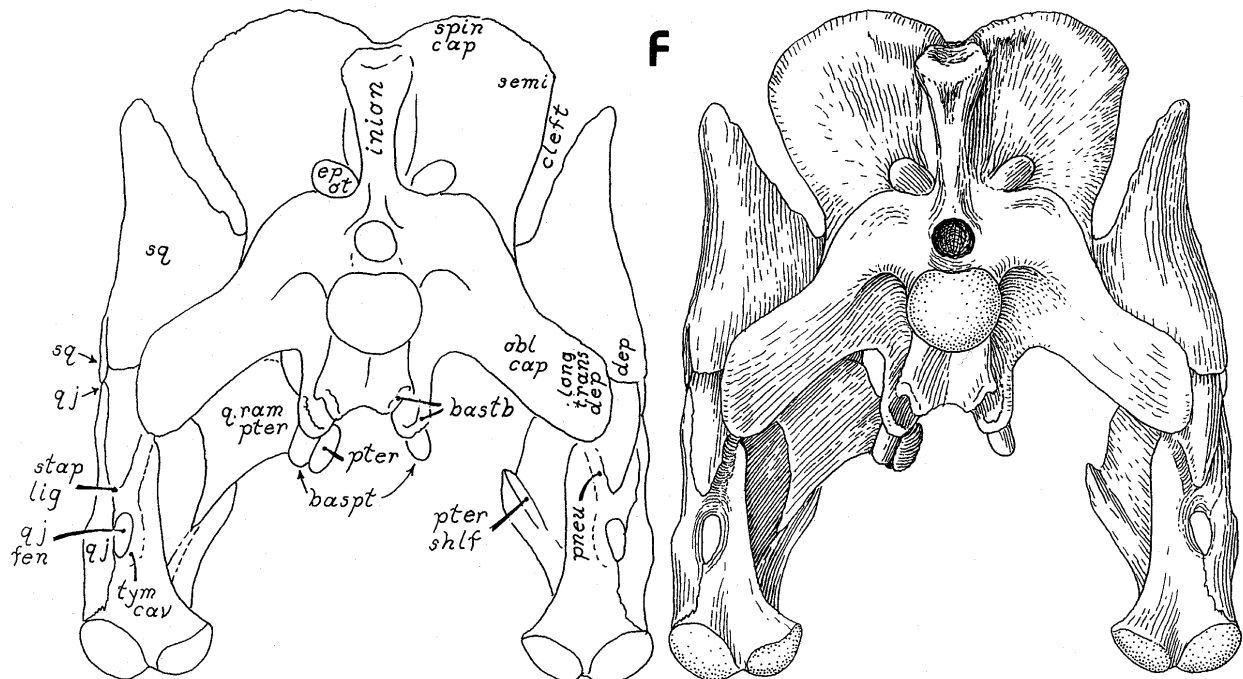

Fig. 4 (**continued**) - **F** - Occipital view of an allosaurid, AMNH 600, with muscle attachments. Terminology as in EVANS (1939) and OLSON (1936). Abbreviations: baspt, bstp - basipterygoid process; bastb, bstb - basituberal process; cerv - cervical division; crsp - crista prootica; dep - m. depressor mandibulae; epot - epiotic; fen - fenestra; il cos - m. iliocostalis; il cos cerv - m. iliocostalis cervicis-capitis; lev scap - m. levator scapulae; long - m. longissimus; obl cap - m. obliquus capitis; om hy - m. omohyoideus; para - parasphenoid rostrum; paroc - paroccipital process; pneu - pneumatic space; pter post - m. pterygoideus posterior; pter shlf - pterygoid shelf; qj - quadratojugal; q.ram.pter - quadrate ramus of pterygoid; rec cap ant - m. rectus capitis anterior (=m. longus colli et capitis); rhom - m. rhomboideus; scal - m. scalenus; semi spin - m. semispinalis; ser pos - m. serratus posterior; spin cap - m. spinalis capitis (= m. biventer of avian terminology); sq - squamosal; stap lig - stapedial ligament; stern hy - m. sternohyoideus; stern mas - sternomastoideus; sup scap - suprascapular cartilage; trans - m. transversarius; tymp cav - tympanic cavity.
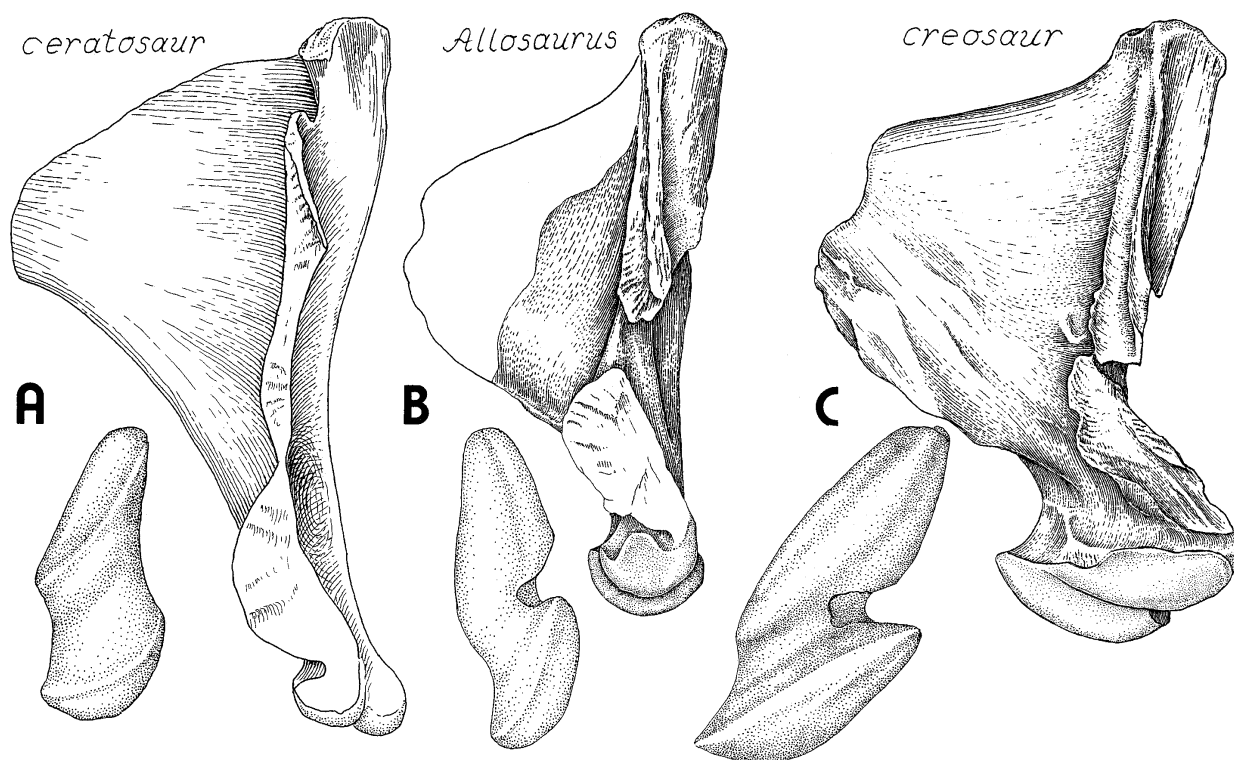
Fig. 5 - Quadrate adaptations for great gape. Outer and distal views of left quadrates. **A** - *Ceratosaurus* MARSH USNM 4735. **B** - True *Allosaurus* MARSH WDIS 911. **C** - Creosaur-style allosaurid WDIS 011.

skulls show that the jaw can be opened well beyond 90° with the quadrate surface still firmly pressed into the mandibular joint surfaces (Fig. 2).

REINFORCEMENT OF THE BASITUBERA

Besides the long lateral head-neck flexors, there two additional muscle groups that can be recruited into the killing stroke - the m. rectus capitis anterior, which runs along the lower surfaces of the cervical centra and cervical ribs, and the m. ilio-costalis, which runs downward and forward along the lateral surface of the neck. Both insert on the basitubera on the underside of the braincase (Fig. 4). The sabre-tooth marsupials of South America show unusual strengthening of the basitubera (TURNBULL, 1978). Megalosaurids and ceratosaurids show no special structures in this area, but allosaurids and sinraptorids do (CURRIE & ZHAO, 1993): a set of transverse thickenings develop in the bone boxwork behind the basitubera ("basisphenoid web" of CURRIE & ZHAO, 1993), indicating that unusual stresses were incurred during head ventral-flexing.

TRANSFORMATION OF TEETH INTO MEGA-SERRATIONS

Normal biting cats have opposing canines of virtually identical size and shape, a condition nearly universal among today's mammalian predators,

from aardwolves to zorillas. Sabre-tooth mammals show an increase in the crown height of the upper canine at the expense of the lower canine. The earliest archosauromorphs differed from most mammals and mammal-like reptiles in having an emphasis on upper teeth. In nearly all predatory Triassic archosaurs, including erythrosuchids, rauisuchians, ornithosuchids, proterosuchids, the upper tooth row is longer and the tooth crowns taller than their opposite numbers below, a condition passed down to all early theropods. Consequently, I conclude that the primitive predatory archosaur behavior included swinging the upper jaw down as the lower jaw was swung up. This style of biting can be observed among extant crocodilians who raise the skull far more than they lower the jaw in preparation for biting.

At first sight, the teeth of allosaurids are paradoxical; unlike the situation in sabre-tooth mammals, the teeth are reduced in size, not enlarged. Compared to ceratosaurids and megalosaurids, all allosaurids appear definitely micro-dont in uppers and lowers; relative to skull length, allosaurid tooth crowns are only 50-60% as large as those of ceratosaurids (Fig. 2-3). Why? Certainly allosaurids were not using their upper teeth to stab deeply into prey.

I suggest that the entire upper jaw of allosaurs functioned as one huge, saw-edged Samoan war-club, with each small, individual tooth acting as a
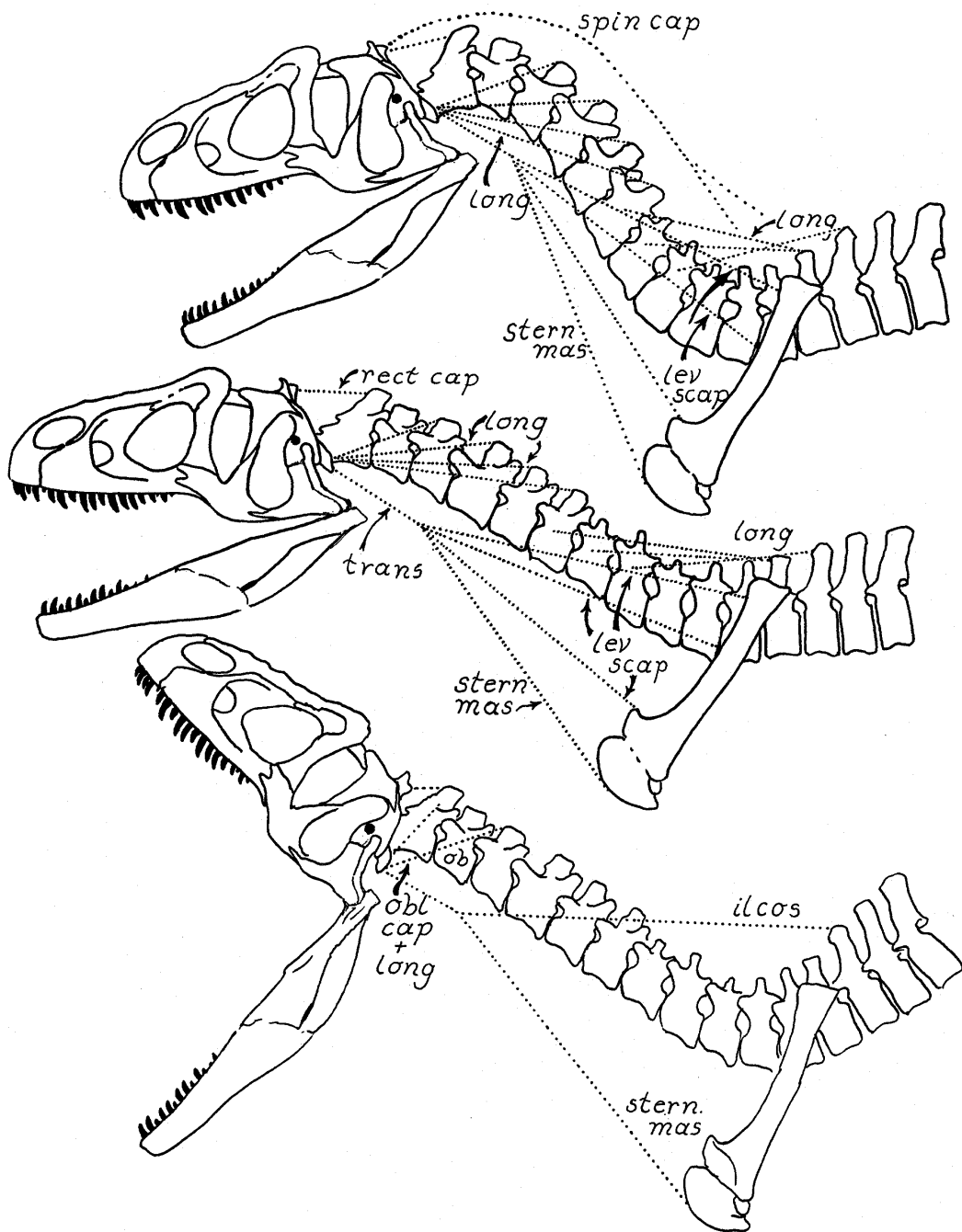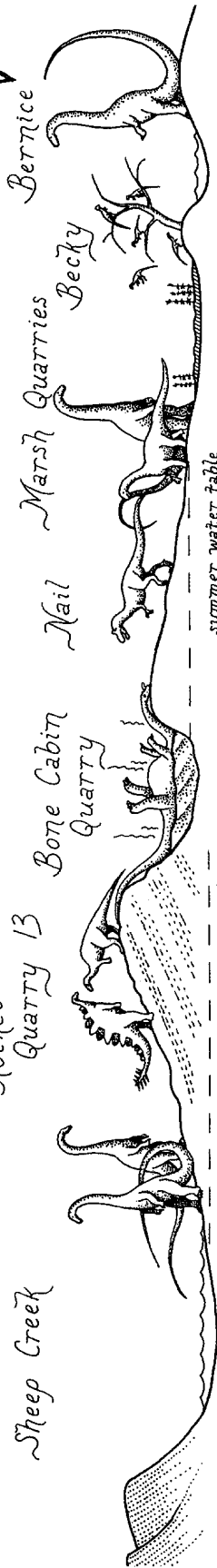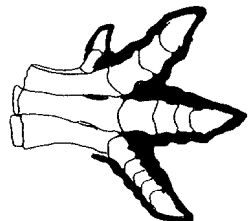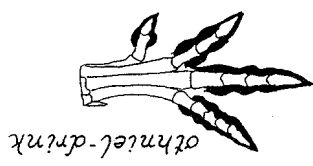
Fig. 6 - Skull, neck and shoulder in a creosaur-type allosaurid. Dotted pathways show lines of action of long muscles in various head-neck postures. Note the convergence of muscle lines of action at the location below the neck where the rib shafts overlap.

mega-serration. Polynesian warriors glued shark teeth to clubs, and the individual shark tooth functioned as a mega-serration that was, on a much smaller scale, also serrated. Such a club inflicts a long, jagged wound with concomitant trauma and blood loss, especially if the mega-serrated blade is pulled backward as it strikes its target. I would envision that an allosaurid would not kill a sauropod in a single bite, but would rather weaken large prey by re-peated attacks, a strategy that would not require a two-ton predator to hold onto a twenty-ton target. Blows from the allosaurid skull may have come from one side or both sides of the tooth row, depending on the diameter of the victim's body part.

Allosaurid head-neck mechanics would not preclude using normal biting to kill smaller prey, such as juvenile sauropods or adult camptosaurs.

othniel-drink

sauropod

stegosaur

camptosaur

dryosaur

Bernice

Becky

Marsh Quarries

Nail

Bone Cabin Quarry

Rocket Quarry 13

Sheep Creek
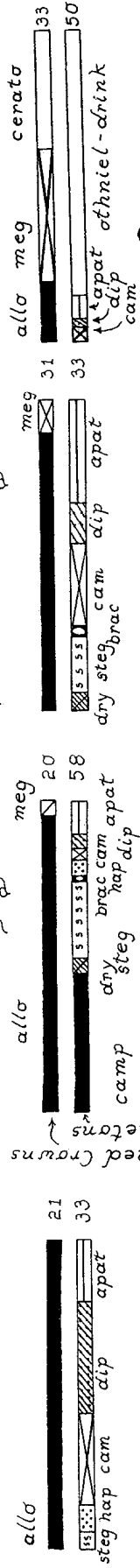
Swamp River

Long-Lived Large Swamp

Poorly Drained Flood Plain

Large Channel

Well Drained Flood Plain

Short-Lived Shallow Lake
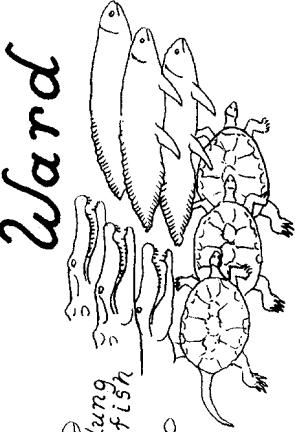
Dunes

summer water table

summer water table

allo meg cerato 33
apat othniel-drink 50
dip cam

meg 31
dry steg apat 33
brac cam dip
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steg hap dip
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steg hap cam dip apat 33

Shed Crowns
Skeletons

Ward

Carlin

9-Mile

Arrowta!!

lungfish

lung fish
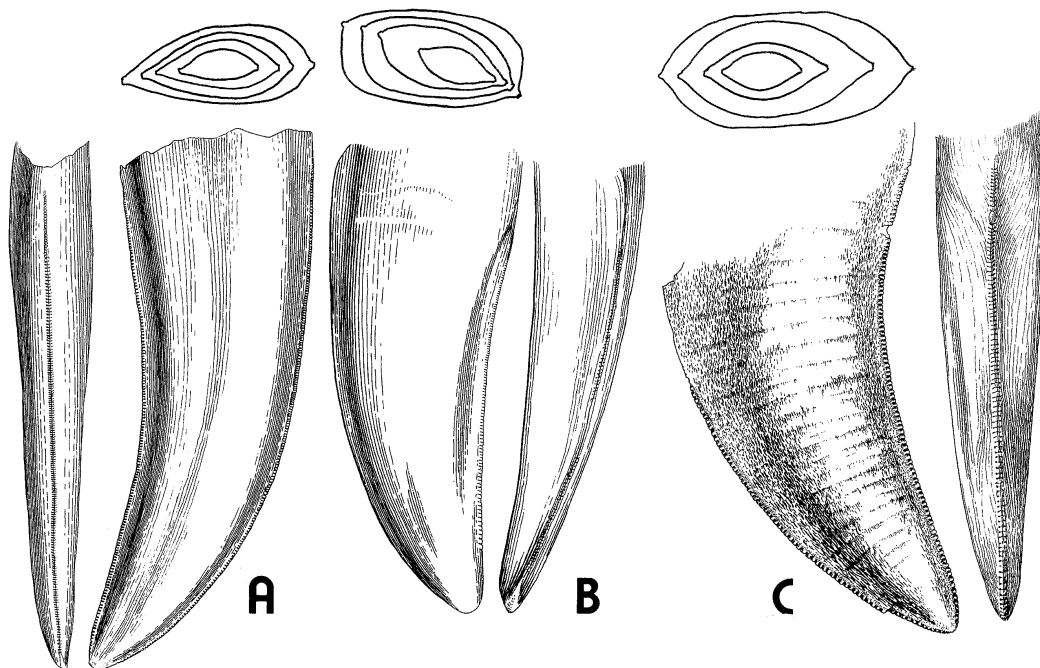
Clam

Turtle

Croc

Turtle

Snails
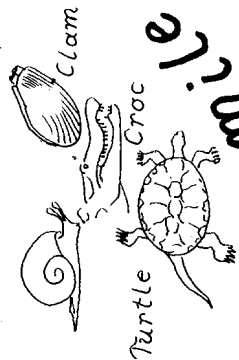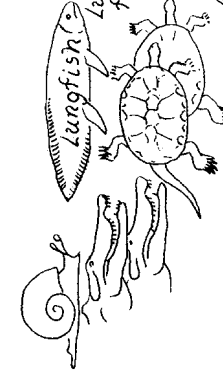
Fig. 8. - Upper teeth of Como theropods. **A** - *Ceratosaurus* MARSH, WDIS 538, middle maxillary row, crown height 80mm. Ward Facies. **B** - Allosaurid, WDIS 536, middle maxillary row, crown height 58mm. Carlin Facies. **C** - Megalosaur, WDIS 537, middle maxillary row, crown height 75mm. Carlin Facies.

Some confirmation of this theory is provided by the shape of allosaurid tooth crowns, which are thicker medial-laterally for their height than are ceratosaurid and megalosaurid crowns (Fig. 8; BAKKER, 1997). Consequently, allosaur crowns are blunter, stronger, and would have been better able to resist breakage when the tooth row was drawn backwards through the prey's hide. Allosaurid serrated keels are twisted more than in other Jurassic theropods, with the posterior keel passing outwards from the crown tip and the anterior passing inwards; during attack, the twist would keep shallow wounds open.

ECOLOGICAL SEGREGATION OF COMO BLUFF ALLOSAURIDS

The ecological context of theropod samples from Como Bluff, Wyoming, provide a test of the idea that allosaurids were specialized sauropod-killers (BAKKER, 1997)(Fig. 7-9). Four broad habitats can be defined by sediments, by the foot shape of common herbivores, and by aquatic fossils (snails, clams, turtles, crocodiles, lungfish): 9-Mile Facies - red-green mottled soils, few pond limestones, no swamp mudstones, few aquatic snails or clams, few aquatic ver-

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Fig. 7 - Habitats and predators in the Morrison Formation at Como Bluff Wyoming. **Top row**: Hind feet with silhouettes of footpads, as shown by footprints. Compact Feet, common at 9-Mile Facies: dryosaurs, camptosaurs, stegosaurs. All Terrain Feet, common everywhere except the Ward Facies: Sauropods. Wide Spreading Feet, common at the Ward Facies: *Othnielia* GALTON and *Drinker* BAKKER & GALTON. **Second row**: Habitats sampled by the Morrison Formation at Sheep Creek and Como Bluff. Names of selected famous quarries given above the habitat cartoons: Sheep Creek - Carnegie Mus. Rocket/NASA - Wyoming Dinamation Society. Bone Cabin Quarry - American Mus. Nail - Wyo. Dinamation. Soc. Marsh Quarries - Yale. Becky, Bernice - Wyo. Dinamation Soc. The Arrowtail Facies samples dune fields adjacent to shallow, short-lived lakes and poorly drained floodplains. The 9-Mile Facies samples red-green mottled, well drained soils and episodic sheet floods. The Carlin Facies samples drab, poorly drained soils and small, short-lived ponds and swamps. The Ward Facies samples huge, long-lived swamps and adjacent poorly drained floodplains plus scattered river channels. **Third Row**: Composition of samples of shed theropod teeth and potential prey skeletons. Sample size given to right of bar diagram. Theropod shed teeth: allo - allosaurs; cerato - ceratosaurs; meg - megalosaurs. Prey dinosaurs, sampled by skeletons: apat - apatosaurs; brac - brachiosaurs; cam - camarasaurs; camp - camptosaurs; dip - diplodocines; hap - haplocanthosaurs; othniel-drink - big footed ornithopods; steg - stegosaurs. **Bottom row**: Abundance of aquatic fossils. Single cartoon, number of specimens = 1-10% number of dinosaur skeletons. Double cartoon, number of specimens = 10-50% number of dinosaur skeletons. Triple cartoon, number of specimens = 50-500% + number of dinosaur skeletons.
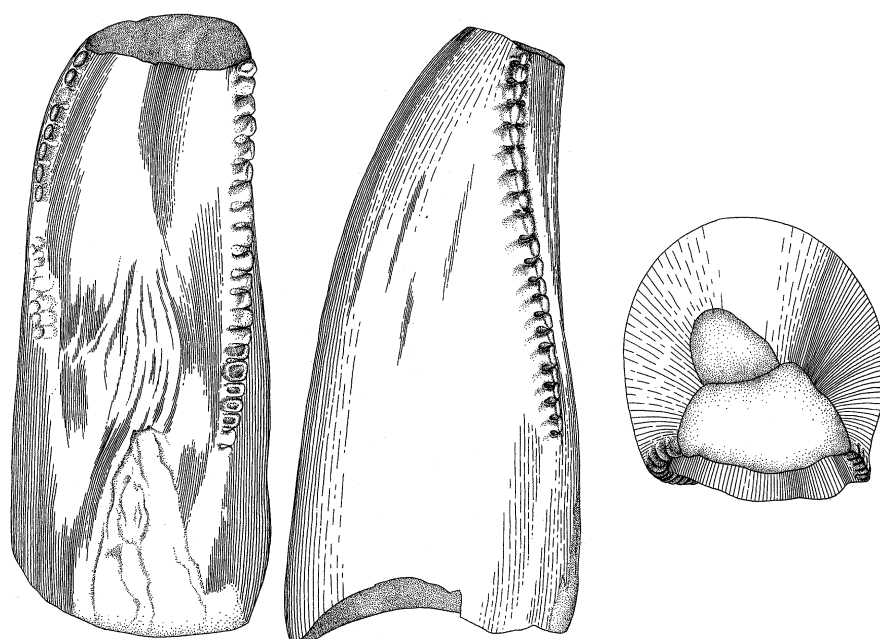
Fig. 9. Dromaeosaurid, WDIS 539, anterior premaxillary tooth, crown height restored 12 mm. Ward Facies. This specimen is the earliest known dromaeosaurid.

tebrates; Arrowtail Facies - wind-blown sand dunes, many pond limestones, drab floodplain muds, abundant aquatic snails, few aqautic vertebrates; Carlin Facies - drab floodplain mudstones, many small pond limestones and dark swamp mudstones, local patches of abundant snails and aquatic vertebrates; Ward Facies - wide and deep laminated dark swamp mudstones, super abundant aquatic vertebrates. Large herbivorous dinosaurs with small feet - camptosaurs, dryosaurs and stegosaurs - are common only in the 9-Mile Facies where red/green mottled paleo-soils indicate firm substrate. Sauropods, equipped with large, padded feet with gripping claws, are common in the 9-Mile, which samples well-drained soils, and in the Arrowtail Facies and Carlin Facies, which sample poorly-drained floodplains and small swamp-pond systems. Ornithopod dinosaurs with large, spreading feet dominate in only one habitat, the Ward Facies, a huge swamp/lake system.

Shed theropod teeth show where feeding activity took place. In these three facies with abundant sauropods - 9-Mile, Arrowtail, and Carlin - allosaurs make up most of the shed theropod tooth sample. The Ward Facies is the only habitat where sauropod bones are very rare, and this facies is the only habitat where allosaurid shed teeth are greatly outnumbered by megalosaurids and ceratosaurids (Fig. 7). Thus the predator families were ecologically segregated: allosaurids fed on sauropods, stegosaurs and camptosaurs on floodplains, while non-allosaurids fed on aquatic and semi-aquatic prey in

and around swampy terrain (Fig. 7, 8). The Ward Facies also represents the final stage of Morrison Formation deposition, at the Jurassic/Cretaceous boundary, and here are the first records of some characteristic Cretaceous theropods, such as dromaeosaurids (Fig. 9). The rarity of allosaurids in the Ward Facies suggests an interesting scenario: allosaurid reduction and ultimate extinction during the Jurassic-Cretaceous transition and the radiation of new theropod groups were caused, in part, by a temporary shift in habitat away from the open floodplains where allosaurids had enjoyed numerical dominance.

PRE-ALLOSAURID FAUNAS

A test can be found in the faunas immediately older than those with allosaurids. In the Tendaguru, East Africa fauna, that immediately predates the earliest Morrison faunas, gigantic sauropods are common and diverse. Unfortunately, good cranial material from large theropods is lacking. Fortunately superb theropod skulls have been recovered from the Mamenchisaur Faunas of China, probably of early Late Jurassic age (DONG, 1992, CURRIE & ZHAO, 1993). Sauropods dominate the herbivore sample but average body size is smaller than that of the Tengaguru and Morrison. No true allosaurids are present; the commonest big predators are sinraptorids, with femora in the range seen in allosaurids, 800-1200mm. If the theory is correct, then sinraptorids should show at least some of the adaptations fully developed later among allosaurids. The predic-

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tion is confirmed. Sinraptorids have paroccipital processes more deflected downwards than those of ceratosaurids but less than in allosaurids; sinraptorids also have an accessory transverse web of bone reinforcing the basicranial axis where the ventral-most head flexors attach.

POST-ALLOSAURID FAUNAS

If the Kowalevskian theory is correct, adaptations for killing prey huge compared to predator size should become less common as the predator-prey size disparity decreases in Cretaceous dinosaur faunas. In the early Early Cretaceous (Neocomian) of England, a mixed sauropod+ankylosaur+iguanodont fauna occurs with the last known genuine allosaurids. In the later Early Cretaceous (Aptian-Albian) of Texas and Oklahoma, a mixed medium-size-sauropod+ankylosaur+iguanodont fauna occurs with the large theropod *Acrocanthosaurus* STOVALL & LANGSTON, femur length 1.2 m; average herbivore size is far smaller than that of the Late Jurassic. Although *Acrocanthosaurus* sometimes is referred to the allosaurids, it has large, laterally compressed, sharp teeth and lacks the down-turned paroccipital process and enlarged lower quadrate condyle; this genus did not have the extreme head-as-war-club adaptations seen in Late Jurassic allosaurids (STOVALL & LANGSTON, 1950).

In North America in the Late Cretaceous, the average large herbivore size falls to near that of the average top predator, because the giant sauropods are replaced nearly entirely by duckbills, horned dinosaurs, and ankylosaurs, herbivores who rarely achieve a femur length greater than 1 m. The commonest large predators in these Late Cretaceous faunas are tyrannosaurids, with femur lengths of 1m to 1.38 m. Tyrannosaurids show none of the war-club adaptations seen in allosaurids. Tyrannosaurid lower and upper temporal bars are long, tooth crowns are long, paroccipital processes are not bent, and lower quadrate condyles do not develop bulging, twisted surfaces with ligament pits. Tyrannosaurid jaw adductor chambers were wide medial-laterally and long anterior-posteriorly at the top and bottom; clearly the biting muscles were very strong and were not sacrificed in favor of neck ventral-flexors.

The overall composition of Laurasian Cretaceous faunas confirms the theory that when predators are nearly the same size as the prey, sabre-tooth style adaptations become rare.

A special case is presented by Cretaceous faunas where dromaeosaurid raptors are the largest common predators. Raptors may be termed "Sabre-Toed" predators: another group of body muscles - that of the hindleg - is recruited to power a killing weapon, the huge slashing claw, allowing the raptors to kill prey far larger than themselves. In most samples, dromaeosaurids are dwarfed by acrocanthosaurids or tyrannosaurids, and it's hard to identify which herbivores were the core prey species for the raptors and which for the giant theropods. However, a few samples do exist where raptors are the biggest common carnivore, and the theory would predict that the average large herbivore would be far larger than the raptors. Case in point: in the Cloverly Formation, late Early Cretaceous, the medium-size raptor *Deinonychus* OSTROM is the only common predator, adult femur length 320 mm, adult weight calculated from models of 70 kg; larger theropods are represented only by scraps (OSTROM, 1970). If *Deinonychus* were adapted for harvesting relatively large prey, then the common herbivore should be an order of magnitude larger than *Deinonychus*. This prediction is met. By far the commonest Cloverly herbivore found with shed raptor teeth is the ornithopod *Tenontosaurus* OSTROM, with an adult femur length of 580 mm and a body weight, calculated from scale models, of about 1300 kg.

South American Cretaceous faunas contain a far richer assemblage of large sauropods than does contemporaneous Laurasia (RUSSELL, 1993). Therefore one would predict that selection would favor the evolution of allosauroid adaptations. The horned predator *Carnotaurus* BONAPARTE from Argentina does show convergence with true *Allosaurus* MARSH: the tooth height is reduced, snout length is shortened, the upper rim of the occiput is strengthened by a web of bone connecting the supraoccipital with the squamosal, and the lower temporal fenestra is compressed anterior-posteriorly (BONAPARTE, NOVAS & CORIA, 1990). *Carnotaurus* does not show downward deflection of the paroccipital process; nonetheless, the strong occiput and small teeth suggest that the upper jaw was used as a club.

The better known Cretaceous faunas thus seem to confirm the general thesis that when the commonest herbivores are very much larger than the commonest top predator, some top predators evolve weapons for slashing. There are Gondwana Cretaceous dinosaur faunas in Brazil, India and Madagascar where huge sauropods are common and diverse, and hence it would be most intriguing to examine the top predators for evidence of slashing features.

CONCLUSION

I'm persuaded that Kowalevsky was fundamentally correct. Evolution of land vertebrates is neither chaotic nor adaptively capricious. The selective pressures upon top predators have an especially narrow focus. Whenever there are repeated cycles of changing prey resources, we should see distantly

related predator clades evolving structures that are functionally analogous. When giant herbivores make up a very great proportion of the potential prey, skull or claws do become modified to permit a top predator to slash at its target without holding on.

ACKNOWLEDGEMENTS

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