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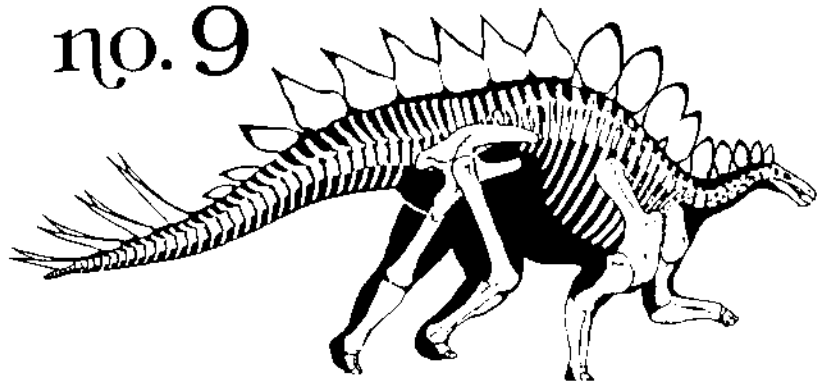
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**EDMARKA REX, A NEW, GIGANTIC THEROPOD DINOSAUR
FROM THE MIDDLE MORRISON FORMATION, LATE JURASSIC
OF THE COMO BLUFF OUTCROP REGION**

*With comments on the evolution of the chest region and shoulder in theropods and birds,
and a discussion of the five cycles of origin and extinction among giant dinosaurian predators*

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ABSTRACT

Edmarka rex, a new species of torvosaurine megalosaurid, is described from specimens found in the middle levels of the Morrison Formation at Como Bluff, Wyoming. The Como torvosaur differs from *Torvosaurus tanneri*, from Dry Mesa Quarry, in western Colorado, in having a jugal with a wider, triangular, tyrannosaur-like postorbital process, much narrower medial-lateral width, and relatively longer, lower lateral profile. Although the Como jugal is close in size to that from Dry Mesa, the postcrania associated with the Como torvosaur is 30% larger than most of that ascribed to *T. tanneri*, suggesting that the Dry Mesa vertebrae and hindlimb material do not belong to the huge skull and forelimb from that quarry. All primitive theropod jugals differ from those of thecodonts in having a more cylindrical quadratojugal process, indicating that the lower temporal bar was used to protract the face to some extent, an adaptation fully expressed in birds. The torvosaurine scapula-coracoid agrees with that of *Megalosaurus* in the following: a wide scapula blade of nearly constant width, not expanded dorsally as in allosaurs and ceratosaurs; an evenly rounded coracoid that lacks the posterior hook of allosaurs; a glenoid that does not face as strongly downwards as in ceratosaurs. Progressive narrowing of the scapular blade in theropods and birds was made possible by the strong tilt of the blade which provided the teres and deltoid muscles with a wide origin. Torvosaur ribs were not hollow-cored, unlike those of ceratosaurs and *Megalosaurus*. Yangchuanosaurs may well have coexisted with megalosaurs in the early Late Jurassic of Europe. Contrary to previous impressions, giant torvososaurs are not uncommon in the lower two-thirds of the Morrison Formation. Giant allosaurs (*Epanterias amplexus*) appeared during Morrison times after giant torvososaurs had already disappeared. Five or six different theropod families evolved giant predator species with femur length 1100 mm or greater, but at no time did giant predators from two families coexist. Maximum theropod size was not controlled by prey size or prey defenses. When one family replaced another as giant predator, the new giant predator usually was more advanced in the degree in which avian-like characters were developed in skull and postcrania.

INSTITUTIONAL ABBREVIATIONS

AMNH — American Museum of Natural History, New York, New York. BYU — Brigham Young University, Provo, Utah. CPS — Wyoming-Colorado Palaeontographical Society (collections temporarily at University of Colorado but will be transferred to Wyoming institutions for permanent repository). USNM — United States National Museum, Washington, D.C. UUV — University of Utah Vertebrate Paleontology, Salt Lake City, Utah.

INTRODUCTION

Myth of *Tyrannosaurus* Superiority To judge by popular books and television programs — including a question on the popular quiz show *Jeopardy* — the Late Cretaceous carnivorous dinosaurs of the tyrannosaur family exceeded greatly in size any carnivore from the Jurassic Period. But, in fact, in 1878, long before any tyrannosaur species was described, a gigantic theropod was named from the latest Jurassic of the Morrison Formation at Oil Creek, Colorado. This specimen, the type of *Epanterias amplexus* Cope 1878, represents an allosaurid species with a nose-to-tail length as great or greater than that of most adult *Tyrannosaurus* skeletons (Bakker, 1990; Osborn and Mook, 1920). So large are the *Epanterias* bones that Cope himself was misled into believing that they were those of a sauropod. A second giant allosaur was found in the 1930s in the Morrison of western Oklahoma, a third near Fort Collins, Colorado, in 1988 (Bakker, 1990); all *Epanterias* specimens come from the highest dinosaur-bearing levels of the Morrison known at the sites.

Here we report the discovery of *Edmarka rex*, another gigantic Morrison theropod that would rival *T. rex* in total length. *E. rex* and its close kin, *Torvosaurus tanneri*, seem to be relatively common only in the middle and lower levels of the Morrison. These torvosaurines are the last and largest members of the megalosaurid family, as redefined by Galton and Jensen (1979). The presence of a giant megalosaurid in the Como Bluff Morrison suggests several revisions of standard views about dinosaur evolution: 1) The body size category occupied by *T. rex* was filled repeatedly, in succession, by species from five or six separate families, and this size probably reflects a natural ceiling for dinosaurian meat-eaters. 2) At no time did two giant carnivore species from two different families coexist in one place. 3) In most cases, when one family replaced another as giant carnivore, the new top predator was more advanced than the old in skull and limb characters and comes closer to an avian level of organization. 4) When one family replaced another as top predator, the incumbent giant carnivore went extinct before the replacement giant species appears; therefore occupancy of the top predator role seems to confer an advantage in suppressing the evolution of another giant carnivore from any other family.

Discovery Two quarries have produced the giant torvosaur in the Como outcrop area. Siegwarth and Filla excavated a series of huge theropod ribs from Louise Quarry in early summer 1989. Bakker, in an error recalling Cope's mistaken allocation of *Epanterias*, misidentified the ribs as those of a small sauropod. James Madsen was the first to suggest theropod affinities. The ribs are 20% larger than those of any other Morrison theropod except *Epanterias*. Kralis and Bakker discovered Nail Quarry during mid summer 1990. Kralis uncovered a very large left theropod scapula-coracoid, which Bakker removed; the shape of the scapular blade was recognized as being megalosaurid. In August, 1991, Kralis was assisting Bakker in teaching a field course organized by Mike Perry of the Dinamation International Society. Kralis and members of the field course discovered and excavated a left jugal that shared several peculiarities with that referred to

Torvosaurus tanneri from Dry Mesa Quarry in western Colorado (Britt, 1991) and a coracoid with a shape close to that of megalosaurs from the Mid Jurassic Stonesfield Slate Quarry, the type locality of *Megalosaurus*. Theropod ribs, agreeing in size and shape with those from Louise Quarry, were also excavated at Nail, as well as a first caudal vertebra. All of the giant theropod bones from Nail and Louise have linear dimensions close to that of *Epanterias* but show the distinctive shape of the Megalosauridae.

A third Como region quarry has produced a giant megalosaur that may represent *Edmarka*, *Torvosaurus* or some closely related species. In August, 1991, Mr. Ron Jones of Bartlesville, Okla., a member of the Dinamation International Society field course, discovered a very rich locality, Zane Quarry, within the lacustrine limestones of the lowermost two meters of the Morrison Formation. Large megalosaurid ribs and fragments of vertebrae were recovered (Field #Z-1). This locality is by far the earliest known site of abundant dinosaurs yet known for the entire Morrison outcrop region in the Colorado Front Range and adjacent Wyoming, and the only rich locality known for the lowermost Morrison anywhere.

Edmarka rex, genus et species novum

Diagnosis for genus and species: Closest to *Torvosaurus tanneri* but differs in retaining the primitive condition of a jugal that is thin medial-laterally, relatively longer and lower in lateral view, and with an orbital margin that is wider front-to-back. Further differs in the derived character of a much wider postorbital process on the jugal, with an enlarged, recessed facet on the outer surface for an expanded ventral ramus of the postorbital.

Type: CPS 1005, left jugal, missing only the extreme dorsal tip of the postorbital process and the posterior tip of the lower quadratojugal process. CPS 1004, dorsal ribs, and CPS 1002, left adult scapulocoracoid with closed suture, may belong to the type individual — all these bones were found in a 3 m x 2 m area in the quarry. CPS 1005, proximal caudal, with tightly coossified centrum-arch suture, was found 5 m away from the jugal and may belong to the type. Nail Quarry.

Referred specimens: CPS 401, six right dorsal ribs, Louise Quarry. CPS 1003, subadult left coracoid, Nail Quarry, found underneath the anterior edge of the type jugal.

Provenance: Middle to Late Tithonian, Late Jurassic, Morrison Formation, Como Bluff outcrop region. Maps are available from the authors for reputable scientists. We refrain from publishing these maps here because of the very real danger from vandals and unscrupulous rock hounds. Both Louise and Nail Quarries are from an interval below the "Main Marsh Upper Gray Mudstone", the interval where most of Marsh's quarries were located (including Quarry 9, the mammal quarry), but far above Marsh's Quarry 13 (the stegosaur-camptosaurus quarry). Only one Como quarry has been reported previously from this middle interval — Marsh's Quarry 7 (Bakker, 1990). In the measured section presented by Bakker (1990), Louise Quarry is at 44 m; Nail is at 48 m.

Etymology: *Edmarka* — "belonging to Edmark", in honor of Dr. Bill Edmark, University of Colorado alumnus, who has made notable contributions to science and technology, * *rex* — Latin "king" in reference to the top predator status of the species. The combination of a first declension — *a* ending with *rex* — follows the usage of Queen Elizabeth the First, who signed her own name "Elizabeth rex".

Description and Comparisons

For the following discussion the Family Megalosauridae is defined by the species *Poikilopleuron bucklandi* and *Torvosaurus tanneri*, taxa that share the derived condition of very short, thick forearm and metacarpus, as noted by Galton and Jensen (1979). *Megalosaurus bucklandi*, the type for the Family, is assumed to be close to *Poikilopleuron* because of the overall similarity of vertebrae and limbs of the latter to the disassociated remains referred to *M. bucklandi* from the type quarries at Stonesfield (Eudes-Deslongchamps, 1838; Huene, 1926; Gilmore, 1920; Taquet and Welles, 1977; Walker, 1964). Galton and Jensen (1979) suggested that the short forelimb elements of *Poikilopleuron* and *Torvosaurus* were primitive, but, since very primitive theropods, such as podokesaurs and herrerasaurs and staurikosaurus, have forearm bones of less abbreviated structure, it is more probable that the megalosaur condition is advanced. *Eustreptospondylus oxoniensis* is here referred, with some doubts, to the megalosaurids, because of the close similarity of the lacrimal and maxilla to those of *Torvosaurus*, similarities that may be primitive retentions. We use "torvosaur" and "torvosaurine" as the informal category for the largest and most specialized megalosaurids, *Torvosaurus* and *Edmarka*, distinguished from all other Late Jurassic theropods by the great depth of the jugal.

Jugal, main body and quadratojugal joint (Fig. 1-4). The Nail Quarry jugal is nearly complete (Fig. 1A,B). The two jugals from Dry Mesa Quarry ascribed to *T. tanneri* are missing large pieces from the anterior (maxillary-lacrimal) processes (Fig. 1C); as we restore them, these jugals are 5% shorter fore-to-aft than the one from Nail Quarry. If other skull elements were similar in relative size (Fig. 3B), then *Edmarka* had a total skull length exceeding 1300 mm, as large as that of *Tyrannosaurus rex*. In general, the jugals of *T. tanneri* and *E. rex* are distinguished from those of ceratosaurs and allosaurs by a greater dorsal-ventral depth. In *T. tanneri* the jugal is both absolutely deeper and deeper relative to bone length than in *E. rex* (Fig. 1C,D). In both the Nail and Dry Mesa jugals the upper quadratojugal process is relatively much longer fore-to-aft than in allosaurs, agreeing with the condition in ceratosaurs. Long quadratojugal processes indicate a very long lower temporal bar and a voluminous adductor box, behind the orbit and in front of the quadrate, where most of the adductor mandibulae originates (Fig. 3B). Allosaurs are one of the very few large theropods to show reduction of the anterior-posterior length of the lower temporal fenestra (Fig. 3C), but such reduction is common among small theropods — for example, ornithomimids and *Coelophysis*. Allosaurs are also unusual in having tooth crowns that are small for their jaw length compared to the condition in ceratosaurs and megalosaurs. It is becoming clear that allosaurs took a markedly divergent path in occupying the top predator role.

The jugal in *Edmarka rex* agrees with that of most other large theropods, including albertosaurs, in being quite thin medial-laterally. *Torvosaurus tanneri* is most unusual in the spectacularly increased medial-lateral width — in vertical cross sections the width is two or three times greater than in *E. rex*, even though the jugal in *E. rex* is longer (Fig. 1A-C). The massive jugal in *T. tanneri* implies that the stresses induced across the lower cheek region were far higher than was typical in theropods — either exceptionally wide temporal muscles or some sort of head-bumping behavior may be suspected. It is intriguing that *Tyrannosaurus rex* also displays massive cheek bones, and this species shows both great temporal width and swollen, reinforced areas on the skull roof for head-butting.

In the jugal of *E. rex* the two quadratojugal processes are exceedingly different in size, shape and function (Fig. 1A,B). The upper process is extremely thin side-to-side and certainly could bend when the animal was alive. The lower process is long but massive with a cross-section

wider than tall; little bending would be possible. The upper process has smooth surfaces all over; the lower process has roughened lines covering the convex ventral surface and the concave dorsal surface which makes up the main articulation for the ventral edge of the quadratojugal. Ligamentous sheaths must have bound the lower jugal process to the quadratojugal. The degree of roughening of the bone surface suggests that these sheaths bound the two bones tightly and that fore-to-aft sliding was not possible. However, the quadratojugal probably could twist around an axis passing through the jugal-quadratojugal joint, and the thin upper process of the jugal would bend to accommodate the twisting. This twisting would be necessary if the quadrate were to swing outwards and slightly forwards at the quadrate-squamosal joint. In most theropods, the quadrate head has a cylindrical joint surface that produces an outward and forward movement on the squamosal. Movement of this joint would enlarge the distance between the distal ends of the right and left quadrate, thus increasing the gullet size.

In *Torvosaurus tanneri* the quadratojugal processes are more massive than those of *E. rex* and most other theropods (Fig. 1C). The upper process is thicker medial-laterally and the lower margin is more strongly twisted outwards and has a bevelled outer edge. The lower quadratojugal process in *T. tanneri* is much deeper than wide, in sharp contrast to the condition in *E. rex*.

The lower quadratojugal process of the jugal in theropods is a region of interest to studies of bird origins (Fig. 2,4). As Chatterjee (1991) points out, the avian quadrate-temporal-bar mechanics are unique among modern vertebrates. Indeed, modern birds and colubroid snakes represent the highest grade of adaptation for mobility of the quadrate, facial bones and snout. In the primitive reptile condition, the pterygoid-quadrate joint is a sheet-to-sheet contact and the quadratojugal-quadrate joint is extensive and immobile. The avian quadratojugal has a pivot joint with the quadrate on the outer surface, and the pterygoid has a hinge joint along the anterior-inner quadrate surface. The bird pterygoid and quadratojugal are parts of an inner and outer compression strut system; when the quadrate is protracted, the inner and outer struts push the palate and beak forward and upward relative to the braincase + orbitotemporal region. All birds have a highly mobile quadrate-squamosal joint that is synovial. The most primitive diapsid reptiles, including the extant *Sphenodon*, lack a highly mobile quadrate-squamosal joint: the quadrate head does not have a distinct articular surface in the shape of a ball or cylinder; the descending process of the squamosal is very wide and extends far ventrally to obtain an extensive overlapping contact with the quadratojugal; this long, ventral squamosal-quadratojugal contact would hinder any outward movement of the quadrate.

Thecodonts and primitive theropods show how the avian system evolved from that of a *Sphenodon*-grade reptile (Fig. 2,4). In primitive thecodonts, such as erythrosuchids, the quadrate head has a convex joint surface for the squamosal; the quadratojugal process of the jugal is one undivided sheet; the pointed posterior part of this sheet fits into a dorsal-ventrally deep depression in the outer surface of the quadratojugal. All primitive theropods — torvosaurus are good examples — have a more advanced system (Fig. 4) where the quadratojugal process is divided into upper and lower prongs, and the upper prong is sufficiently thin to permit twisting of the quadratojugal. The lower quadratojugal process in primitive theropods is modified into a stout prong of semi-circular cross section that resembles the tubular lower temporal strut of birds and could function in a similar manner, transferring the thrust of the quadrate to the maxilla and lacrimal. It is unclear exactly what sort of movement at the snout and face would be produced by outward and forward movement of the quadrate in torvosaurus and other primitive theropods. In most birds, the snout can be raised by quadrate

sb sc — subcoracoscapularis. sc delt — scapular deltoid. sc hu pos — scapulo-humeralis posterior. ser pos — serratus posterior. sprcor — spracoracoideus. sq — squamosal. stern mas — sternomastoideus. sup cor — spracoracoideus. sup scap — suprascapular cartilage. sur — surangular. sut spin — sutural spine of coracoid. ter — teres. trap — trapezius. tri — triceps. tub — tubercle. wedge — re-entrant wedge on jugal.

abbreviations: for all figures: an — angular. ant — anterior. ant rim — anterior (outer) glenoid rim. art — articular. bi — biceps. bra — brachialis. cap — articular capsule. capt — capitulum. cart rib — cartilage ribs, connecting osseous rib to sternum. cone — cone-in-wedge joint of coracoid-scapula suture. cor bra — coracobrachialis. cos cor — costocoracoideus. delt — clavicular deltoid. den — dentary. dor — dorsal. ect — ectopterygoid. evert — everted edge of jugal. gla — glenoid long axis. grv — groove. il cos — illocostalis. in micos — inner intercostalis. j — jugal. l — lacrimal. lat — latissimus dorsi. lev — leverage. lev scap — levator scapulae. max — maxilla. n — nasal. out int cos — outer intercostalis. pect — pectoralis. pm — premaxilla. pn — pneumatic cavity. po, porb — postorbital. prf — prefrontal. pt — pterygoid. q — quadrate. qj — quadratojugal. res — restored. rhom — rhomboideus.

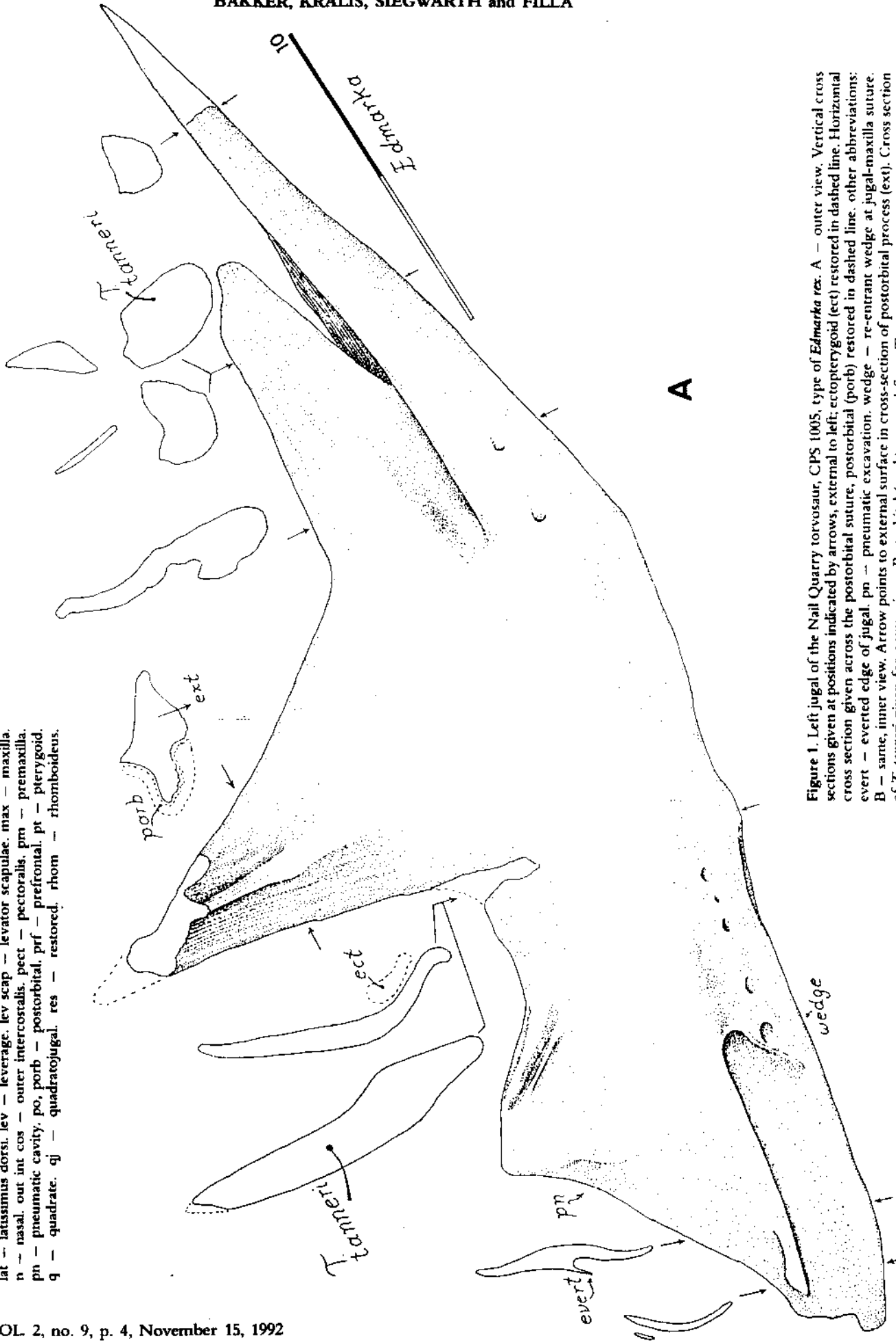


Figure 1. Left jugal of the Nail Quarry torvosaur, CPS 1005, type of *Edmarkia* res. A — outer view. Vertical cross sections given at positions indicated by arrows, external to left; ectopterygoid (ect) restored in dashed line. Horizontal cross section given across the postorbital suture, postorbital (porb) restored in dashed line. Other abbreviations: evert — everted edge of jugal. pn — pneumatic excavation. wedge — re-entrant wedge at jugal-maxilla suture. B — same, inner view. Arrow points to external surface in cross-section of postorbital process (ext). Cross section of *T. tannieri* given for comparison. Postorbital (porb) restored from *Tannierosaurus*.

EDMARKA REX OF COMO BLUFF

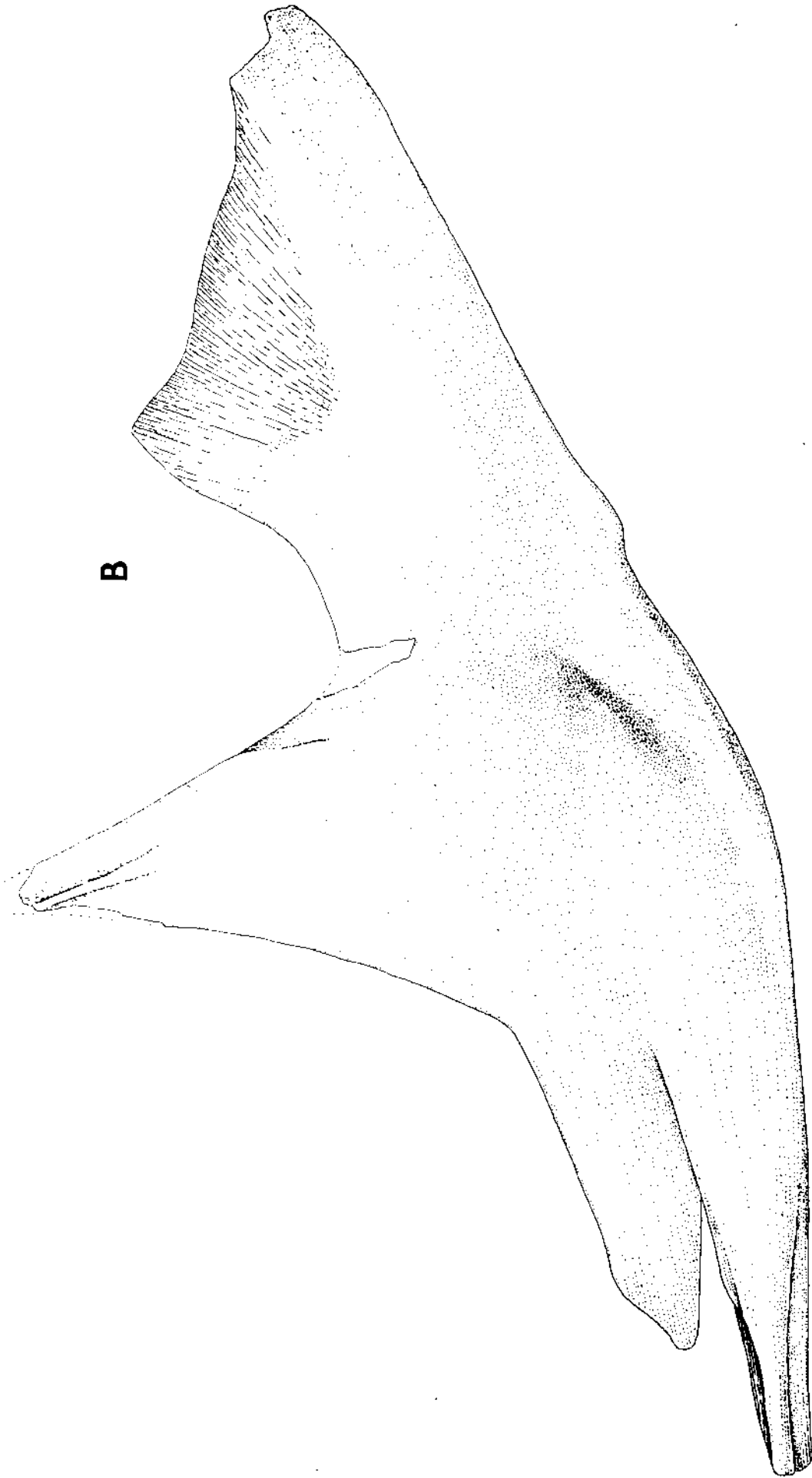


Figure 1 continued. Left jugal of the Nail Quarry torvosaur, CPS 1005, type of *Edmarka rex*. B — inner view.

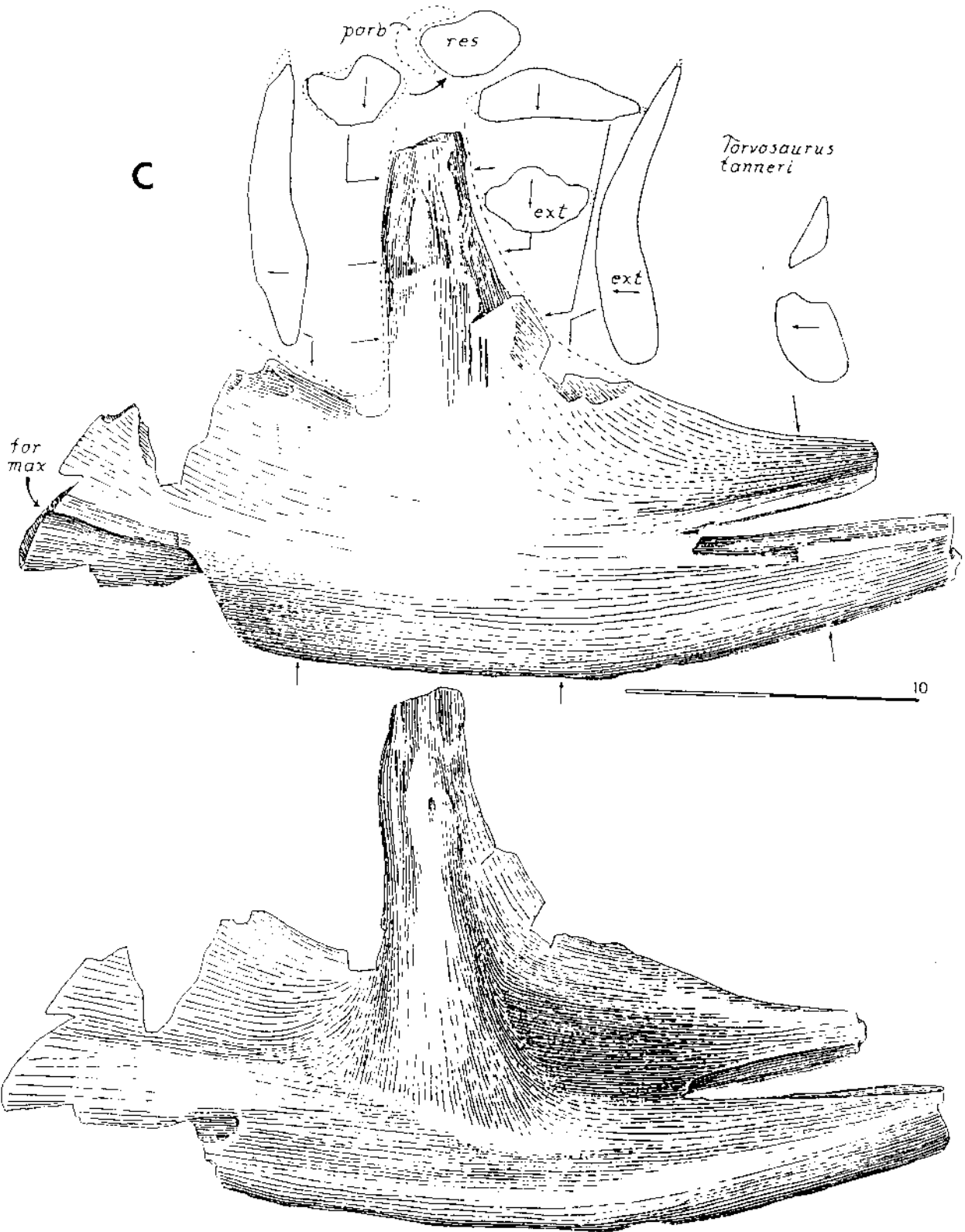
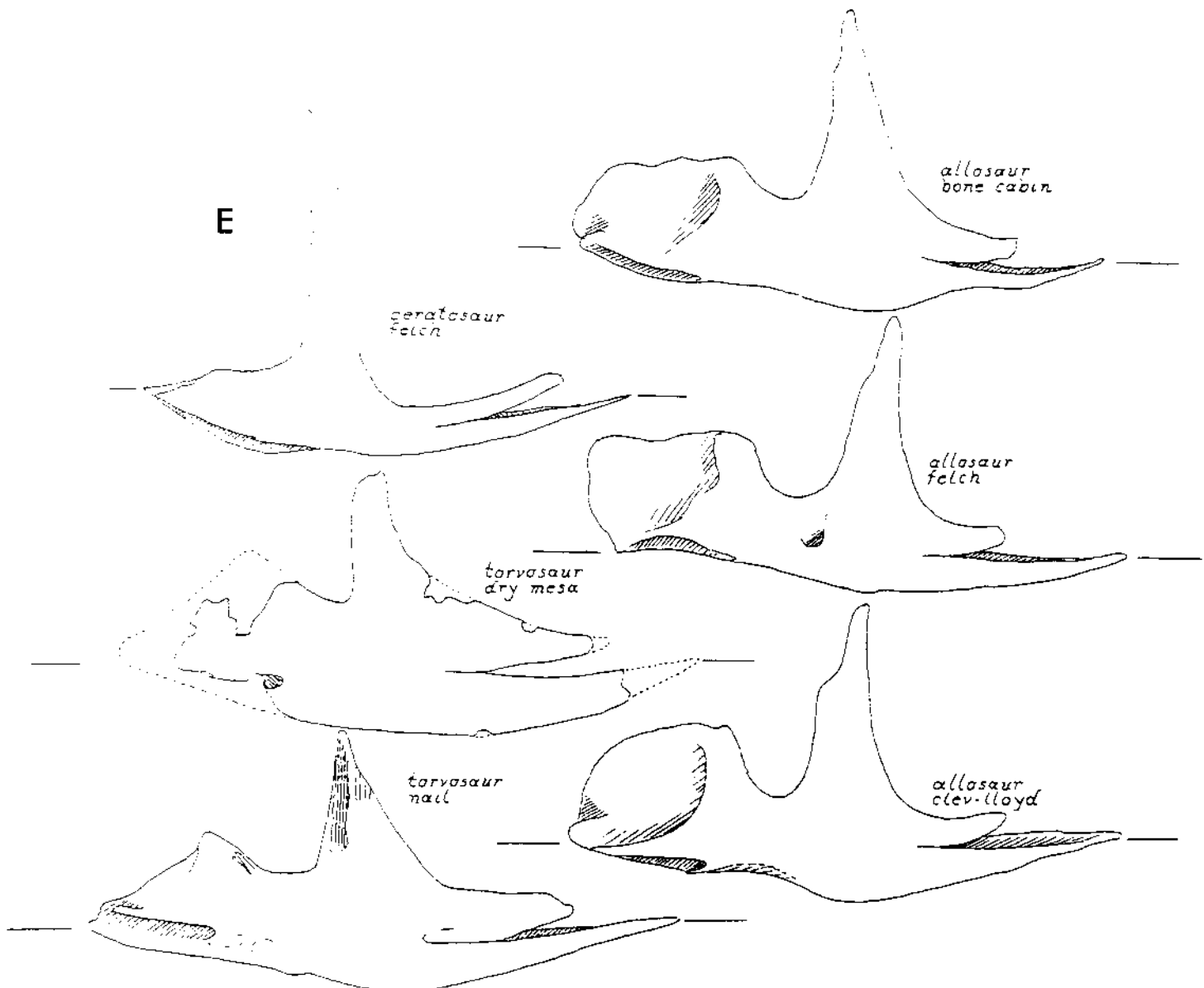
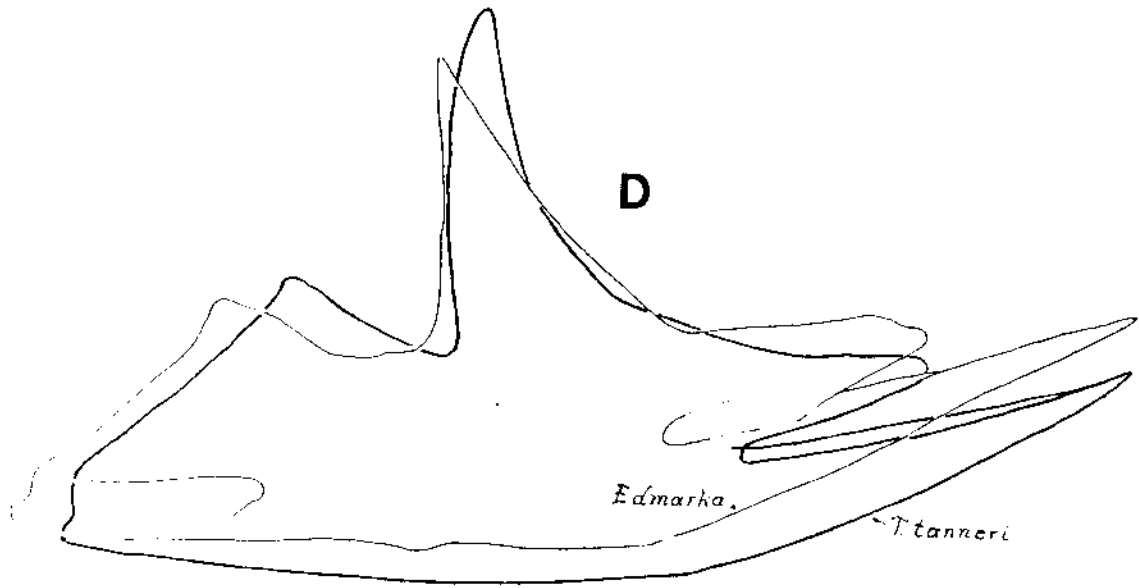


Figure 1 continued. C — outer (reversed) and inner views of the Dry Mesa jugal ascribed to *Torvosaurus tanneri*. Eroded surfaces on postorbital process restored in dotted lines. Horizontal cross-sections given across postorbital process as preserved and restored (res.). Upper limit of joint facet for maxilla indicated by arrow (for max). Postorbital (porb) shown restored from *Torvosaurus*. Arrows in cross sections point towards external surface (ext).

Figure 1 continued. D — outer outlines of the jugals of *T. tanneri* (heavy line) and *E. rex* (fine line). E — outer views of left jugals. Felch allosaur — USNM 4734 (topotype of *A. fragilis*). Cleveland-Lloyd allosaur from Madsen, 1976. Bone Cabin allosaur, AMNH 600. Felch ceratosaur — USNM 4735 (type of *Ceratosaurus nasicornis*).



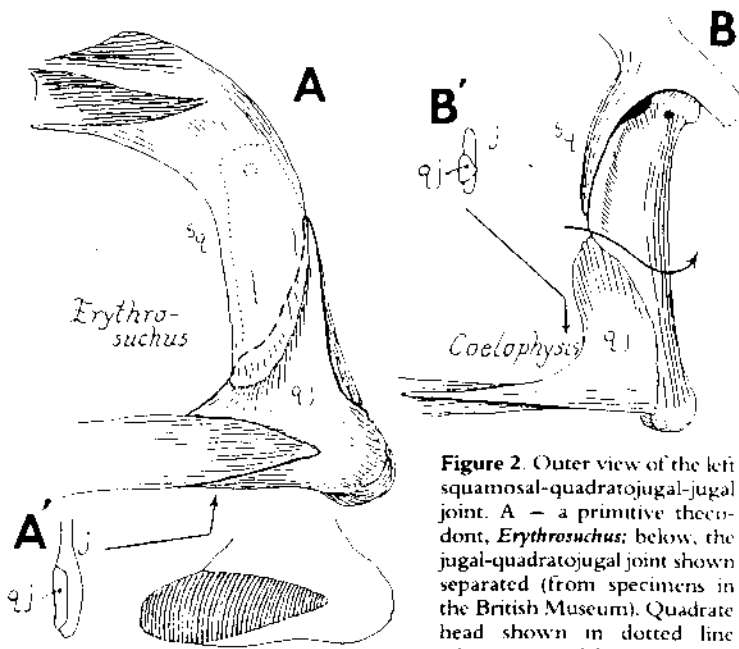


Figure 2. Outer view of the left squamosal-quadratojugal-jugal joint. A - a primitive thecodont, *Erythrosuchus*; below, the jugal-quadratojugal joint shown separated (from specimens in the British Museum). Quadrate head shown in dotted line where covered by squamosal.

B - a primitive theropod, *Coelophysis* (from specimens at the U.S. National Museum), arrow shows inferred course of the auditory meatus. A', B' - inset shows vertical cross section through quadratojugal-jugal joint. abbreviations: q - quadrate, qj - quadratojugal, sq - squamosal.

protraction at a joint near the frontal-nasal contact or within the nasal. However, in most theropods, the frontal meets the nasal in an extensive overlapping joint that would permit only modest flexure. It may well be that the quadratojugal compression strut was used to push the maxilla-lachrymal outwards, as part of the mouth-widening movements. It is significant that in theropods the ventral lachrymal process and the anterior jugal process are thin sheets that fit into narrow slots in the maxilla. The maxilla-nasal contact is along a narrow sutural zone that also would permit some twisting. To make a modern bird, the theropod jugal must lose its upper quadratojugal prong.

In summary, the stages in the evolution of the modern avian system may be as follows (Fig. 4): 1) **The pre-archosaur stage**; the quadrate-squamosal joint has limited mobility, and the extensive squamosal-quadratojugal contact, located far ventrally, and immobile quadratojugal-quadrate contact prohibit outwards and forwards displacement of the lower temporal bar. 2) **The primitive thecodont stage**; the quadrate has a spherical joint for the squamosal that permits some outward and forward movement, but the squamosal-quadratojugal contact is still low and extensive. 3) **The primitive theropod stage**; the squamosal-quadratojugal contact is reduced and displaced dorsally, increasing the freedom of movement of the quadrate, and the jugal has two prongs for the quadratojugal, permitting more twisting and outward displacement of the jugal and transference of quadrate thrust to the maxilla-lachrymal. 4) **The modern bird stage**; the lower temporal bar is transformed into a tubular strut, the upper quadratojugal prong of the jugal is lost, pivot and hinge joints develop between lower temporal bar and the quadrate, and between quadrate and pterygoid.

Jugal, postorbital process (Fig. 1). The postorbital process in the jugal of *E. rex* differs in quite striking ways from that of the Dry Mesa jugals ascribed to *T. tanneri*. The Dry Mesa jugal has a process that contracts in width rapidly upwards; the anterior margin is vertical and straight;

the posterior margin is concave. The cracking and erosion suffered by the Dry Mesa jugal obscures the surface details where the contact with the postorbital would occur. But the descending process of the postorbital is narrow and U-shaped in horizontal cross section, showing that the postorbital wrapped around the thick, rounded, anterior edge of the postorbital process of the jugal. In the Nail jugal, the postorbital process is developed as a wide triangle, with straight anterior and posterior margins. The articular area for the postorbital wraps far around onto the outer surface where there is a deeply recessed articular facet, ornamented with vertical ridges and striae that indicate a strong ligamentous suture. *Torvosaurus tanneri* shows little, if any, development of an outer, recessed postorbital facet on the jugal.

The inner postorbital facet on the jugal in *E. rex* is composed of an elongated sulcus with a swollen posterior edge. In the Dry Mesa jugals there is a slight swelling in this region, but poor preservation obscures details of the inner postorbital facet. A wrap-around postorbital-jugal joint may be primitive for theropods, since the podokesaur *Dilophosaurus* shows this feature, as well as do ceratosaurs. In allosaurids the postorbital contact is limited to the inner surface of the jugal, where there is a recessed facet, and the anterior edge of the jugal. In tyrannosaurids there is an extensive recessed facet on the outer surface of the jugal but little wrap-around onto the inner surface.

The difference between the Nail and Dry Mesa jugals is greater than that between daspletosaurs and albertosaurs among the tyrannosaurids and would seem to justify the recognition of two distinct torvosaur genera.

Jugal-maxilla-lachrymal connections (Fig. 1A,3). The anterior ramus of the jugal is completely preserved in the Nail specimen. The attachment site for the lachrymal is indicated on the inner surface by a flat zone with fine, raised lines radiating forward and up-and-forward. This surface texture indicates that the lachrymal-jugal connection was carried out by relatively delicate ligamentous tissue that might permit some rotation of the two bones at their suture. The articular area for the maxilla on the outer surface of the jugal is unexpectedly complex. The ventral edge of the anterior jugal process is narrow, rounded and smooth, and would fit into the outer groove in the maxilla. Running along the outer jugal surface is an everted edge of bone with a razor-sharp lower margin (evert in Fig. 1A); the jugal is deeply excavated upwards between this edge and the main sheet of the jugal. The maxilla must have had a tall outer edge that fit into this excavation; a similar situation occurs in ceratosaurs and allosaurs, although the depth of the jugal beneath the everted edge is less in allosaurs. At its posterior termination, the everted edge meets a forwardly directed wedge of bone (wedge in Fig. 1a); in ceratosaurs this re-entrant wedge articulates into a notch in the maxilla; hence the maxilla-jugal contact is zig-zag in this zone. The zig-zag maxilla-jugal contact indicates that fore-to-aft sliding was not possible; however, some outward-inward flexure would be permitted. In the jugals from Dry Mesa, most of the maxillary contact region is broken but the parts preserved do show a section of the everted edge and the excavated groove below (Fig. 1C).

At the dorsal-anterior corner of the outer jugal surface in the Nail specimen, the everted edge terminates in a thin, free prong of bone that must have clasped the maxilla. The upper edge of the anterior process of the jugal makes an obtuse triangle in lateral view; the posterior side of this triangle is the lower margin of the orbit. In the Dry Mesa specimen the lower margin of the orbit is more compressed fore-to-aft. A compressed orbital margin probably is derived within theropods, since ceratosaurs and most Triassic taxa have more widely open orbits. In allosaurs and most Cretaceous theropods the outer surface of the anterior jugal ramus is excavated for a large pneumatic sinus. But in the Nail jugal there is only a small excavation below

the anterior edge of the postorbital process (pn in Fig. 1); this excavation would continue dorsally onto the lacrimal (Fig. 3B). In the Dry Mesa lacrimal there is an extensive pneumatic zone on the outer surface, as in ceratosaurs.

Posterior to the re-entrant wedge for the maxilla on the outer surface of the Nail jugal are a series of four exits for the cutaneous branches of the maxillary nerve (V_2). Further posteriorly, at the root of the lower quadrato-jugal process, are two more exits for the same nerve. Extant iguanid and monitor lizards have a similar exit pattern for the cutaneous nerves, but extant crocodylians have a very different arrangement where the exits are much smaller, much more numerous, and emerge from the deeply pitted outer bone surface. The similarity of the cutaneous exits in theropods to those of lizards indicates that a thick, muscular band of lip tissue bordered the upper and lower alveolar margin in predatory dinosaurs. Unlike the condition shown in many restorations, theropods differed from crocodylians and did not have a thick, horny skin closely adherent to the pitted bone surfaces around the mouth.

Edmarka has a small, rounded, protuberant process on the ventral margin of the jugal below the orbit, and such protuberances are common among tyrannosaurs but are absent in *T. tanneri* and most, if not all, other large Jurassic theropods. The function is obscure — possibly the jugal process was part of the species-recognition features developed around the orbit, as is common among extant birds and many lizards.

Jugal-ectopterygoid joint (Fig. 1A-C). In the Nail jugal the inner surface is deeply concave below the postorbital process; in ceratosaurs and allosaurs the outer wing of the ectopterygoid fits snugly into this depression. The Nail jugal has a smooth surface here and there is no evidence of any strong ligaments or suture. The ectopterygoid must have been free to slide and rotate in the jugal depression. The inner jugal surface in *T. tanneri* is also concave, although to a lesser degree than in *E. rex*.

Jugal, measurements. (CPS 1005) length, as restored: 444 mm. Height through postorbital process, as restored, 209 mm.

Comparison with *Eustreptospondylus* and emendations to the restoration of the torvosaurine skull (Fig. 3). Britt (1991) presented a restoration of the skull of *Torvosaurus tanneri*, based on the Dry Mesa Quarry material. Several additions and corrections can be made. Britt did not compare the torvosaur skull in detail with that of *Eustreptospondylus oxoniensis* Walker (1964) from the Upper Callovian of England; there are striking similarities (Fig. 3). The following features are noteworthy: 1) In both of these theropods, the anterior part of the tooth-bearing branch of the maxilla, the ramus anterior to the ascending nasal process, is longer than in *Ceratosauros* (USNM 4735) and *Allosaurus fragilis* (USNM 4734), and about as long as in the long-faced allosaurs, such as AMNH 666 and 5727. 2) In allosaurs, ceratosaurs, and yangchuanosaurs the outer surface of the maxilla is excavated below the antorbital fenestra, and this excavation has a ventral border that is raised and lightly striated, indicating the

attachment of pterygoideus muscle here: In torvososaurs and *Eustreptospondylus* the ventral excavation and its raised rim are absent. 3) Torvososaurs and *Eustreptospondylus* have premaxillae that are lower dorsal-ventrally than in yangchuanosaurs and ceratosaurs. 4) Torvososaurs and *Eustreptospondylus* have lacrimals of extraordinary simplicity — the upper edge of the horizontal ramus is straight, without any hint of the horns or crests or swollen pneumatic spaces seen in all ceratosaurs, yangchuanosaurs, and allosaurs. 5) Torvososaurs and *Eustreptospondylus* agree with ceratosaurs and yangchuanosaurs in having extremely tall quadrate shafts.

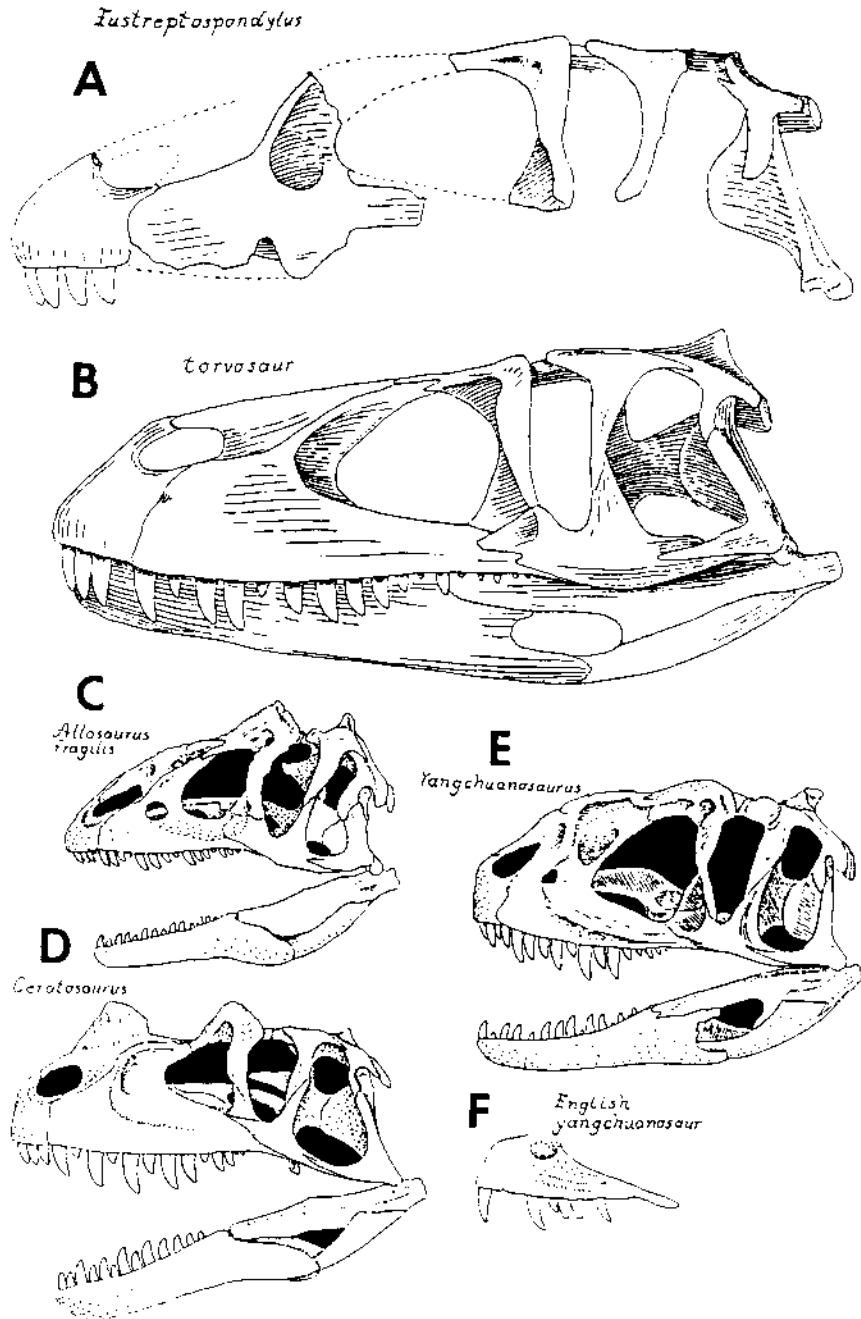


Figure 3. A — outer view of type of *Eustreptospondylus oxoniensis*, Oxford Univ. Mus. J 13558, redrawn from von Huene (1926) and from photographs supplied by Amanda Renzi. B — same for *Torvosaurus*; jugal from Nail Quarry; premaxilla, maxilla, lacrimal, postorbital, quadrate, dentary from Dry Mesa Quarry; squamosal, frontal-parietal from *Eustreptospondylus*, other bones restored from *Yangchuanosaurus*. C — same for a short-snouted allosaur, USNM 4734, Felch Quarry (topotype of *A. fragilis*). D — same for *Ceratosauros*, USNM 4735 (type of *C. nasicornis*). E — same for *Yangchuanosaurus shangyuensis*, drawn from the type, Sichuan Museum 00215. F — maxilla of yangchuanosaur-like theropod from England, redrawn from Huxley, 1869.

6) Both theropods have quadrates that lack a pneumatic excavation on the posterior face at the quadratojugal suture (This opening is the so-called "quadratojugal foramen"; in fact, the opening probably was spanned by connective tissue and therefore should be called a "fenestra" since it was not a true foramen that transmitted nerves or blood vessels; in extant *Sphenodon*, which shows a huge fenestra here, no nerve or blood vessel penetrates the connective tissue sealing the bony opening.) Allosaurs have short quadrates with a large pneumatic excavation.

In the first five of these features, torvosaur and *Eustreptospondylus* resemble primitive thecodonts and the primitive herrerasaurid theropods of the Triassic and thus the torvosaur condition probably is primitive for theropods. Lack of a quadratojugal-quadrata fenestra is probably derived, since most early diapsids have a large fenestra. Ceratosaurids also lack an opening here. Torvosaur has three premaxillary tooth positions, one less than *Eustreptospondylus*, but in the torvosaur there is a long gap in the premaxillary alveolar margin behind tooth three, as if a tooth had been suppressed, and the proportions of the premaxillae are quite similar in the two theropods. Four is probably the primitive theropod premaxilla tooth count, as in podokesaurs.

The question remains: Do yangchuanosaurids, ceratosaurids and megalosaurids deserve status as three separate families? These taxa are confusingly similar in postcrania, showing much less difference between any two than there is between allosaurids and any one of the three. New descriptions of yangchuanosaur braincases, being prepared by Currie and Bakker, show the presence of many allosaurid characters that justify establishing yangchuanosaurs as a separate family of allosaurids. Ceratosaurids seem to share one derived feature with megalosaurs — reduction of the quadratojugal-quadrata fenestra. The braincase of *Eustreptospondylus* is much more advanced than that of ceratosaurids in possessing basitubera that are displaced backwards and in an occipital condyle that is excavated above for passage of the spinal cord (Fig. 6). Both differences are adaptations for greater ventroflexion at the head-neck joint. Forward placement of the basitubera gives the longus colli muscle (= rectus capitis anterior) maximum leverage when the muscle is pulling at a high angle to the underside of the braincase (Fig. 6). Excavation of the condyle permits the spinal cord to bend downward. The braincase of the medium-size theropod *Piveteausaurus* (Taquet and Welles, 1977), a genus sometimes allocated to the megalosaurids, from the Middle Jurassic of France, agrees with that of ceratosaurids in having the primitive condition of an unexcavated condyle and basitubera located far posteriorly (Fig. 6). Hence *Piveteausaurus* may be a ceratosaurid and not a megalosaurid. There are no braincases definitely referable to *Megalosaurus*, *Poikilopleuron* or torvosaur, and thus it is not known whether these large megalosaurids had eustreptospondylid features.

Yangchuanosaurs in England (Fig. 3E,F). Yangchuanosaurs share many primitive features with megalosaurs, as just noted. Yangchuanosaurs have not been reported outside China; however, a large theropod upper jaw described by Huxley (1869), from the early Late Jurassic of England, shows the highly abbreviated anterior process of the maxilla that distinguishes yangchuanosaurs from all other large Jurassic theropods. This specimen is evidence that yangchuanosaurids coexisted with megalosaurids in Europe.

Scapula-coracoid, megalosaurid characters (Fig. 5,7,8). The Nail scapula-coracoid shares several characters with that from the type localities of *Megalosaurus* in the Stonesfield Slate of the English Middle Jurassic (Fig. 5); the blade has nearly parallel anterior and posterior margins and shows little flare at the upper end; there is a gentle expansion of the blade at mid height; the coracoid lip of the glenoid is far posterior to the scapular lip, so that the glenoid long axis (a line passing through the center of scapular and coracoid lips) slopes up and forwards relative to the scapular blade; the coracoid has an evenly rounded outline without the posterior hook seen in allosaurs and many other theropods and in many ornithopods as well.

In the type of *Eustreptospondylus oxoniensis*, a juvenile specimen, the scapula-coracoid has an outline very similar to that of *Edmarka* — the scapular blade is parallel-sided and narrower than that of the Stonesfield megalosaur. Allosaurs have a glenoid where the coracoid lip is much further forward and the upper end of the blade is very narrow, as in tyrannosaurs and most other Cretaceous theropods. In ceratosaur the blade is wide, with a straight posterior and concave anterior margin, and the upper end is expanded. Newly discovered material of yangchuanosaurs, being studied by Currie, indicates a wide, parallel-sided scapular blade that is close in outline to that of *Megalosaurus*.

Scapula-coracoid, muscle attachments (Fig. 7,9-11). Theropods show an intermediate stage in the evolution of an avian-style scapular blade and its muscles. During the transformation from primitive thecodont to bird, the blade became longer, much thinner, and strongly inclined posteriorward, a rearrangement

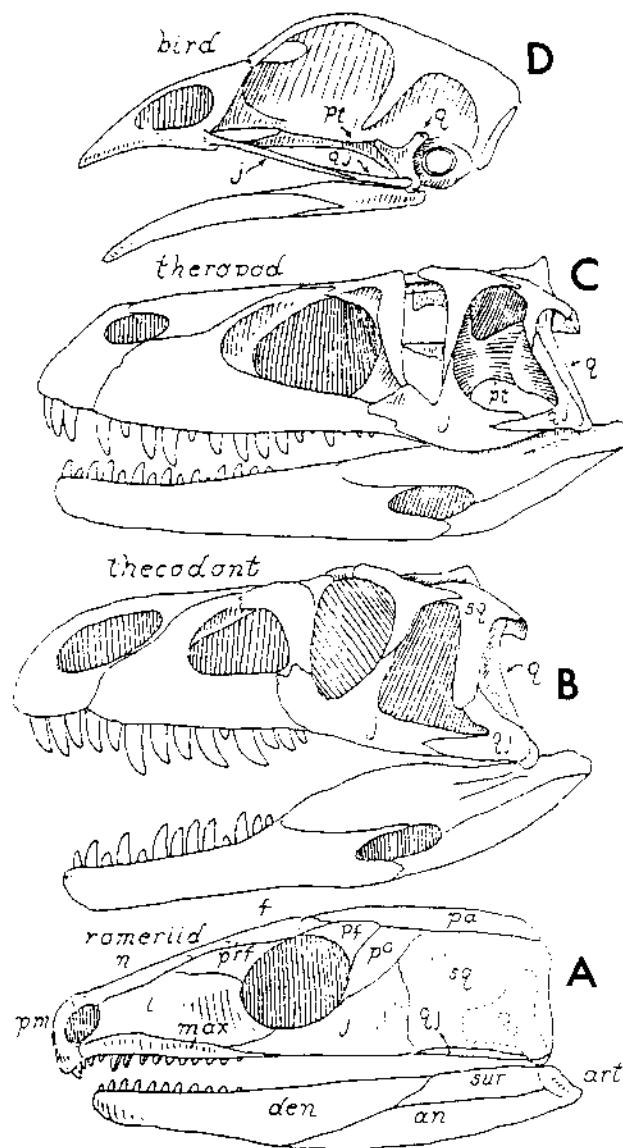


Figure 4. Stages in the evolution of the avian quadrate-quadratojugal-ptyergoid struts. A — primitive reptile stage (romeriid). B — primitive thecodont stage (erythrosuchid). C — primitive theropod (megalosaurid). D — bird (*Gallus*). abbreviations: q — quadrate. qj — quadratojugal. Others as in Fig. 1.

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that required fundamental changes in how muscles originated (Fig. 11). The muscles attaching to the scapula-coracoid and ribs in torvosaurus have been restored by comparison with dissections of lizards, *Sphenodon*, chickens and crocodilians, carried out by Bakker (see muscle maps in Bakker, 1987). The upper end of the scapular blade is continued, in the living animal, as a suprascapular cartilage (Fig. 9). The rhomboideus originates from the outer surface and anterior edge of the suprascapular cartilage; the deep serratus originates from the inner surface; the scapular deltoid originates from the anterior part of the suprascapula and the osseous upper blade; the teres (anterior division of the latissimus dorsi) originates from the posterior part of the upper blade. In primitive diapsids, including chasmatosaurid thecodonts, the scapular blade is wide and short; the teres, rhomboideus and scapular deltoid must have had wide bellies (Fig. 11). In extant diapsids with short, wide scapular blades, such as monitor lizards and sphenodontids, the humerus works mostly in a horizontal plane and the scapular deltoid and teres (when present) pull nearly vertically, parallel to the scapular blade. The width of the origin of the muscles is controlled by the width of the scapular blade and suprascapula.

Crocodylians and most thecodonts have more elongated scapular blades with constricted mid-shafts. In crocodylians and probably in most thecodonts the scapular blade is tilted backwards, an orientation that changes the geometry of the muscle origin. Instead of pulling parallel to the scapular blades, the scapular deltoid and teres pull at an angle. Since the muscle fibers are arranged oblique to the scapular blade, the width of the origin is no longer controlled only by the width of the blade but by the length too (Fig. 11). In birds the scapular blade

is tilted into a horizontal position and the scapular deltoid and teres pull at right angles to the blade; here the width of the origin is controlled entirely by the length of the blade.

In nearly all theropod dinosaurs the scapular blade is longer and narrower than that of most thecodonts, and articulated specimens show that the blade was tilted backward as strongly as in crocodylians or more (Lambe, 1917; Matthew and Brown, 1923). Since the blade was tilted strongly, the blade could be reduced in width without interfering with the widths of the muscle origins. Everything else being equal, reduction of unnecessary bone is an advantage because the material saved can be put into those skeletal regions where stress is greatest. Allosaur humeri are as long relative to the shoulder height as are megalosaur and ceratosaur humeri, and the muscle attachment sites are as strong on the allosaur humeri. Hence there is no reason to believe that the allosaur teres and deltoid muscles were weaker than in ceratosaurs and megalosaurs, and the thin allosaur scapular blade was sufficient to provide deltoid origin. According to this view, the narrow allosaur shoulder construction is more thrifty than that of megalosaurs and ceratosaurs, which wasted bone on wide scapular blades.

The unexpanded upper end of the megalosaur scapula indicates that the suprascapular cartilage was relatively small, implying reduction of the rhomboideus (among extant diapsids, a greatly expanded suprascapular blade is accompanied by a strong expansion of the upper end of the osseous scapula blade). Similar dorsal reduction of the scapular blade occurs in advanced sauropods, such as apatosaurs, and advanced ornithischians, such as hadrosaurs, and in all modern birds. The functional significance is not clear.

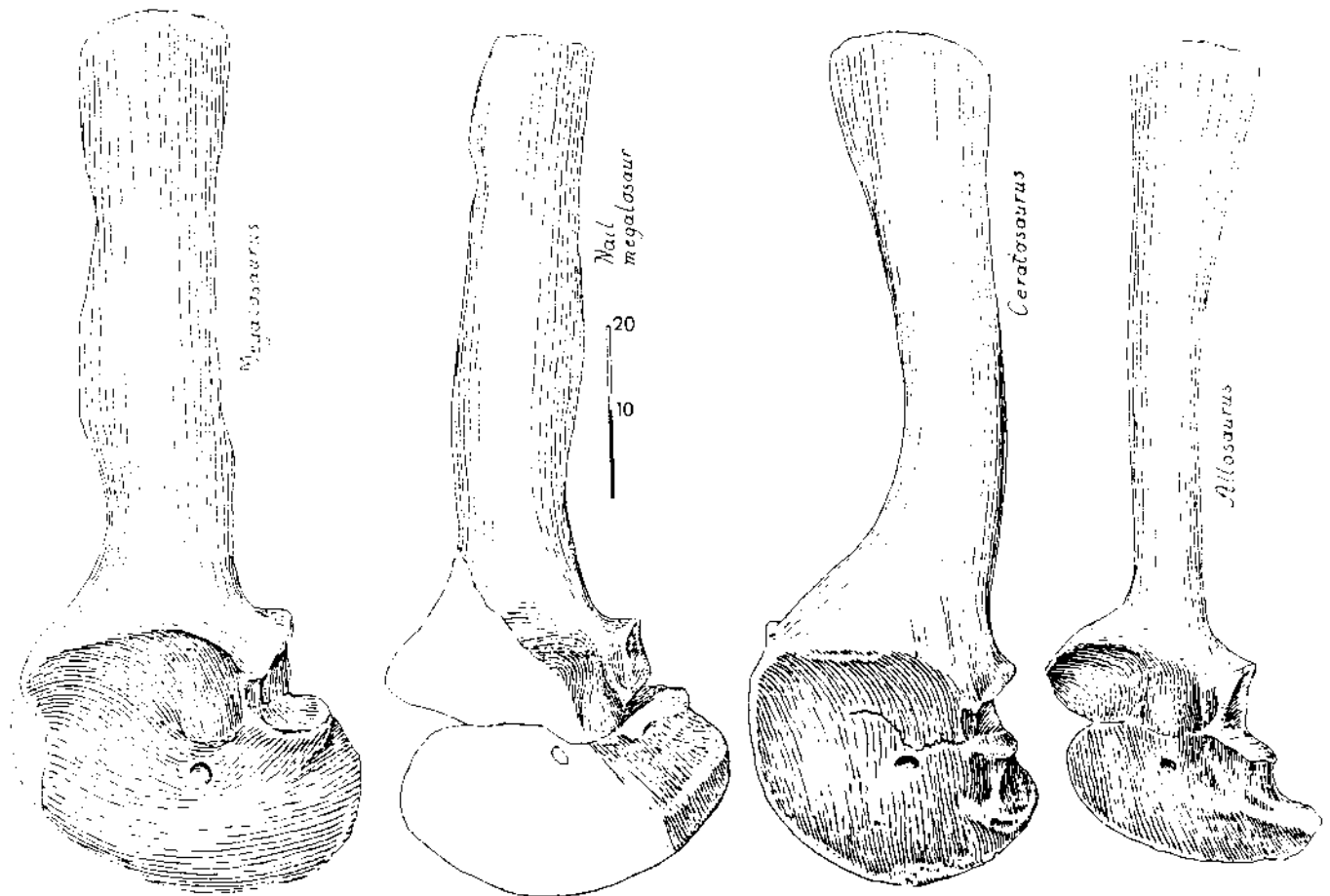


Figure 5. Scapula-coracoid drawn to a common length (chord). *Megalosaurus* from Stonesfield, Oxford University Museum 13574 (photograph provided by Amanda Renzi). *Ceratosaurus* - UCVP 317. *Allosaurus* redrawn from Madsen (1976). Nail megalosaur (torvosaur, *Edmarka rex*) CPS 1002 (scale bar applies only to Nail specimen).

In the Nail scapula the origin of the scapular triceps is indicated by a ridge, rounded in cross section, that forms the outer edge of the posterior face of the scapula, just above the glenoid (Fig. 7,8); this is the crocodilian condition, but in the Nail scapula the ridge is not strongly scarred, as it is in crocodiles, and the triceps must have been relatively weak. Since use of the hands to apprehend prey requires more power in flexion than in extension at the elbow, a weak triceps is not unexpected in a theropod. Medial to the triceps ridge in the Nail specimen is a small, slightly excavated triangular area, corresponding to the supraglenoid buttress of Romer (1956); the articular capsule of the shoulder probably extended over this area, as in extant crocodilians (Fig. 10). The posterior scapular edge becomes narrower and narrower dorsally above the glenoid and becomes sharp-edged for the dorsal two thirds of the scapular blade height. In crocodilians the transition to a sharply edged posterior border marks the beginning of the serratus insertion, which continues dorsally to the top of the suprascapular cartilage (Fig. 7). The levator scapulae must have attached along the anterior edge of the blade in the torvosaur scapula, as is the case in all living diapsid species.

In the Nail scapula the origin of the scapulohumeralis posterior probably was on the outer scapular surface just anterior to the glenoid, as in extant crocodilians (Fig. 7-10). The subcoracoscapularis probably covered the inner surface of the scapula and coracoid. Both of these muscles insert onto the posterior face of the inner tuberosity of the humerus. The origin of the subcoracoscapularis too is transformed by the backward tilt of the scapula — in the primitive diapsid state, with a wide, vertical blade, this muscle has an origin controlled by blade width; as the tilt increases, the muscle origin width is controlled more by scapula length.

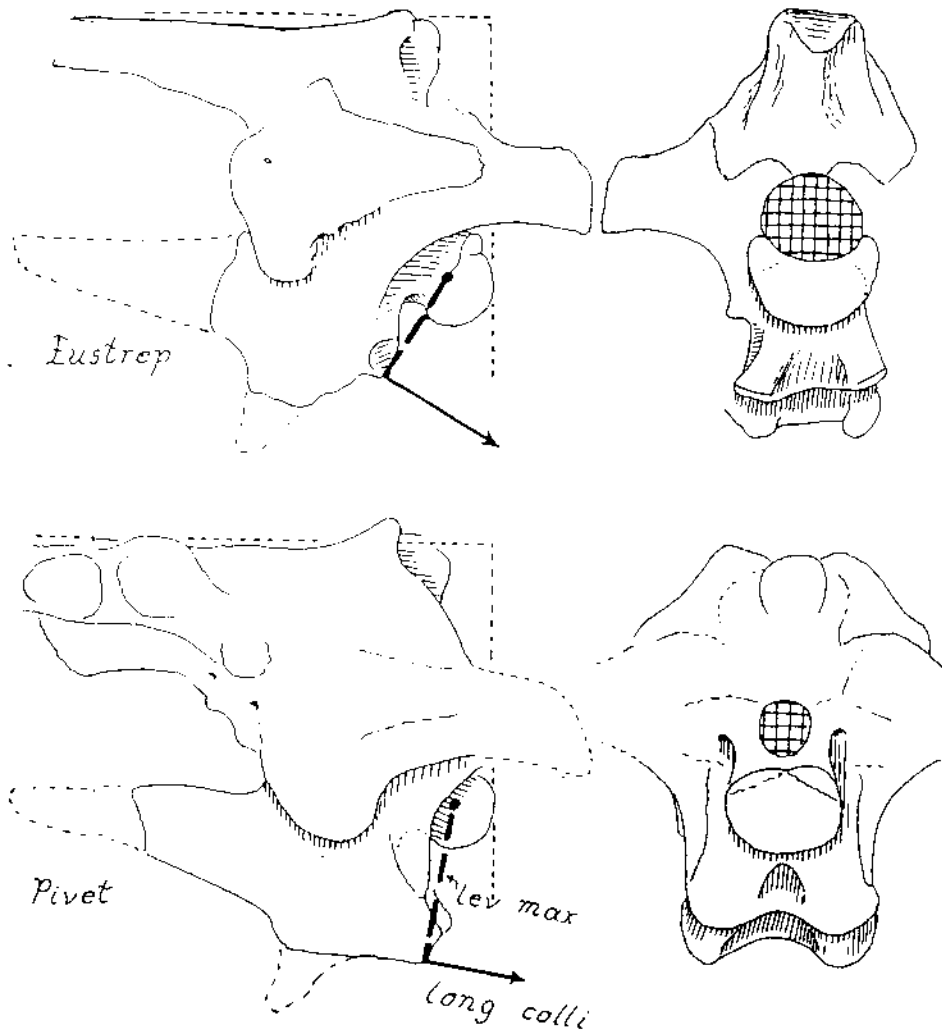


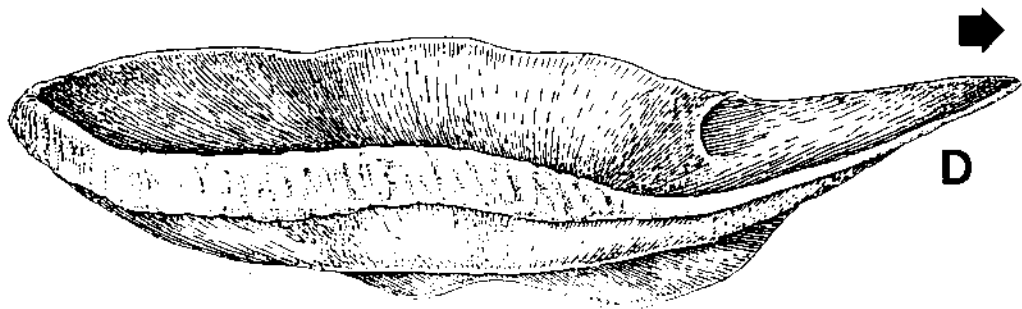
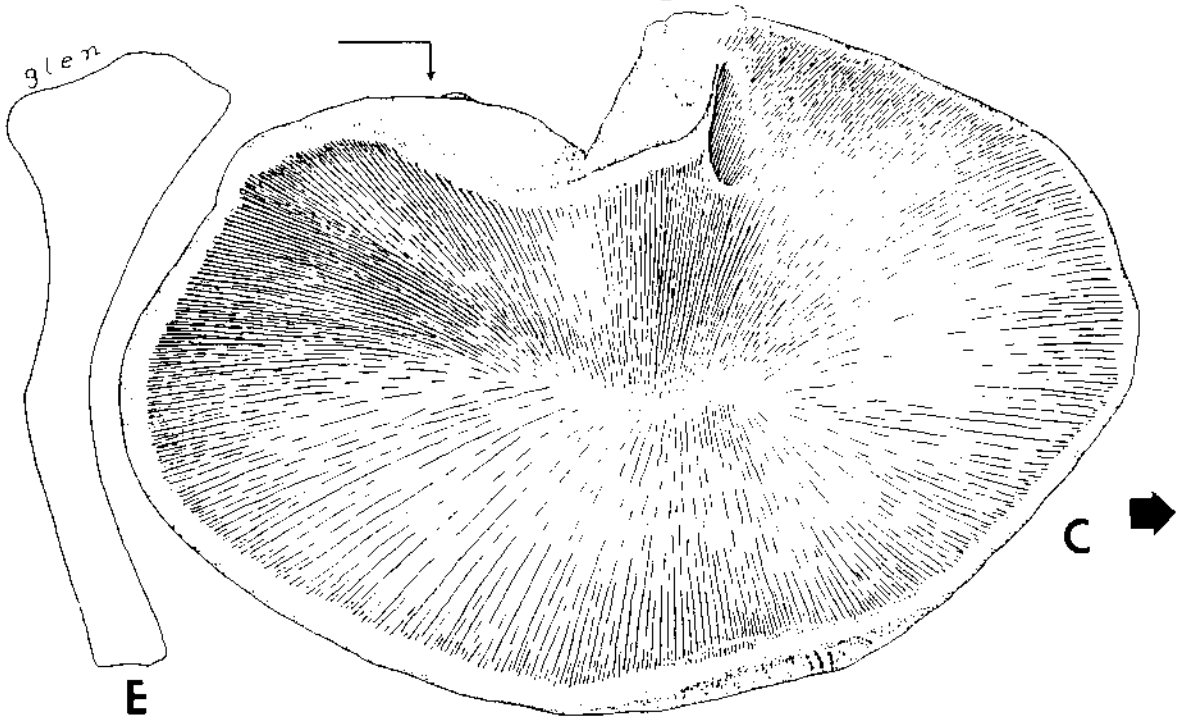
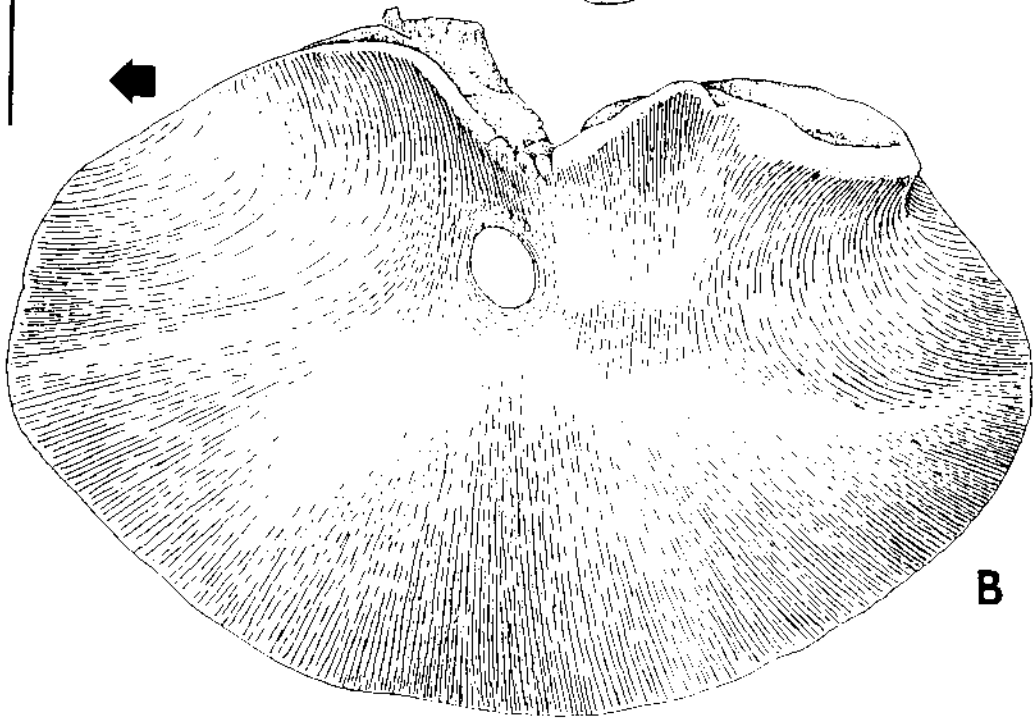
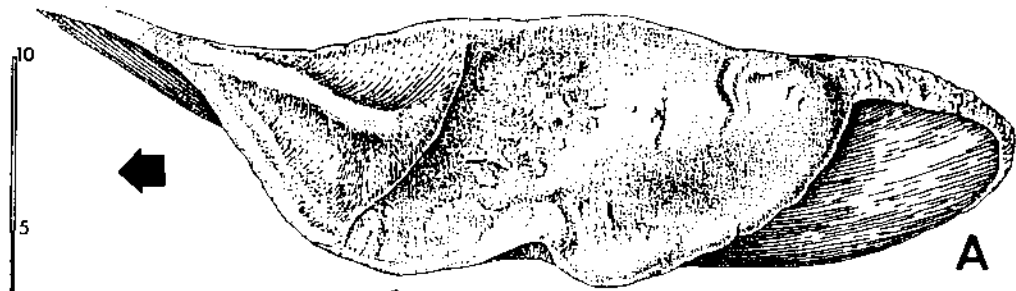
Figure 6. Geometry of head-neck flexure in *Eustreptospondylus* (above) and *Piveteausaurus* (below). Posterior (right) and lateral (left) outlines of braincase. Arrow shows line of pull of longus colli et capitis muscles (=rectus capitis anterior) at head-neck flexure where the leverage is maximized. lev — leverage. Heavy dashed line shows leverage. Light horizontal dashed line shows plane of frontal-parietal; light vertical dashed line shows position of condyle relative to frontal-parietal plane.

The Nail scapula shows little development of an acromial process — the anterior expansion at the ventral end of the anterior edge, an area in crocodilians covered by the upper part of the supracoracoideus and coracoid division of the deltoid muscle (Fig. 7,9). Dorsal-ward expansion of the supracoracoideus origin occurs most prominently among quadrupedal dinosaurs, such as sauropods, stegosaurs, and nodosaurs. In these quadrupeds the upper division of the supracoracoideus probably functions as a lateral brace to the humerus as it swings in a vertical plane, preventing the upper arm from collapsing inwards. Such a function is unnecessary in the grasping arms of a bipedal predator.

The torvosaur coracoid is at present known from the complete subadult specimen from Nail and the incomplete adult specimen found coossified with the scapula at Nail. The part preserved in the adult coracoid is 25% larger than the same region in the subadult specimen. The subadult coracoid has a well marked longitudinal ridge located on the posterior part of the outer surface below the glenoid lip (Fig. 7); this ridge is very strong in allosaurs and podokesaurs. Madsen (1976) identified the ridge as the biceps origin, as have other theropod workers. But, in fact, the biceps origin in all extant lizards, sphenodontids and crocodilians is located much further forward, at the anterior-ventral quadrant of the coracoid (Fig. 7,9). The posterior coracoid ridge of theropods is located exactly where the costo-coracoideus muscle attaches in lizards, *Sphenodon* and crocodilians; this muscle pulls the scapula-coracoid backwards towards the ribcage, assisted by the sterno-coracoideus that attaches to the inner surface of the coracoid. In crocodilians and *Sphenodon* this ridge also marks the attachment of the coracoid head of the triceps, reduced to a narrow tendon with few contractile fibers.

In the torvosaur coracoid, there is a surface developed below and anterior to the costo-coracoideus ridge. This surface is the origin of the coraco-brachialis in crocodilians and lizards, and certainly in theropods too (Fig. 7,9). The muscle inserts along the anterior surface of the humerus shaft, medial to the deltopectoral crest. The development of a posterior coracoid prong in allosaurs moves the origin of the coraco-brachialis posteriorly relative to the center of rotation at the glenoid, increasing the leverage of the muscle for adducting the humerus, thus increasing the strength of the arm for drawing prey in towards the predator (Fig. 5,9).

The origin of the biceps in the Nail coracoid is indicated by a flat, smooth zone developed in the central area of the outer surface, below the coracoid foramen (Fig. 7,9). The lack of a tuberosus rugosity indicates that the origin was fleshy, as is the case in *Sphenodon* and many lizards. The origin of the supracoracoideus on the Nail coracoid is on the anterior quadrant of



E

C

D

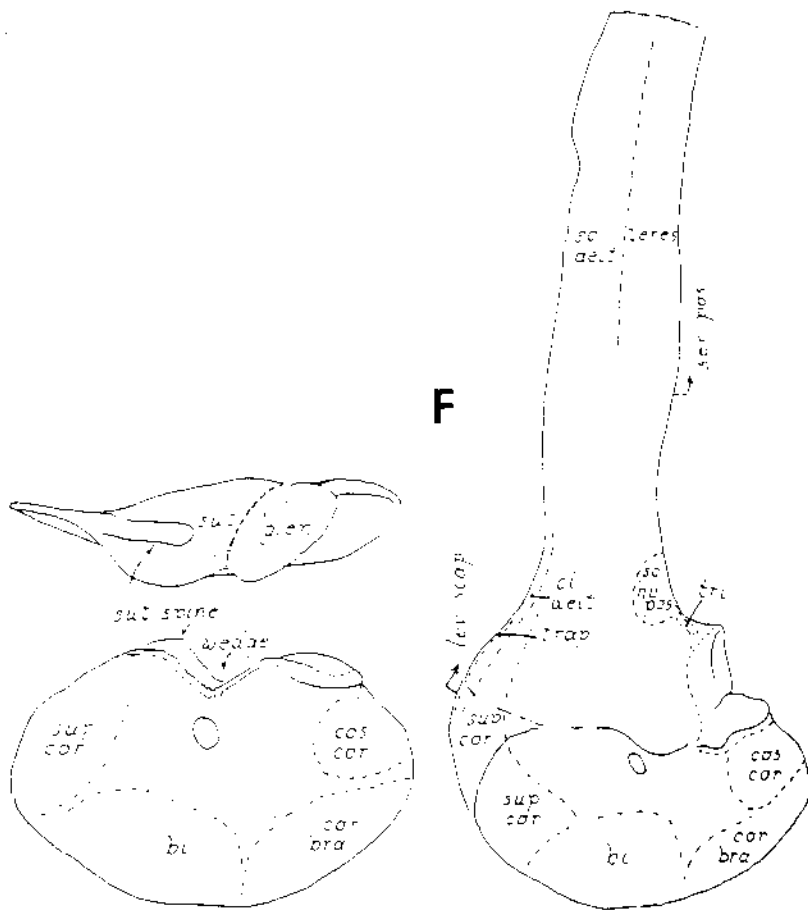


Figure 7 continued. Left coracoid of torvosaur, *Edmarka rex*, Nail Quarry, CPS 1003. F - outline of outer surface of scapulocoracoid, and outer and sutural surfaces of the isolated coracoid, showing joints and muscle attachments. sut spin - sutural spine of coracoid. Other abbreviations as in Fig. 8,9. In the sutural view, the limit of the glenoid is shown by dashed line.

the outer surface, as in *Sphenodon*, crocodiles and lizards. In *Edmarka* there would have been a wedge-shape gap in the anterior edge of the scapula-coracoid where coracoid met the scapula, a condition present in allosaurs; in life, this gap must have been bridged by a sheet of cartilage, as is the case in crocodylians. In the *Megalosaurus* scapula-coracoid from Stonefield, the gap is small (Fig. 5).

Scapula-coracoid - joints (Fig. 7-10). The torvosaur coracoids could be confused with those of a young camarasaur, but are easily distinguished by the following (Fig. 8): 1) In megalosaurs, as seen in lateral or medial view, the glenoid lip is in line with the coracoid-scapula suture; in camarasaur and all other sauropods the coracoid glenoid lip is tilted downwards relative to the coracoid-scapula suture; this orientation is part of the rearrangement of the shoulder joint to make the glenoid face more strongly downwards. 2) On the outer side of the scapula-coracoid in megalosaurs and some other theropods there is a strong conical wedge of the scapula (cone, wedge in Fig. 7,10) that fits into a wedge-shaped notch in the coracoid along the coracoid-scapula suture just anterior to the glenoid; this wedge is much less prominent in sauropods. 3) The outer edge of the scapular glenoid lip is much wider medial-laterally in sauropods than in megalosaurs and other theropods, and the main plate of the coracoid bone is everywhere thinner in theropods.

The exceptionally well developed cone-in-wedge joint at the coracoid-scapula contact in *E. rex* and *Megalosaurus* requires comment. The cone on the scapula and its recipient wedge-shaped notch on the coracoid are both swollen outwards, as in allosaurids. But in podokesaurs, ceratosaurids, and most other theropods there is little outward bulging in this zone. A swollen contact is probably derived and augments the strength of the joint to resist bending inward or outward. Such stresses could be induced by exceptionally powerful arm abductors (deltoid and supra-coracoideus muscles) or by external forces that would compress the thorax top-to-bottom (struggles with prey). It is significant that megalosaurs and allosaurs have massive arms with relatively huge thumb claws, suggesting that the arm musculature did produce unusual stresses on the shoulder girdle. In tyrannosaurs the cone-in-wedge is weakly developed, as expected in species with weak arms.

Additional stiffening of the coracoid-scapula suture is obtained in *Edmarka* by a tall spine of the coracoid (sut. spine in Fig. 7) that fits into a notch in the scapula just anterior to the cone-in-wedge joint. Such sutural spines are developed to a less degree in allosaurs.

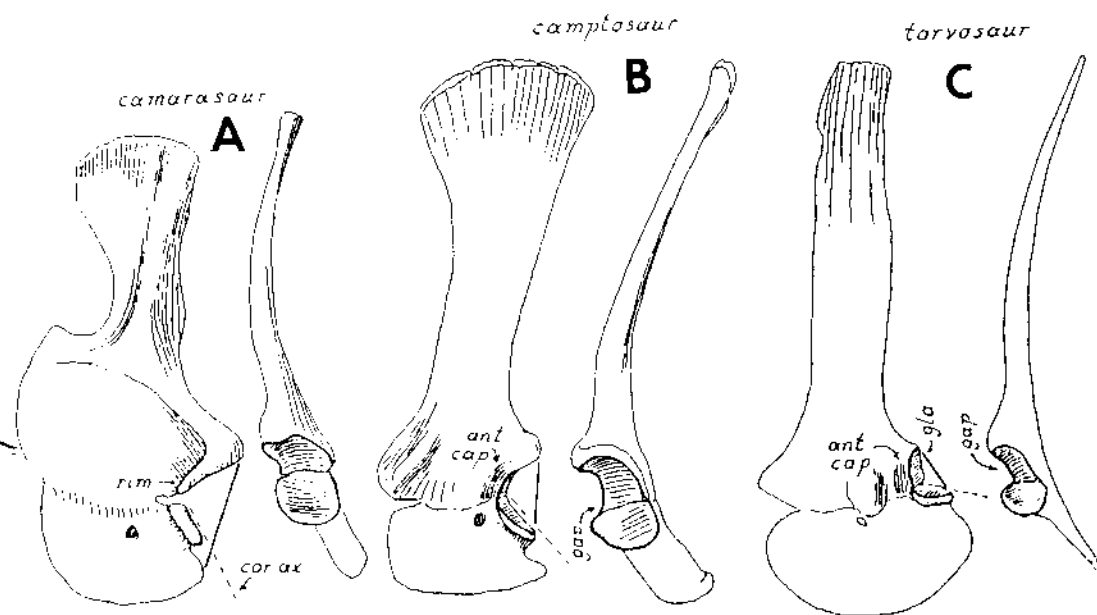


Figure 8. Orientation of glenoid lips. Outer and posterior views of scapula-coracoids. A - a camarasaur. B - a camptosaur. C - a torvosaur, *Edmarka rex*. abbreviations: rim - anterior (outer) glenoid rim. ant cap - anterior extension of joint capsule. dashed line - coracoid lip axis (cor ax). heavy line - glenoid long axis (gla). Note gap in glenoid rim, as seen in posterior view.

Glenoid (Fig. 7,8,10). The upper, scapular lip of the glenoid is completely preserved in the mature specimen from Nail Quarry, and

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the lower, coracoid lip is completely preserved in the smaller, subadult coracoid. The glenoid surface in the mature specimen is smooth, but the surface in the subadult coracoid is furrowed and pitted, indicating thicker cartilage. The scapular lip of the glenoid is turned outwards in the Nail specimen about to the degree seen in extant monitor lizards and far less than in crocodylians (Fig. 10). In horizontal cross section, the surface for the humerus on the scapular lip is very slightly concave. Anterior to the joint surface, and posterior to the conical wedge that locks into the coracoid, the outer surface of the scapula is depressed for the zone of non-articular bone contained within the joint capsule (cap in Fig. 8,10). This anterior non-articular zone within the capsule also occurs in crocodylians and most lizards, and indicates a loose anterior capsule that permits the humerus to be protracted and abducted.

In the torvosaur glenoid, as viewed from the rear, the outer (anterior) rim of the scapular lip is strongly concave; the inner (posterior) rim is convex (Fig. 8). The ventral part of the outer scapular-glenoid rim, at the coracoid-scapula suture, is very weak and does not project outwards or form a ridge of any sort. This glenoid

shape is the rule for theropods and bipedal ornithopods (see Galton and Powell, 1980, for figures of camptosaurus). The weak ventral part of the anterior scapular lip matches that of most lizards and *Sphenodon*, where the glenoid permits the humerus to be protracted in a horizontal plane and there are no anterior ridges or rims to obstruct forward movement. In all quadrupedal dinosaurs, including ceratopsians, the outer (anterior) glenoid margin is less concave, as seen in posterior view, and there is a raised rim that runs along the outer (anterior) lip (Fig. 8), continuing without interruption across the scapula-coracoid suture (Bakker, 1987). In these quadrupeds the depressed zone anterior to the glenoid lip is not present, and so the articular capsule must not have extended forward beyond the glenoid lips. The glenoid of the quadrupedal dinosaurs would not permit the humerus to be protracted as close to the horizontal plane as was the case in theropods and ornithopods.

The coracoid lip of the glenoid in *Edmarka* has a thick, protruding outer edge, and a vertical cross section that is concave in the outer half of the joint surface (Fig. 7). This concavity is stronger than that seen in extant crocodylians and most lizards, where the coracoid lip

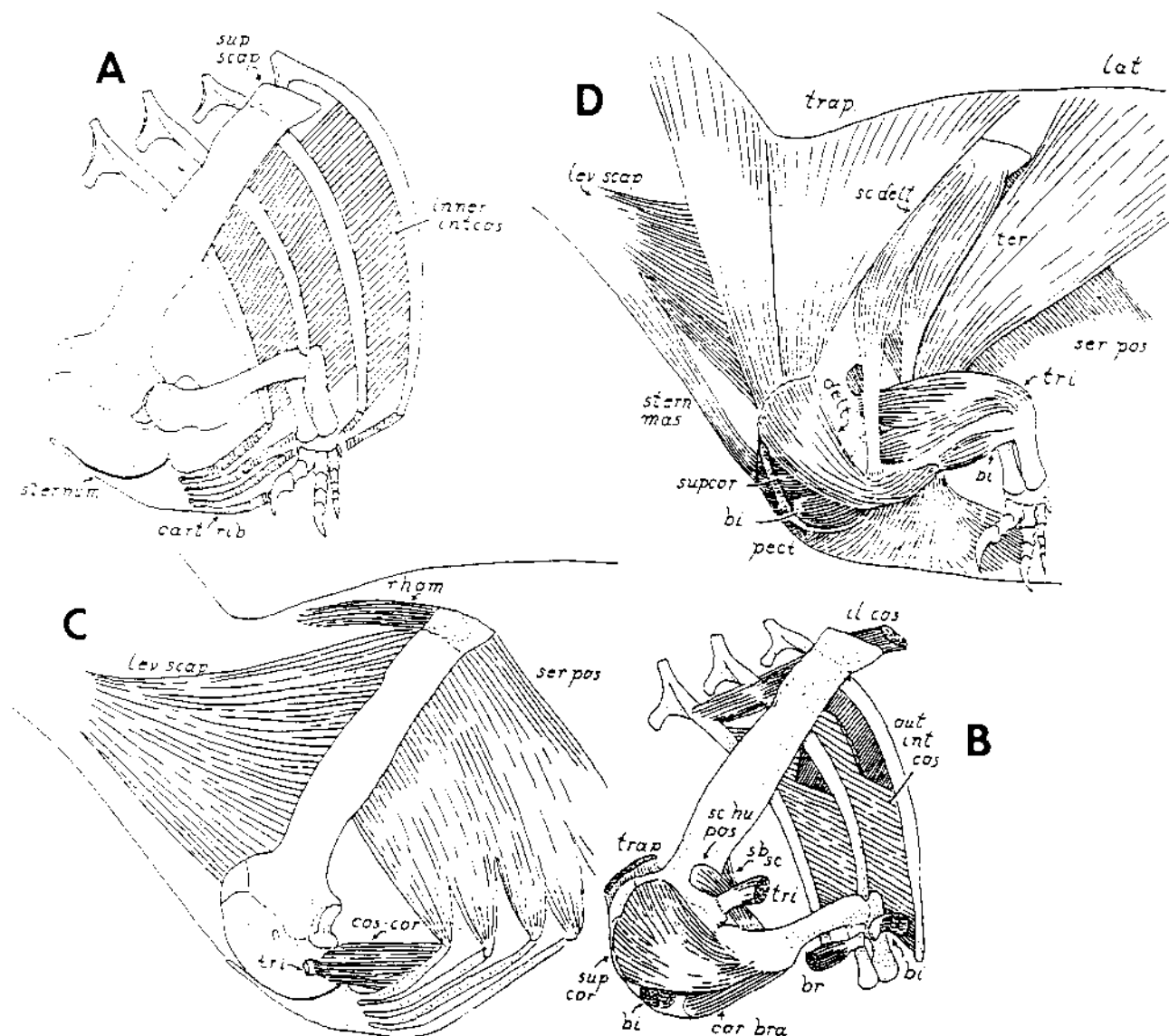


Figure 9. Muscle attachments on the Como torvosaur, *Edmarka rex*. A — forelimb composite, based on Nail scapulocoracoid, Louise ribs and Dry Mesa humerus, forearm, and hand. Internal intercostals shown. B — same, hand and sternum removed. Various muscles shown. C — same, arm removed, deep muscles moving the scapulocoracoid shown. D — same, superficial muscles shown; anterior part of pectoralis cut away to show biceps and supracoracoideus. Abbreviations given in Figure 1.

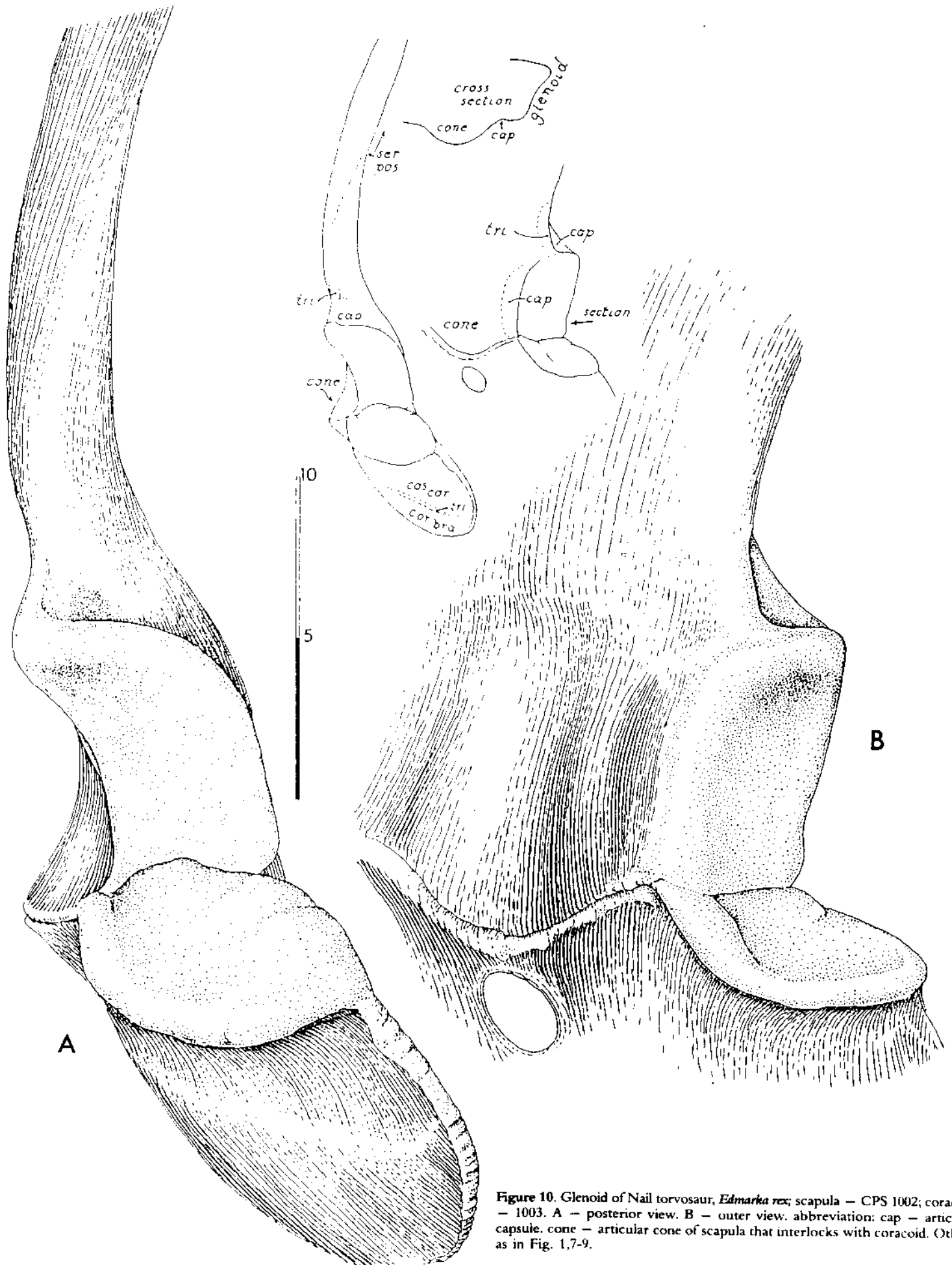


Figure 10. Glenoid of Nail torvosaur, *Edmarka rex*; scapula - CPS 1002; coracoid - 1003. A - posterior view. B - outer view. abbreviation: cap - articular capsule. cone - articular cone of scapula that interlocks with coracoid. Others as in Fig. 1,7-9.

is evenly convex. The stronger concavities in both the scapula and coracoid lips give the torvosaur shoulder joint more of a ball-and-socket character, as opposed to extant lizards, where the glenoid may be described as saddle-shaped.

The senior author (R.T.B.) must, at this point in the description of the shoulder in *Edmarka*, enter some remarks about recent discussions of shoulder function in ceratopsian dinosaurs. At the 1991 Society of Vertebrate Paleontology meeting, several papers were presented on the forelimb posture among horned dinosaurs. It was a surprise to the senior author that these discussions were deficient in data taken from dissections and ligament preparations of extant vertebrates (see Bakker, 1987). A glance at any well-preserved shoulder socket of *Triceratops* or *Monoclonius* shows that the topography differs in two obvious ways from that of sprawling lizards and that of semi-erect crocodylians and chameleons: 1) the glenoid lips in the dinosaurs are more concave in transverse sections, forming a continuous, elongated socket across the coracoid and scapular surfaces; 2) an anterior capsular depression is never developed in the dinosaurs. Therefore, horned dinosaurs were neither sprawlers nor semierect; their carriage was as fully erect as that of rhinos.

Coraco-d-sternum joint (Fig. 7,9). The continuous posterior, ventral and anterior edge of the Nail subadult coracoid is covered with a matte-finish bone that indicates the presence, in life, of a covering of cartilage. This edge is widest and flattest in cross section along its posterior half where it has a topography of deep dimples, knobs, transverse furrows and ridges, indicating especially thick cartilage (Fig. 7). Elsewhere the edge is rounded in cross section; the coracoid is thinnest anteriorly. The articular surface for the sternum must have been located along the thick posterior half of the ventral coracoid edge, as is the case in crocodylians, lizards, and *Sphenodon*. The shape of the megalosaur sternum probably was like that seen in sphenodontids, lizards and crocodylians — a small diamond concave-up in the transverse plane (Lambe, 1917).

Coracoid foramen. In the Nail coracoid the coracoid foramen, for the suprascapular nerve (= suprascapular nerve), is completely enclosed by the coracoid and passes backward and outward: the outer opening is slightly compressed fore-to-aft; the inner is slit-like.

Scapula-coracoid — measurements. Coracoid (CPS 1003): anterior-posterior length — 291 mm; greatest depth — 198 mm. Coracoid (CPS 1004) anterior-posterior length, restored from CPS 1003; 363 mm. Scapula (CPS 1005): dorsal-ventral length: 895 mm as preserved, 950 as restored; max. breadth of blade: 141 mm.

Thoracic Ribs — theropod characters (Fig. 12-14). It is sobering to note that the first-discovered specimen of the Como torvosaur was a series of thoracic ribs, initially misidentified by Bakker as those of a small sauropod. All too often ribs are not accorded the respect deserved — costal morphology not only provides enough information to identify specimens to subfamily or genus, but also displays fascinating patterns of functional design.

To our knowledge, all ribs from large theropods, including those from Louise and Nail, are distinct from those of other Morrison large dinosaurs in having the following combination of features: posterior shafts that are not expanded very much to make barrel-stave-like structures; a neck, connecting the upper edges of tuberculum and capitulum, that is exceptionally thin along its upper edge; a tuberculum that rises little above the level of the tuberculum-capitulum web; capitulum and tuberculum strongly compressed fore-to-aft; posterior-lateral edge of tubercular thickening, below tuberculum, devoid of the excavation seen in sauropods.

Judging by articulated series of yangchuanosaur ribs, the Louise torvosaur series represents thoracic 10, 9, and 4 with complete or nearly complete heads; ribs 3 and 11 are preserved with the capitulum missing. When theropod ribs are articulated with their respective vertebrae, the plane passing through the tuberculum and capitulum is oblique, passing inwards and forwards. To show the full width across the rib heads, the ribs in Fig. 12 and 13 are shown drawn in the plane of greatest width. In Fig. 14 the external and posterior views of the ribs are drawn as they would be articulated in life.

The shaft is widest in rib 3, nearly as wide in 4, much narrower in 9, 10 and 11. The tuberculum in all the ribs faces upwards and backwards and there are very strong scars below the joint surface for the articular ligament joining the tuberculum to the transverse process (Fig. 12,13). Along the anterior edge of the tuberculum there is a raised area of bone that must represent the limit of the articular cartilage; below this articular lip is a depressed zone with pitted bone surface that must indicate the extension of the joint capsule. In all the ribs the inner edge of the tuberculum rises only slightly above the level of the thin web of bone along the top edge of the neck of

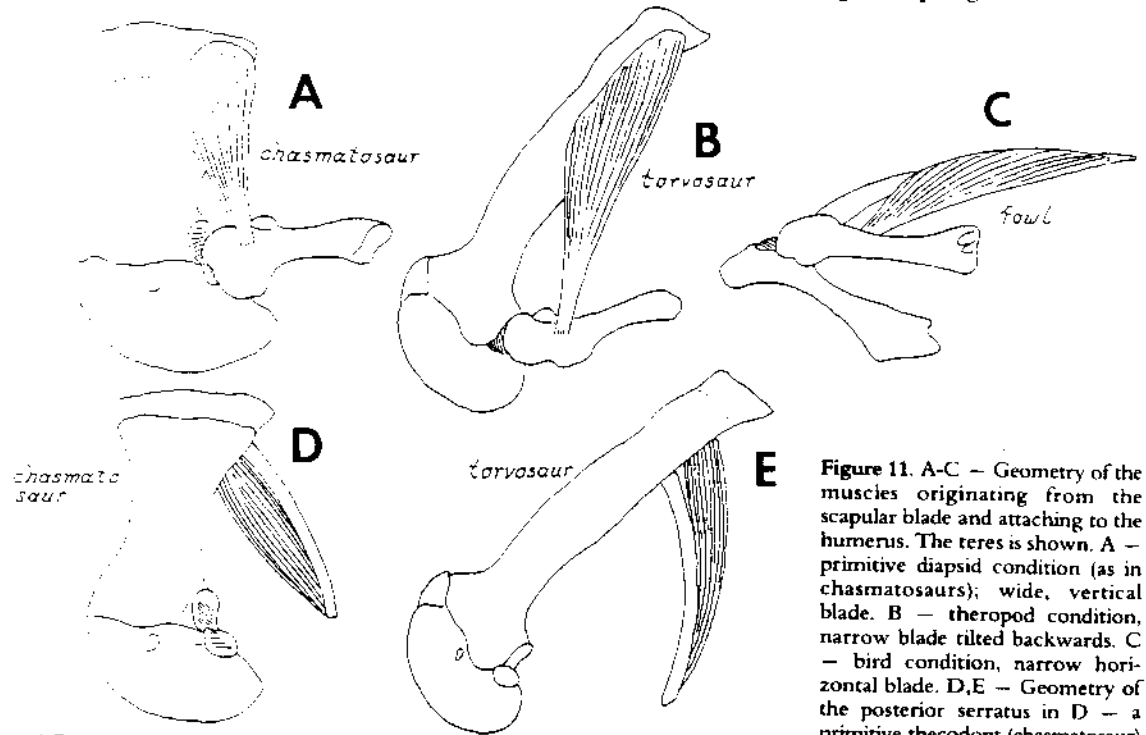


Figure 11. A-C — Geometry of the muscles originating from the scapular blade and attaching to the humerus. The teres is shown. A — primitive diapsid condition (as in chasmatosaur); wide, vertical blade. B — theropod condition, narrow blade tilted backwards. C — bird condition, narrow horizontal blade. D,E — Geometry of the posterior serratus in D — a primitive thecodont (chasmatosaur) and E — a theropod (torvosaur). The second thoracic rib is shown, with part of the serratus attached. Note that the strongly tilted blade in the theropod gives the serratus a course leading to the posterior edge of the rib.

and E — a theropod (torvosaur). The second thoracic rib is shown, with part of the serratus attached. Note that the strongly tilted blade in the theropod gives the serratus a course leading to the posterior edge of the rib.

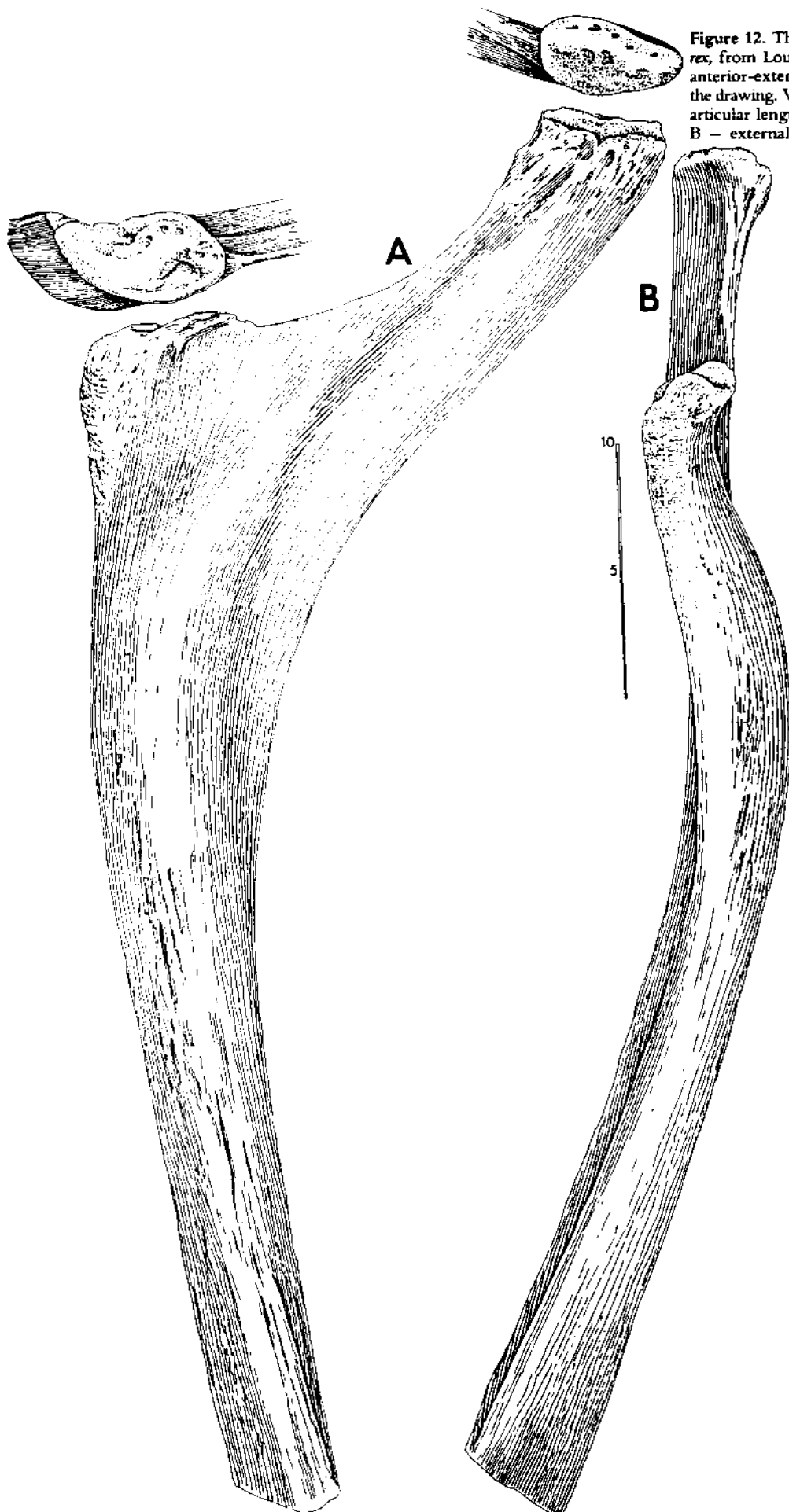


Figure 12. Third thoracic (dorsal) rib of the torvosaur, *Edmarkia rex*, from Louise Quarry, CPS 1001. A — close-up of the head, anterior-external view with the greatest breadth in the plane of the drawing. Views of articular facets, drawn in the plane of greatest articular length, are given above the tuberculum and capitulum. B — external-posterior view, perpendicular to the plane in A.

the capitulum. The capitular neck is longest and most strongly curved upward in rib 4, shortest and least curved upwards in 10. Both capitulum and tuberculum in all ribs have articular areas of oval shape, severely compressed fore-to-aft. There is a slight thickening of bone along the ventral half of the neck. The capitulum has a swollen anterior lip, with a depressed zone beneath for the articular capsule and strong, rugose ridges for the radiate ligament that surrounds the joint between capitulum and vertebra. Unlike mammalian ribs, where a strong ligament connects the anterior edge of the capitular neck to the transverse process of the next vertebra anteriorly, the torvosaur ribs show no marks for a ligament on the anterior face of the neck. The thin dorsal edge of the tuberculum-capitulum web bears some weak rugose lines parallel to the edge; a thin ligament sheet probably passed upwards to the underside of the transverse process (equivalent to the ligament of the neck of human anatomy).

On the outer side of the rib, below the limit of the articular capsule scars of the tuberculum, is a concentrated area of pits and irregular rugose lines (ilcos in Fig. 12-14). In modern birds, the slips of the iliocostalis muscle attach here, and so probably did they in the torvosaur (Fig. 9). In primitive diapsids, such as lizards and *Sphenodon*, the iliocostalis is much thicker than in birds and extends almost halfway down the thoracic rib shaft (Olson, 1936). The reduction of the iliocostalis is a distinctively avian feature and is part of the transition from a primitive tetrapod, where lateral flexion of the vertebral column was the strongest component of walking and running, to an advanced dinosaur-bird, where the lateral trunk flexors are diminished in bulk in favor of much augmented limb muscles.

Ribs — anterior intercostal ridges (int int, out int in Fig. 12-14). The ribs from Louise and Nail Quarry agree with those of allosaurs and differ from those from the Stonesfield megalosaur quarry and from those of ceratosaurs in lacking a clearly-defined cavity in the shafts. In most dinosaurs, there is a strong outer ridge on the anterior margin of the rib shaft, marking the attachment of the outer intercostal muscle. There is also an inner anterior ridge, less strongly developed, for the inner

intercostal. The outer ridge in theropods usually continues all the way proximally to the tuberculum, reinforcing that joint. The Como torvosaur ribs differ from those of the Stonesfield megalosaur, Morrison allosaurs and ceratosaurs in the way the anterior intercostal ridge dies out proximally far below the tuberculum. In the Louise Quarry ribs the ridges are most rugose in ribs 9 and 10, indicating strong intercostal tendon sheets; in ribs 3 and 4 the outer ridge is broadly rounded in cross section and the inner ridge is suppressed.

Ribs – posterior intercostal ridges (Fig. 12-14). On the posterior side of the shafts in the Louise Quarry ribs there are inner and outer rounded ridges, marking the attachment of the intercostal sheets; these sites are especially well developed in ribs 9 and 10. The posterior ridges are less rugose than the anterior ridges, indicating that the muscle was fleshy at the posterior attachment. Between inner and outer posterior ridges is a wide channel, the intercostal groove, for the intercostal blood vessels and nerve. In ribs 3 and 4 the intercostal groove is strongly developed only at the proximal end; distally, the outer border of the groove is much sharper than the inner border.

In ribs 9 and 10 the shaft is roughly equidimensional in cross section. In ribs 3 and 4 the shaft becomes much wider anterior-posteriorly than thick and has a rounded-triangular cross section, with apex facing forward. The shafts in ribs 3 and 4 have a strong forwardly-convex curvature in the proximal part of the shaft, immediately below the tuberculum.

Serratus attachment (Fig. 11-14). In ribs 3 and 4 there is a strong, rugose muscle scar on the external edge of the posterior margin, about two thirds down the shaft (Fig. 14). The only major muscle attaching in this region is the posterior serratus. In *Sphenodon* and most lizards and primitive thecodonts as well, the scapula is located over the anterior part of the thoracic ribcage, and hence most of the posterior serratus runs backward and downward towards the anterior edges of the ribs. But in birds, the long, nearly horizontal scapular blade extends for nearly the full length of the ribcage, so part of the serratus passes directly downwards from the scapula toward the uncinate processes on the posterior edges of the ribs. The serratus origin in torvosaur is strong evidence that the scapular blade was strongly tilted backwards – the strong tilt would place the scapular attachment of the posterior serratus much further aft than is the case in primitive thecodonts (Fig. 11D,E). The extreme development of the scar in the torvosaur indicates a very strong serratus here.

Ribs – measurements Louise ribcage (CPS 1001): Width across the tuberculum-capitulum: rib 4 – 251 mm; rib 9 – 220 mm. Maximum width, middle third of shaft: rib 3 – 60.1 mm; rib 4 – 58.3 mm; rib 9 – 43.2 mm.

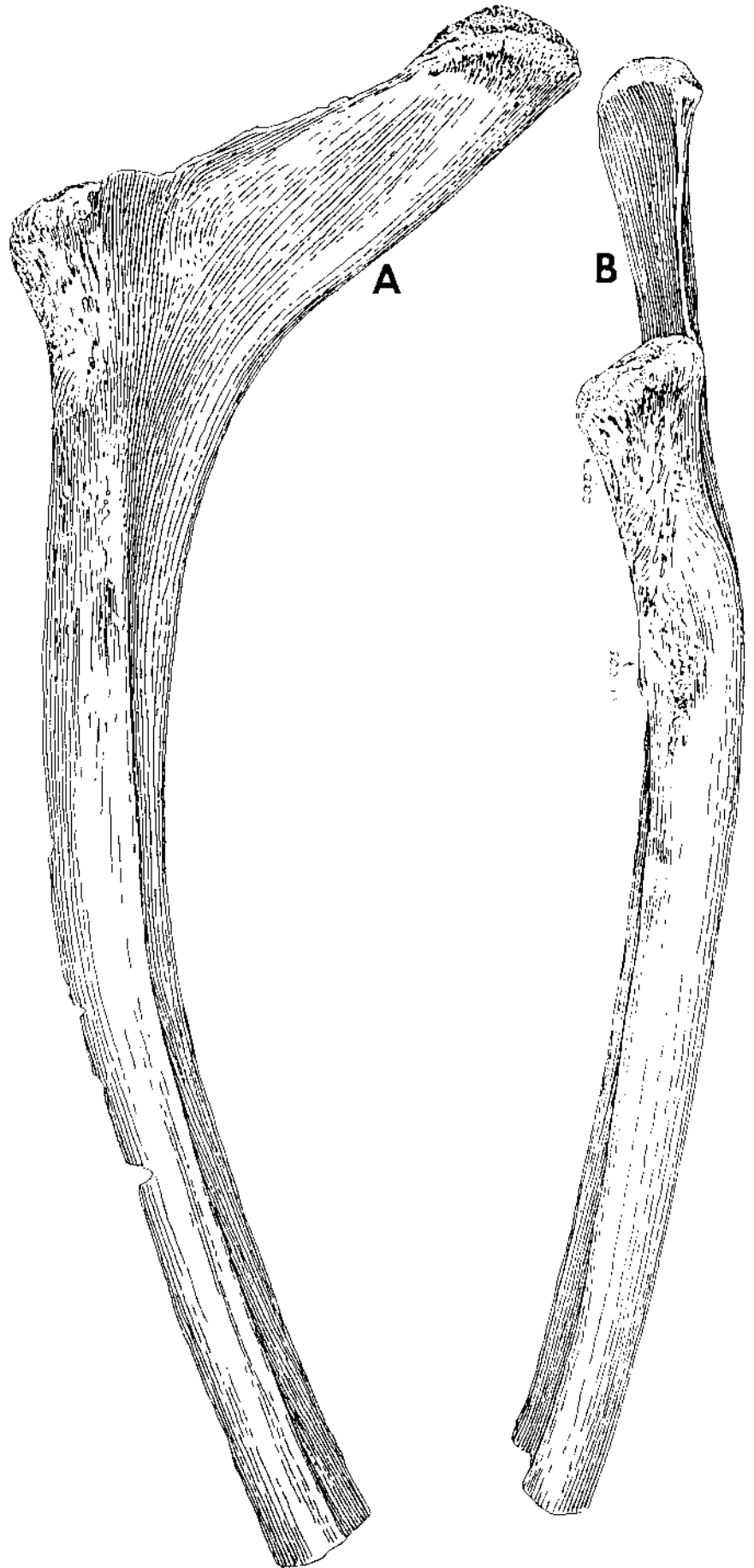


Figure 13. Ninth thoracic rib, *Edmarka rex*, CPS 1001. Views as in Fig. 12. Abbreviations listed in Fig. 1.

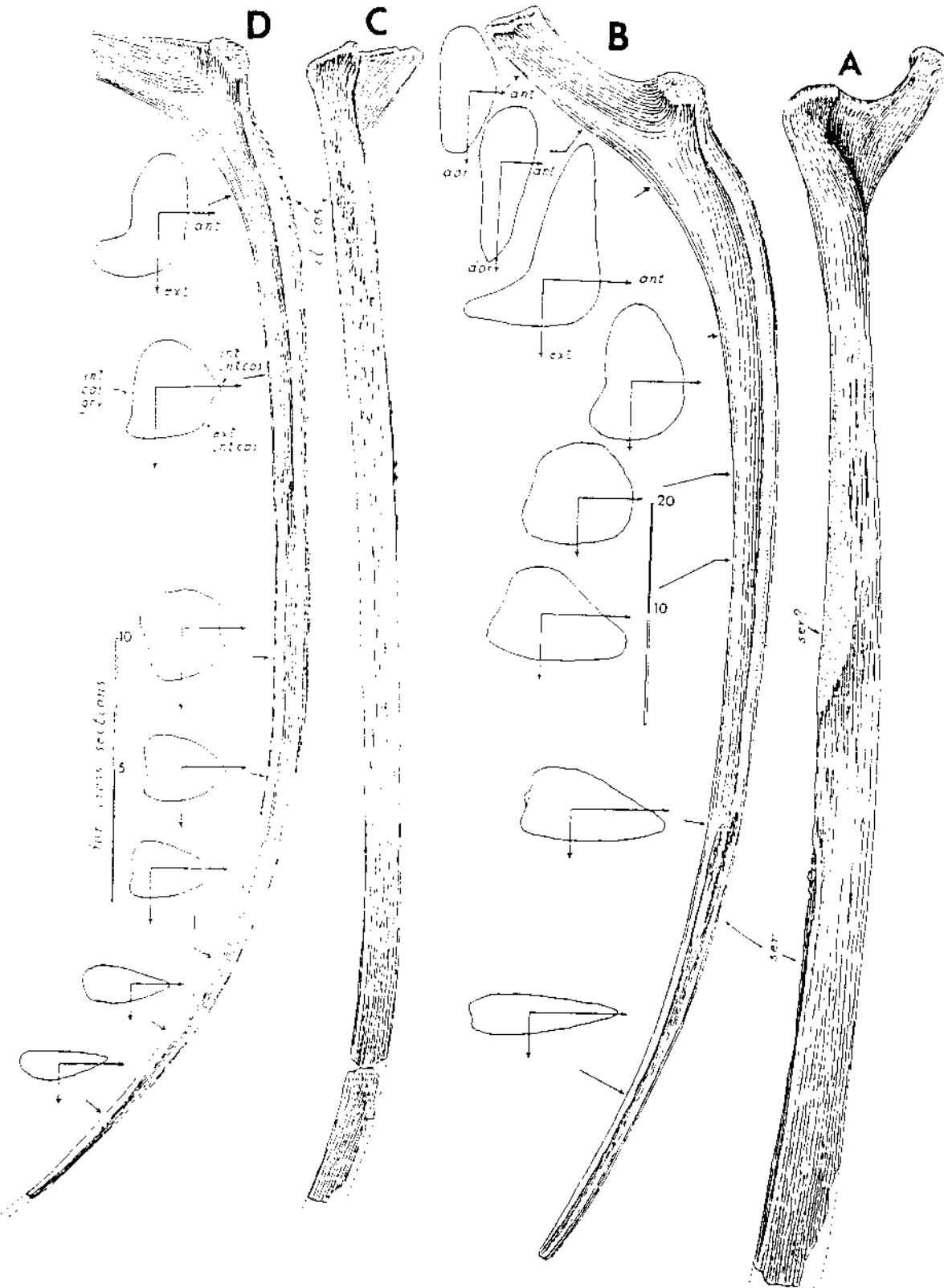


Figure 14. Thoracic ribs from Louise Quarry, *Edmarka rex*, CPS 1001. A,B — Third thoracic rib. A — external view, rib positioned as if articulated with the vertebra. B — posterior view, perpendicular to A. Enlarged cross-sections shown at locations indicated. Note that the plane of the greatest width of the head (plane passing through center of tuberculum and capitulum) is oblique. Scale bar for the external and posterior views; scale bar for cross sections shown in D. C,D — same views for thoracic rib ten. Scale bar for the cross sections. Abbreviations given in Fig. 1.

Pubis (Fig. 15). A left pubis (CPS 1010), of primitive "saurischian" construction, was found 1 m east of the scapula-coracoid at Nail Quarry (Fig. 15). In the field, the specimen was identified as that of a sauropod. However, the Nail pubis differs from that of all Morrison sauropod pubes in lacking the anterior thickening at the proximal end ("ambiens process"), in being far narrower across the thin sheet of bone that connects right and left pubes ("pubic apron"), and in being only about half as wide across the iliac articulation, relative to the proximal-distal length of the pubis. The total pubic length and the breadth across the iliac articulation are appropriate for a megalosauroid with a scapulocoracoid of the size found at Nail. Therefore the Nail pubis may be referable to *Edmarka rex*.

Because of severe weathering damage on the outer surface, the pubis must remain in the plaster jacket that covers the outer surfaces, and only the inner surface is free. The distal half of the pubic shaft is thick and cylindrical, relatively more massive for the pubic length than in *T. tanneri*. At the distal extremity the pubis is expanded posteriorly to make a pubic foot of modest anterior-posterior length; the medial-lateral width of the foot is relatively larger than in *T. tanneri*. In distal view, the foot has an ovoid outline, strongly pinched in the posterior third, as in *T. tanneri*. The distal surface of the foot is set at a right angle to the pubic shaft, unlike the condition in *T. tanneri* where the distal surface slopes slightly backwards relative to the shaft. Generally among theropods, the distal foot surface is parallel to the line of the sacral vertebrae, and in species where the pubic shaft is vertical (perpendicu-

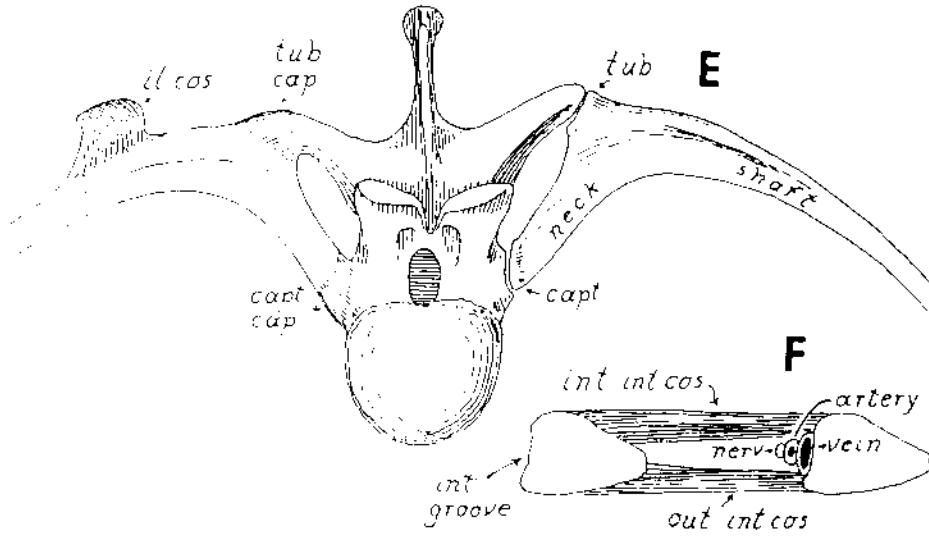


Figure 14 continued. Thoracic ribs from Louise Quarry. *Edmarka rex*, CPS 1001. E - schematic front view, showing how rib attaches to the vertebra. F - cross-section through adjacent thoracic rib shafts, showing relations of soft structures. capt - capitulum. tub - tuberculum. other abbreviations as in Fig. 1.

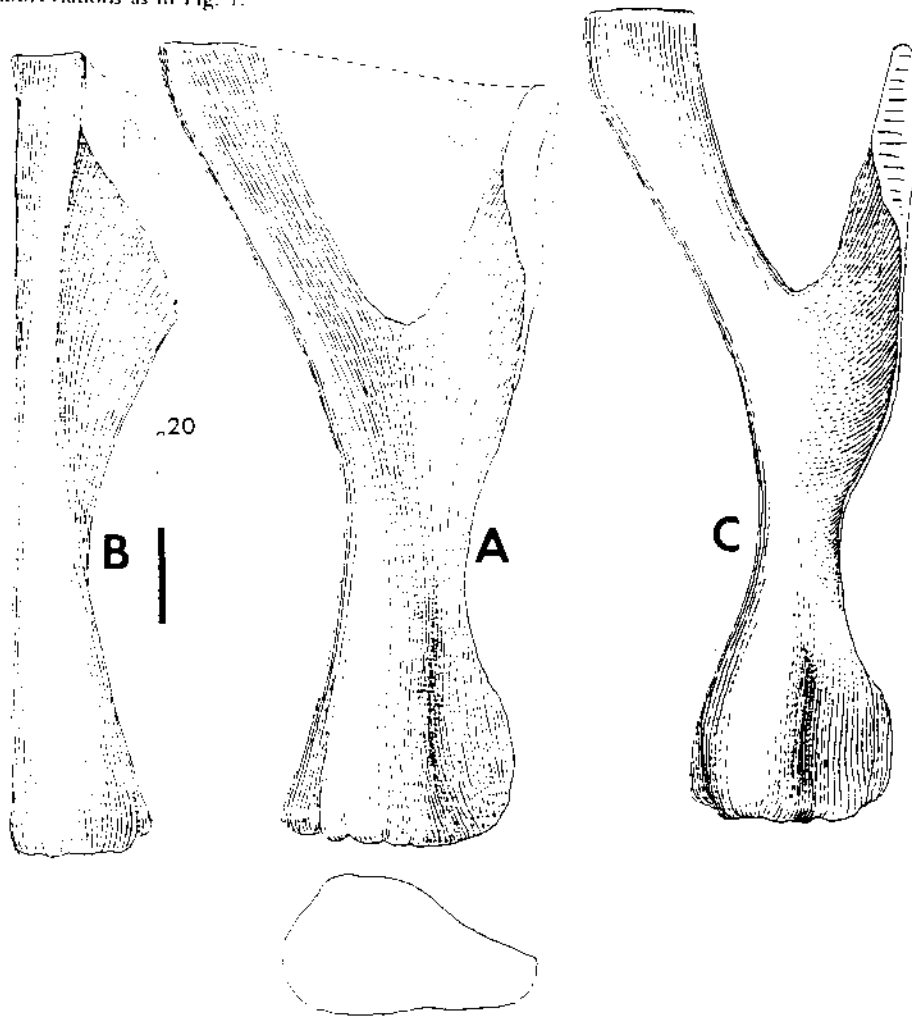


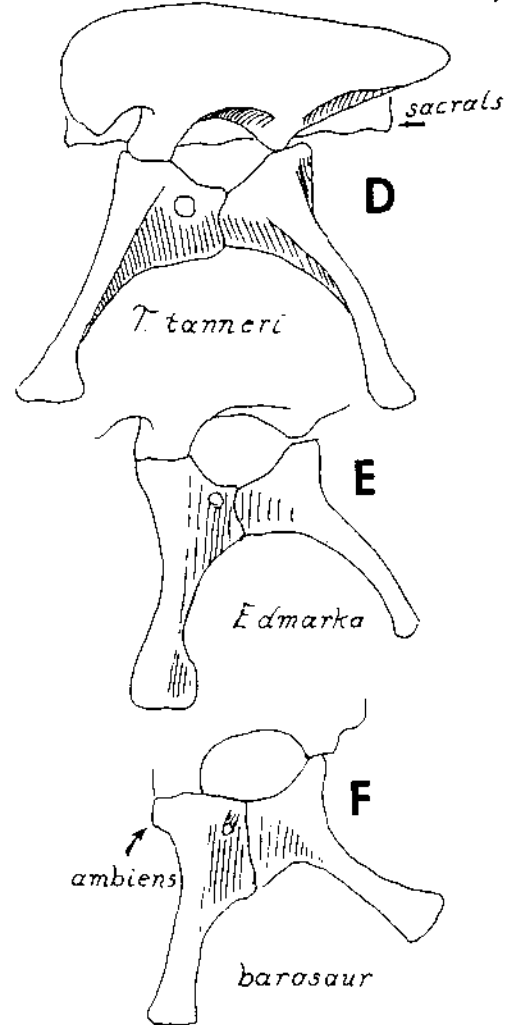
Figure 15. Left pubis CPS 1010 (reversed) attributed to *Edmarka rex*. A - medial-anterior view, drawn in the plane of greatest width, with outline of distal end. B - anterior-lateral view (perpendicular to A). C - inner view, as articulated in the living animal. D - outline of pelvis in *T. tanneri*, to show relations of distal pubic surface. E - tentative outline of pubis-ischium in *E. rex*. F - outline of pubis-ischium in a sauropod (*barosaur*), arrow points to ambiens process.

lar to the sacrum) the distal foot surface is at right angles to the shaft; in species where the pubic shaft is set obliquely downward and forward from the pelvis, such as *T. tanneri*, the distal surface is bevelled. In the Nail pubis the proximal iliac articular surface is also at a right angle to the shaft. In lateral view, the Nail pubic shaft is more strongly concave along the anterior margin than that of *T. tanneri*.

Overall, the Nail pubis is thicker and more massive for its length than that of *T. tanneri* but much lighter and thinner than that of any known sauropod. If correctly allocated, the Nail pubis reinforces the case for generic separation of the Nail megalosaur from *T. tanneri*.

Pubis - measurements. (CPS 1010) proximal-distal length: 866 mm. Minimum width at mid-shaft: 142 mm. Anterior-posterior length of distal end: 250 mm.

Size of skull relative to postcrania (Table 1). The data from the Como torvosaurus suggest that the Dry Mesa Quarry material recently redescribed by Britt (1991) belongs to two quite distinct sizes of megalosaur - the skull, atlas and humerus may



represent an individual or individuals 30% smaller in linear dimensions (Table 1). All the postcrania from Nail and Louise Quarries, except for the subadult coracoid, are of appropriate size to match the jugal, if the proportions of the Como torvosaur are those of a normal large theropod. In allosaurs, ceratosaurs, yangchuanosaurs, and tyrannosaurs the skull length is close to the length of scapula-coracoid, femur length, and maximum rib length (Table 1). The Nail jugal is only slightly longer than that of Dry Mesa Quarry, and our restoration of the Dry Mesa skull yields a premaxilla-quadrant length of 1223 mm. Hence the skull length for both the Nail and Dry Mesa specimens is only about 10% longer than the Nail scapula-coracoid and the longest rib from Louise Quarry, both of which are 1100 mm or more. However, the post-atlas vertebrae and hindlimb elements from Dry Mesa are much too small to be appropriate for the restored skull. The Dry Mesa tibia is 725 mm long; by comparison with *Ceratosauros*, the femur ought to be about 860 mm (Table 1) and the scapula-coracoid about 932 mm. But a normal large theropod with a 1200 mm skull should have a femur and scapula-coracoid 1100 mm long or longer.

The size of the anterior caudal vertebrae also indicates that the Dry Mesa column is too small for the Dry Mesa skull. The Dry Mesa proximal caudal vertebrae average about 120 mm centrum length (Britt, 1991), the same size as the allosaur AMNH 5727, which has a femur length of 920 mm (Table 1). The first caudal centrum from Nail Quarry (CPS 1006) is 140 mm long, and since the first caudal is usually the shortest among proximal caudals, the average proximal caudal centrum length probably was 145 + mm, the same size as the giant allosaur (*Epanterias*) in the University of Oklahoma Museum

Table 1. Some useful measurements of large theropods. caud L = length at mid height of anterior caudal centrum. skull L = skull length premaxilla to quadrate. rib L = length of longest thoracic (anterior dorsal) rib. scpr L = scapula-coracoid length (chord). UUVP measurements from Madsen, 1976. Dry Mesa torvosaur measurements from Britt, 1991. AMNH gorgosaur measurements from Matthew and Brown, 1923. NMC gorgosaur measurements from Lambe, 1917. cal – length calculated from other limb bones. res – restored.

| Theropod | caud L | skull L | rib L | scpr L | femur L |
|------------------------------------|--------|---------|-------|------------|---------------|
| torvosaur Nail & Louise | 140 | 1360res | 1275 | 1100 | |
| torvosaur Dry Mesa | 120 | 1223res | | tib | 865cal 725 |
| <i>Ceratosauros</i> USNM 4735 | 68 | 650 | — | 600res | 620 |
| <i>Ceratosauros</i> UUVP 5982 | | 800res | 800 | 825 tib | 765 |
| <i>Allosaurus</i> USNM 4734 | | 670 | — | 795 | 850 |
| <i>Allosaurus</i> Clev-Loyd #33 | 112 | 780 | 735 | 690 | 717 |
| <i>Allosaurus</i> AMNH 5727 | 120 | 950 | 910 | 900 | 920 |
| <i>Gorgosaurus</i> AMNH 5434 | | 1050 | | 965 | |
| <i>Gorgosaurus</i> AMNH 5664 | | 678 | | 620 | 700 |
| <i>Gorgosaurus</i> NMC 2120 | 144 | 970 | 1020 | 1086 | 1040 |
| <i>Tyrannosaurus</i> AMNH 973 | | 1250res | 1300 | 1100 | 1300 |

collections, which has a femur length of 1200 mm. The *Epanterias* specimen from near Masonville, Colorado, also has caudal centra 145-150 mm long (Bakker, 1990).

Proportions among tyrannosaurs are different from those of Jurassic theropods – the proximal caudals are longer relative to the femur, skull and scapula-coracoid, but the caudals decrease in length much more dramatically front-to-back (Table 1).

Whether the Dry Mesa material is compared to that of the Nail-Louise torvosaur, or ceratosaurs, allosaurs or tyrannosaurs, the results are the same – the Dry Mesa skull is much too large to fit the Dry Mesa hindlimb and vertebrae. Galton and Jensen (1979) noted that the radius and ulna in the Dry Mesa specimens were relatively tiny compared to the humerus, a degree of forearm reduction greater than that seen in *Poikilopleuron*. However, if the large Dry Mesa humerus belongs to a full grown individual, and the forearm to a two-thirds grown animal, then the proportions would be similar to those in *Poikilopleuron*.

SIZE-CYCLES AMONG TOP THEROPODS

The very large size of the Como torvosaur adds one more theropod family to the list that produced a species of *T. rex* size. Theropod body configurations show some progressive trends through time – allosaurs have shorter torsos relative to the ilium and femur length than do megalosaurs or ceratosaurs; tyrannosaurs have exceptionally short torsos. Therefore we use femur length rather than total body length as a measure of bulk. Any theropod with a femur length greater than 1100 mm is here considered to be a giant predator. At least five cycles of giant theropod can be documented.

I Yangchuanosaur Cycle. The earliest giant theropod is *Yangchuanosaurus magnus* from the Shangshaximiao Formation (Dong et al., 1983); this genus has a skull that is short relative to postcrania, and therefore the skull length of 1100 mm indicates a femur 1200 mm or more. The estimated age of *Y. magnus* is early Late Jurassic (Dong et al., 1983), roughly Oxfordian or early Kimmeridgian. Yangchuanosaurs are not known from the Morrison Formation, and the data indicate that a great deal of time may well have elapsed between the Chinese yangchuanosaur faunas and the first torvosaur samples from the Morrison.

II Megalosaur Cycle. The evidence for the temporal sequence of giant yangchuanosaurs, torvosaur and allosaurs is as follows. It is generally accepted that the East African Tendaguru dinosaur fauna is slightly older than the earliest Morrison faunas because long-legged stegosaurs, diplodocines (*Diplodocus* and *Apatosaurus*) and camarasaur are absent from the Tendaguru but present in the Lower Morrison. The Tendaguru is well dated by ammonites as latest Kimmeridgian-earliest Tithonian (Arkell, 1956), and therefore the lower Morrison at Como should be early Tithonian. A giant theropod is recorded from the Tendaguru – shed teeth, type of "*Megalosaurus*" *ingens* Janensch 1920. The crowns are much more compressed laterally than in allosaurs and could be ascribed to a megalosaurid, ceratosaurid, or yangchuanosaurid. However, there are no cranial or postcranial bones of mid or late Kimmeridgian Age from anywhere in the world that can be allocated to yangchuanosaurs. Thus it appears quite possible that the Megalosauridae achieved giant size after the giant yangchuanosaurs were already extinct.

III Allosaur Cycle. All the giant torvosaur are from the lower two-thirds of the Morrison. The available evidence indicates that considerable time had elapsed after torvosaur disappeared and before giant allosaurs evolved. There is no trace of any torvosaur, large or otherwise, coexisting with the giant allosaurs of the upper level of

the Morrison in Colorado and Oklahoma. The Bone Cabin Quarry Level-Main Marsh Level in the Cornu region is 15 m above the Nail and Louise Quarries and roughly equivalent in time to the Dinosaur National Monument main quarry (Bakker, 1990). The Bone Cabin-Main Marsh-DNM zone has a very large sample size of predators, and there are no unambiguous records of either giant torvosaur or giant allosaur although medium-size allosaur are common. Therefore it appears that this interval of time marks the gap between torvosaur extinction and the first appearance of *Epanterias*.

IV Acrocanthosaur Cycle. In the late Early Cretaceous (Albian), acrocanthosaurs achieve a femur length of about 1100 mm (specimen at the Black Hills Institute). No true allosaurids are known from any time in the Cretaceous (the definitive allosaurid character is the slender, strongly down-turned paroccipital process). Therefore it seems that all allosaurs, including the giant *Epanterias*, were already extinct before acrocanthosaurs evolved.

An ecological sidebar to the acrocanthosaur cycle is the complex of gigantic aquatic theropods in North Africa in the Early Cretaceous and Cenomanian. *Spinosaurus*, *Bahariasaurus*, and *Carcharodontosaurus* were described from incomplete remains preserved in fluvio-deltaic and near-shore sediments (Stromer, 1915, 1931, 1934). Body lengths and femoral lengths are in the range of *T. rex*. The long, crocodile-like snout of spinosaurs and the shark-like teeth of carcharodontosaurs indicate piscivorous habits, and hence these giant theropods may be a radiation of marine predators analogous to that of the early seals and toothed whales of the Tertiary. Both hindlegs and tail probably were used in swimming in theropods.

V Tyrannosaur Cycle. The earliest well dated tyrannosaurids are late Late Cretaceous, long after the last occurrence of acrocanthosaurs in the Albian. Giant tyrannosaurids are very late to appear – the largest tarbosaur and *T. rex* itself are the only members of the Tyrannosauridae to exceed a femur length of 1100 mm, and these species debut no earlier than about 5 million years before the end of the Cretaceous.

Theropod size-sequences present evidence that replacement of the top predator was possible only *after* the incumbent family went extinct. This ability of the incumbent to discourage other families from evolving gigantic size is especially intriguing because the replacement families usually represent a higher morphologic grade than that of the replaced family. The net result of the succession of replacements was a top predator that became progressively more and more advanced in those cranial and postcranial characters that are fully expressed in birds. Thus the allosaurs are more avian and more advanced than ceratosaurs and megalosaurs in the fore-to-aft shortening of the torso, the narrowing of the scapular blade, and the greater compaction of the metatarsal heads. Acrocanthosaurs and tyrannosaurs show successive increments in the degree of pneumatization of the braincase. It is not unreasonable to suppose that tyrannosaurs were, in a fundamental sense, superior to acrocanthosaurs in adaptations as top predators. And, likewise, allosaurs, with their compact torsos and longer legs, would seem to be superior to megalosaurs and ceratosaurs. So why did allosaurs have to wait, so to speak, to evolve giant species until after giant megalosaurs were gone?

It may be heuristic to think of adaptations as coming in two categories: First there are the general adaptations, such as the degree of pneumatization of skull, shortening of the torso, distal elongation of the limbs, and the reduction of the calcaneum. These improvements in the grade of general adaptations come rarely and require reorganization of morphogenetic systems. Second, there are local specializations, those minor adaptations that fit the species to its particular niche – skin color and prey search image are two examples. A new species, evolving into an adaptive area not previously occupied by its immediate ancestors, may require a period of adjustment while all the adaptive shifts are made to maximize performance in the new role. This process of adjustment may be difficult or impossible if a competing species already occupies the role and already has acquired the adaptive fine tuning. Thus it is not impossible that an incumbent top predator, who has all the refinements in local specialization needed to deal with one set of prey and habitats, would have a suppressing effect upon the production of competing species from a stock that is superior in basic adaptations. For example, it may well be that allosaurs were fundamentally superior in locomotion to megalosaurs, but giant megalosaurs evolved first and natural selection, operating over millions of years, equipped the giant megalosaurs with all sorts of adaptive nuance necessary for the giant predator role. A giant allosaur, if equipped with all the minor adaptations needed, would perform that ecological role better, but, as long as the giant megalosaurs existed, their presence discouraged any allosaur species from evolving giant size – it would be more advantageous for allosaurs to minimize the competitive overlap with megalosaurs.

The pattern of extinction and replacement among the largest theropods demonstrates that the maximum size of the top dinosaurian predators was fixed at a femur length between 1100 and 1350 mm. This maximum size seems to have no relation to the size and armament of the prey – the yangchuanosaurs faced medium size stegosaurs and sauropods small by Morrison standards; acrocanthosaurs are found with medium-size iguanodonts, large nodosaurs and rare sauropods; the largest tyrannosaurs are part of faunas with the herbivore component dominated by duckbills, ankylosaurs, formidable horned dinosaurs and rare sauropods. The aquatic theropod giants of Cenomanian North Africa are especially intriguing – their feeding habits must have been markedly divergent from the theropod norm, and yet the maximum body bulk is not far from that of *T. rex*.

The firm and unyielding ceiling of maximum theropod size suggests that the limit was imposed by some intrinsic feature of the bauplan. Quite possibly the bipedal habitus did not permit evolution of body size greater than that seen in theropods – quadrupedal dinosaurs often exceeded the bulk of *T. rex* and so did the largest proboscideans and rhinos in the Cenozoic.

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ZOFIABAATARIDAE, A NEW FAMILY OF MULTITUBERCULATE MAMMALS FROM THE BREAKFAST BENCH FAUNA AT COMO BLUFF

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Kielan-Jaworowska and Ensom (1992) have suggested that *Zofiabaatar*, from the Breakfast Bench Fauna, deserves allocation to a separate family. I had reached this conclusion independently. Therefore the Family Zofiabaataridae is herein erected, with the following diagnosis: Differs from Allodontidae and agrees with Plagiaulacidae in having fourth lower premolars that are longer anterior-posteriorly, relative to crown height, and crown ridges that are more numerous and make a more acute angle with the cutting edge of the crown. Differs from both Allodontidae and

Plagiaulacidae and agrees with Late Cretaceous families in having a mandibular condyle that faces upwards.

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