GAIA Nº 15, LISBOA/LISBON, DEZEMBRO/DECEMBER 1998, pp. 193-218 (ISSN: 0871-5424)

MECHANICAL FACTORS IN THE DESIGN OF THE SKULL OF *TYRANNOSAURUS REX* (OSBORN, 1905)

Ralph E. MOLNAR
Queensland Museum. South Brisbane, QUEENSLAND 4101. AUSTRALIA

ABSTRACT: **Mechanical analyses, borrowed from mechanical engineering, suggest that the skull of *Tyrannosaurus rex* (OSBORN, 1905) was constructed to resist strong, more or less vertically-directed forces during biting. Space frame analysis indicates that the skull structure was stable under a plausible regime of forces impressed during biting and supporting the weight of the head. Trajectory analysis suggests that major openings (orbits, fenestrae) and sinuses were located in regions away from major stress concentrations. The recurved teeth seem to be curved so that the radius of curvature of the tooth matches the distance from the tooth to the craniomandibular joint.**

KURZZUSAMMENFASSUNG: **Mechanische Analysen, basierend auf Ergebnissen aus dem Maschinenbau, zeigen, dass der Schädel von *Tyrannosaurus rex* (OSBORN, 1905) so konstruiert war, dass er starker, mehr oder weniger vertikal orientierter Krafteinwirkung während des Bisses widerstehen konnte. Verspannungsanalysen deuten darauf hin, dass die Schädelstruktur stabil genug war einer entsprechenden Krafteinwirkung während des Bisses standzuhalten und das Gewicht des Kopfes zu stützen. Die Analyse der Krafttrajektorien zeigt, daß sich die Hauptöffnungen (Orbita, Fenestrae) und Sinus nicht an den Punkten der grössten Belastungskonzentration befanden. Die zurückgebogenen Zähne scheinen so gekrümmt zu sein, daß der Krümmungsradius des Zahnes der Distanz zum Kiefergelenk proportional ist.**

INTRODUCTION

Tyrannosaurus rex (OSBORN, 1905) is so well known to paleontologists and the general public alike that an introduction is unnecessary, but very little structural or functional analysis has been published for this animal. Only three works have appeared: NEWMAN (1970), FARLOW, SMITH & ROBIN- SON (1995) and YAMAZAKI (1995), all dealing with posture and locomotion. This paper presents a preliminary set of analyses of the architecture of the skull and jaws of *T. rex*, based on engineering theory. The results of these analyses are used as bases for speculations on the function of the cranial skeleton, largely in feeding. As most paleontologists presumably are not familiar with engineering theory basic comments on, and references to, the methods and purposes of the analyses precede each section.

Much of this work, in its original form, was part of the requirements for the degree of Ph.D. at the University of California, Los Angeles, in 1973. The descriptive part of that work has already been published (MOLNAR, 1991): this is part of the "contemplated functional study" referred to there. Surprisingly, since 1973 no other work of this kind on dinosaurs (or other fossil animals) known to me has been published, except that of TAYLOR (1992) on the sauropterygian, *Rhomaleosaurus zetlandicus* (PHILLIPS, in ANONYMOUS, 1854). JENKINS (1997a, 1997b) has applied similar techniques to the study of (non-mammalian) synapsids, but that work awaits full publication. This lapse of interest may perhaps be due to the swing of attention to phylogenetic analyses in the 1970's and 80's following the widespread adoption of cladistic methods.

In its form, the cranial skeleton is the most complex skeletal structure in most vertebrates. This complexity probably results from the varied functions of the head: housing of central nervous, sensory, trophic, and respiratory structures; provision of structural support for itself and its attendant structures; and resisting stresses imposed during feeding, fighting, and other activities.

Unlike the mammalian skull, of which the braincase forms a large part, the archosaurian skull seems to consist chiefly of the feeding apparatus. Thus support of the dentition, provision of a framework for the jaw musculature, and resistance to forces imposed by the prey seem to have been major factors influencing its form. Since tyrannosaurids were terrestrial large animals, support of the head against gravity presumably was also a major consideration. The skull is supported by the vertebral column and associated musculature and hence relationships of the occiput to the cervical column are important. Like TAYLOR (1992), I shall assume that the skull and jaws of *Tyrannosaurus rex* were optimized to withstand the forces exerted when obtaining prey and feeding. In addition, since *Tyrannosaurus* was a land-dwelling beast, I assume the cranial skeleton was also optimized - or very nearly so - to withstand the force of gravity, in other words to resist collapsing under the weight of the head. The assumption that the bones did not usually fail when subjected to stresses during feeding or other activities, nor under the force of gravity, may be tested by observation. No theropod skulls have been reported exhibiting any indication of fracture of their component elements attributable to such stresses. Such failure as has been reported is confidently attributed to combat, presumably intraspecific: this kind of failure is not treated here. Looking for evidence of failure of soft tissues, tearing of ligaments or muscles, is much more difficult and has not been attempted. Nonetheless, in view of the rarity of this kind of failure in living animals it seems reasonable to assume that these tissues, too, did not regularly fail. It is also assumed that the cranial joints, excepting the craniomandibular joint, were not significantly weaker than the bony elements themselves, in other words that failure would not preferentially occur at joints. BUSBEY (1995) found that crocodilian skulls damaged during life inevitably fractured across, but not along, the sutures, thus supporting this assumption.

The approach used is adapted from the engineering analysis of structures. These analyses depend upon the application of the laws of physics (specifically, mechanics) to human constructions. As these laws apply equally to organisms, the analyses should provide insights into the construction and design of skeletal structures. Where they do not, it may be assumed that failure of the analysis is not a real failure (which would imply inapplicability of the laws of physics to organisms, and hence vitalism) but stems from incomplete understanding of the structure being analyzed. Thus such analyses serve a dual purpose: they elucidate structure, and point out topics for further research. Analysis of the internal structure of the bones was not conducted, although it would doubtless yield interesting insights. Furthermore although it seems reasonable, from expectations based on evolutionary theory and observation of living animals, to regard the cranial skeleton as stable under the usual stresses (i.e. unlikely to deform and break), such analyses can illuminate details of the structure.

The skull will be considered a frame or truss in order to determine its stability under the various stresses expected to have been imposed during life. Both the skull and mandible are also analyzed by analogy with the trajectory model for cantilever beams. Then specific features of the structure of the skull and jaws are related to the results of these analyses and, in the case of the jaws, to resistance to imposed stresses. Finally the different forms of the teeth of *Tyrannosaurus* OSBORN (1905) will be delineated and related to the bite. There follows some speculation based on these considerations and on analogies with modern carnivores regarding how *Tyrannosaurus* may have attacked prey. This work is based on observation of the skulls of AMNH 5027, LACM 23844 and MOR 008. The use of the term “fenestra” follows that of MOLNAR (1991), that is “fenestra” refers only to an aperture, but not also the fossae often surrounding such apertures.

STRUCTURAL ASPECTS OF THE SKULL

BASIC PRINCIPLES OF FRAME AND TRUSS ANALYSIS

To analyze the ability of the skull to resist imposed stresses, the skull is approximated by a model, a frame (or truss) of bars or struts joined together at their ends. This is a standard technique of engineering statics where, however, the use of bars does not constitute as distant an approximation as here. Most engineered structures are constructed of beams and girders to which bars are a better approximation than to the somewhat box-like structure of a skull, which comprises sheet-like and shell-like elements. The application here follows the exposition of AU (1963). The bars may be considered to be rigidly joined, making up a frame, or joined with pivots (or pins), so they are free to rotate to adjust to applied stresses. This kind of structural model is termed a truss. Rotation in the model represents failure of the structure being modelled, whereas for a frame the bars would be deflected (deformed): if no rotation (or deflection) results from the applied stress, in other words the structure does not deform, it is considered stable under that stress. The stresses are assumed too weak to fracture the bars. The bars of a triangular truss cannot rotate under any applied forces, hence the triangular truss is considered the basic unit of a rigid framed structure. If the frame or truss made up of these bars is two-dimensional, it is a plane frame or truss; if three-dimensional, a space frame or truss (cf. AU, 1963: 12). Useful detailed information on the application of statics to the (mammalian) skull is given in section VI of BADOUX (1964).

Plane Frame Analysis of the Snout

The cross-sectional structure of the snout may be considered as a plane frame, after the fashion of BADOUX (1966a). Its cross-section at the level of the fifth maxillary tooth (Fig. 1A) is a paraboloid arch, with an arched cross-member formed by the palate. This may be approximated by an isosceles triangular plane frame (Fig. 1B). Since the only analyses of this kind known to me have been conducted on mammals (e.g. BADOUX, 1966a), although BUSBEY (1995) approaches this kind of analysis for crocodilians, *Tyrannosaurus rex* will first be compared to carnivorous mammals. If the situation in *T. rex* was analogous to that in mammals (BADOUX, 1966a), most of the forces exerted on the upper teeth in biting would have been generated by contact with the lower teeth. As these teeth are laterally compressed and their sides are nearly vertical, and as the force is exerted normal to the surface of contact, the horizontal component would have been large (Fig. 1C). In turn, this would have exerted strong moments upon the palate at its junctions with the sides of the snout. A triangular frame, under these imposed moments, will be stable if each member is non-deformable. However, if the palate is deformable, it will tend to bow, becoming convex ventrally if horizontal or, in the case of the actual arched palate, to flatten out. Even if the bone itself did not deform the contacts between the elements, which do not appear to have been very strong (cf. MOLNAR, 1991: 158-160), might tend to fail or flex. To reinforce the palate in this model, a tensile member is needed extending from the apex of the triangle to the middle of the palatal member (as does the nasal septum in mammals, BADOUX, 1966a). Therefore given the hypothesis that *T. rex* had a bite like that of mammals, this analysis indicates that it should also have had a nasal septum. However, there is no evidence for such a member in *T. rex*. Thus there are two possibilities: the palate did indeed deform (if only slightly), or the chief forces exerted upon the teeth did not have a strong horizontal component. This last is consistent with the wear patterns of the teeth, discussed below, hence biting in *T. rex* was probably not analogous to that in mammals, a conclusion that - given the form of the dentition - is not surprising.

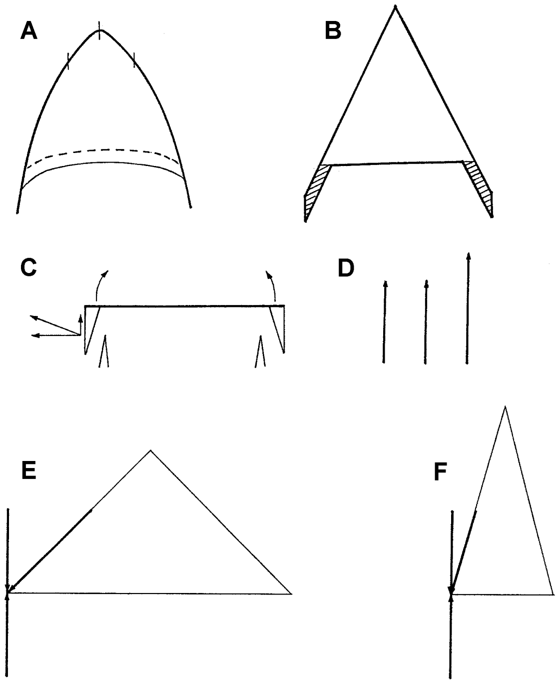

Fig. 1 - **A** - Cross-section of the snout (reconstructed) of *Tyrannosaurus rex* OSBORN (1905) at the level of the fifth maxillary tooth. The level of the palate in LACM 23844 is indicated by the dashed line, and in AMNH 5027 by the continuous line. Vertical bars mark the positions of the nasal symphysis and the nasal-maxillary junctions. **B** - Approximation of the snout section by an isosceles triangular plane frame. The hatched portions represent the robust portions of the maxillae ventral to the palate. **C** - As the teeth have nearly vertical sides, the forces between them have a large horizontal component. This exerts a torque (curved arrow) at the toothrow. **D** - Magnitudes of the impressed force, left, compared to the reactions for the triangular frame of deep snout (F), center, and of broad snout (E), right. **E** - Reaction to an arbitrary impressed force of a triangular frame representing a broad snout. **F** - The reaction is smaller in a frame (representing a deep, narrow snout) with the legs oriented more nearly vertical.

If, on the other hand, the main force exerted on the teeth was from resistance exerted by the food, chiefly by contact with bones or other tough tissues, it would have been directed vertically. Under this condition the triangular frame is stable. This scheme is consistent with the general form of the teeth and the relative lack of wear attributable to tooth to tooth contact. It suggests that the feeding mode in *T. rex* was more similar to that of oras (*Varanus komodoensis* OUWENS, 1912), where the greatest forces presumably are compressive and exerted on marginal snout elements (AUFFENBERG, 1981; BUSBEY, 1995).

The palatal processes of the maxillae, together with the anterior moiety of the vomer, form a secondary palate anteriorly (OSBORN, 1912; MOLNAR, 1991: fig. 9, where A and B have been reversed). This secondary palate is unusual among theropods, being absent in allosaurids, ornithomimosaurs, oviraptorosaurs and dromaeosaurs. An extensive secondary palate is present in *Syntarsus rhodesiensis* RAATH (1969), but absent in *Coelophysis bauri* (COPE, 1887) (COLBERT, 1989: fig. 43). BUSBEY (1995) suggests that in crocodilians the secondary palate primarily functioned in strengthening the snout, which may also have been the case in *T. rex*.

The most effective reaction to such a vertically imposed force is an oppositely directed, vertically

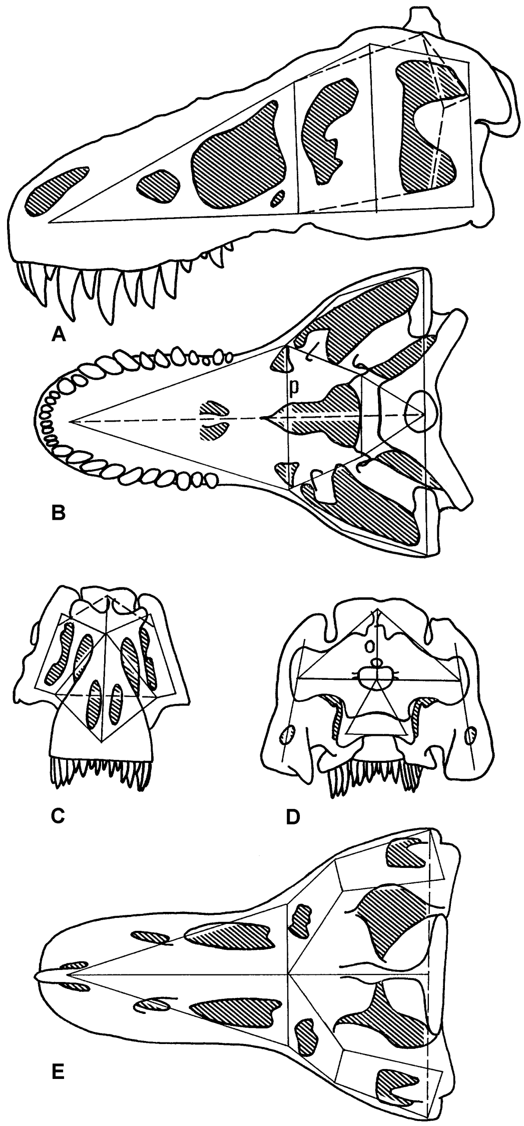

Fig. 2 - The space frame or truss approximation of 29 bars to the skull of *Tyrannosaurus rex* OSBORN (1905) (based on the skulls of AMNH 5027 and LACM 23844). **A** - Lateral view. **B** - Ventral view (p - transverse palatal bar). **C** - Anterior view. **D** - Posterior view (o - supraoccipital bar). **E** - Dorsal view.

oriented reaction force. To exert such reactions however, the rostral cross-section would have to be rectangular, and a rectangle would be unstable were the forces to deviate from the vertical. But a triangular cross-section must generate reaction forces greater than the imposed forces, as there will necessarily be horizontal components to the reaction (Fig. 1E-F). The closer the legs of the triangle to vertical, i.e., the more laterally compressed the snout, the smaller these horizontal components will be (Fig. 1D-F). Hence the steeply inclined sides of the snout in *T. rex* appear to be adapted for forceful biting. This is corroborated by the work of ERICKSON *et al.* (1996) who estimated the bite forces exerted on a bone of *Triceratops* sp. bitten by *T. rex*. They conclude that forces of 6,410-13,400 N were exerted, which is greater than any bite forces measured or estimated from modern sharks and (carnivorous) mammals.

This result implies that the snout in *T. rex* was adapted to resisting strong forces impressed by the teeth. Presumably this was due to the effect of selection acting in favor of the capacity to bite strongly. If true, one would expect an increase in snout depth, and in the verticality of the sides, in the lineage leading to *T. rex*. The interpretation of a strong bite is consistent with the expansion of the postorbital region of the skull to accommodate jaw adductors that are relatively larger than in other tyrannosaurids. A strong bite would also be useful, although I suspect not adapted, for intraspecific combat. In this context, it is relevant that a possible bite mark in the surangular of *T. rex* (LACM 23844) has been described (MOLNAR, 1991) and that more severe bite marks to the jaw of *Sinraptor dongi* (CURRIE & ZHAO, 1993) have been illustrated (FARLOW & MOLNAR, 1995: 49), although not yet described.

SPACE FRAME ANALYSIS OF THE SKULL: PRINCIPLES OF ANALYSIS

The skull may be treated as a space frame by approximating its form with a suitable framework of bars, again using the methods of AU (1963). For this analysis, the skull is assumed to have been akinetic: following RUSSELL (1970) this has been generally accepted. Initially, forces are assumed to have been symmetrically applied and to have acted in the sagittal and parasagittal planes. The skull was approxi-

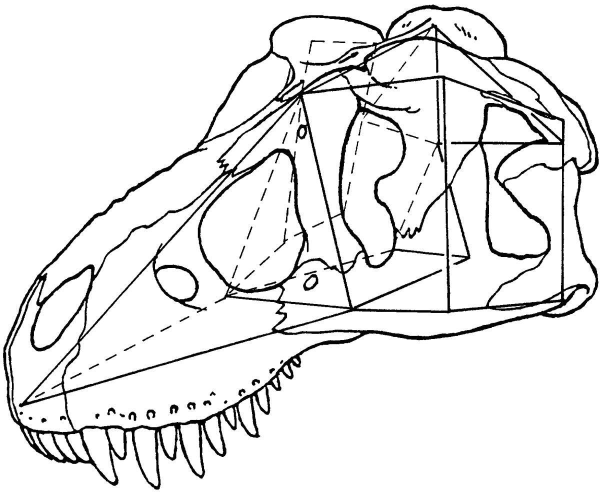

Fig. 3 - Anterior oblique view of the space frame or truss approximation to the skull of *Tyrannosaurus rex* OSBORN (1905).

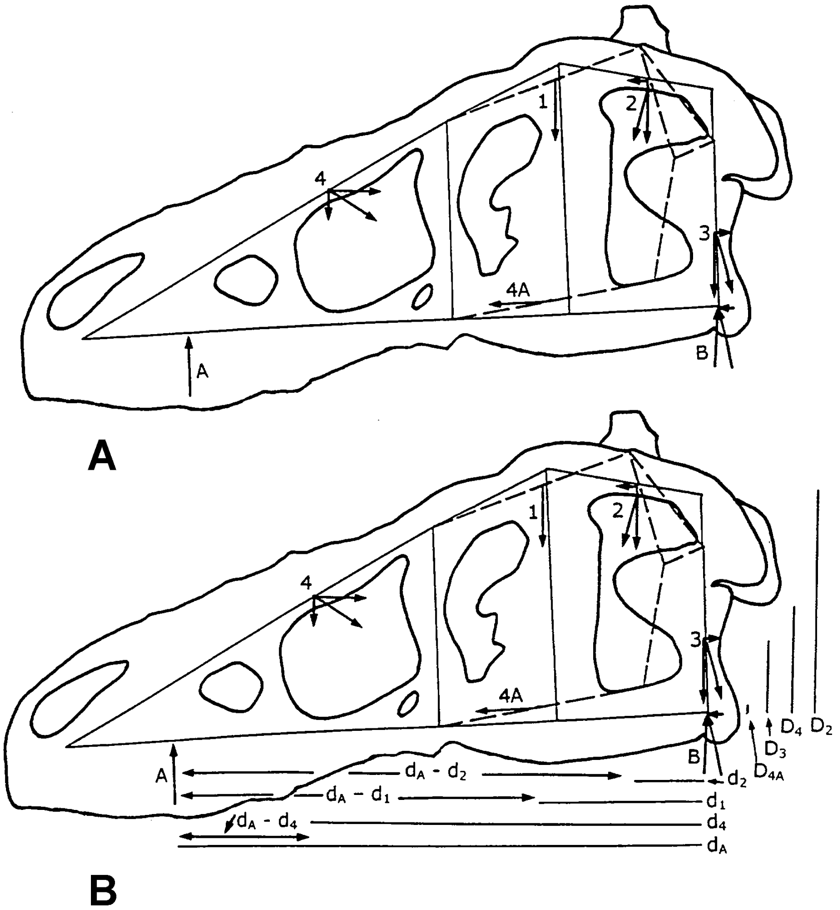

Fig. 4 - Loadings on the space frame used in the free body analyses of the structure under forces imposed in biting. **A** - Forces and reactions. **B** - Moments arms of the forces and reactions. 1 - Force exerted by *Mm. adductor mandibulae externus profundus* and *pseudotemporalis*; 2 - by *M. adductor mandibulae externus superficialis et medialis*; 3 - by *M. adductor mandibulae posterior*; 4 - by *M. pterygoideus anterior*; 4A - reaction of *M. pterygoideus anterior* in passing over the anterior margin of the subtemporal fenestra; A - resistance exerted by food; and B - reaction at the craniomandibular joint. D indicates the vertical moment arms and d the horizontal, and the subscripts refer to the forces and reactions of Figure 4A. The differences used in ADDENDUM II are also indicated.

mated by a set of 29 struts (Fig. 2-3) by inspection, loaded by forces generated by the jaw musculature at eight points, with reactions to the *M. pterygoideus anterior* at two points and other reactions at four points (two points by resistance from the prey, and two by reactions at the quadrate condyles). The reactions from the *M. pterygoideus anterior* are generated as the muscle changes direction passing over the anterior margin of the subtemporal fenestra. Reconstructions of the jaw musculature, very similar to that of the dissertation used for this analysis, are illustrated in HORNER & LESSEM (1993: 105) and FARLOW & MOLNAR (1995: 38).

The concept of degree of redundancy (or statical indeterminacy) is used by engineers to determine the equilibrium of a plane or space frame (rigidity in this context) when given forces are applied. A frame is assumed to consist of nondeformable, rigid, linear members. It is considered to have rigid joints between the members, while in the truss the members are connected by pivots where they intersect (pin-connected), so that they are free to rotate at the joints (which simplifies the analysis). As previously mentioned, the triangular truss cannot rotate about any of its joints as long as the members are non-deformable, thus its position as the basic unit of the non-deformable truss. Any unit consisting of more than three members forms a crank, i.e. can deform by rotations at the joints.

If, for a given frame or truss and set of forces, the equations of statics are insufficient to uniquely determine the values of the tensile and compressive forces of the members the structure is said to be statically indeterminate. Such a structure has more than the minimum number of members necessary to maintain its rigidity under the impressed forces.

Hence, the structure is stable under these forces. The degree of statical indeterminacy is calculated by comparing the number of members and joints to the number of independent components of reaction, i.e. the number of components of the forces acting upon the frame or truss considered as a free body at equilibrium (e.g., TIMOSHENKO & YOUNG, 1962; AU, 1963). A zero or positive value indicates stability.

In the analysis of a truss the forces (loadings) are applied at the pivots, in order that the reactions or deflections of the bars themselves may be safely ignored. In the first approximation a frame analysis was used in part in the interests of precision and of locating where the bars might be expected to fail (Fig. 4). This analysis concerns only what are essentially dead loads, that is static, and static approximations of dynamic, situations.

SPACE FRAME ANALYSIS: STRESSES IN BITING

Stability of frame

With this information the degree of statical indeterminacy of a frame or truss may be determined (AU, 1963): this is done for both models for *Tyrannosaurus rex* in ADDENDUM I. For *T. rex* the frame is statically indeterminate to a positive degree, i.e. it has more members than needed to resist the forces. Hence the skull may be assumed to have been stable under the imposed forces, as expected. For the first approximation, the truss is not stable. However, when the approximations are dropped and transverse components of the muscular forces added, the truss is stable. These results would seem to indicate that in some sense the skull was not optimally constructed. In other words it had more members, more bony structure, than required to remain rigid, assuming the bone was non-deformable.

Reactions at maxilla and jaw joint

Following from this analysis, it is possible to estimate whether the reaction of the food on the maxillae or that of the jaws on the quadrates was the stronger. To do this, an analysis of the space frame as a free body was used (Fig. 4). A free body is one in mechanical equilibrium, that is, not being acted upon by external forces, and hence (from Newton's second law) either stationary or in a state of uniform motion. In such equilibrium the sum of all forces acting upon the body in any direction equals zero, as does the sum of all moments (forces multiplied by their perpendicular distance [the moment arm] from some given point of the body [often an axis of rotation], and hence spoken of as moments about that point). This principle alone is not sufficient for such an analysis, in addition some idea of the relative strengths of the muscles (and the reaction of the *M. pterygoideus anterior*) must be used. I have made the simplistic assumption that the magnitudes of the force vectors of the muscles (and the reaction) are equal (unlike TAYLOR [1992] who assumed two magnitudes, depending on the [reconstructed] mass of the muscle). From the details given in ADDENDUM II it seems that the force of resistance at the condyle was greater than that applied at the maxilla, given this assumption. Bearing in mind the simplistic and unrealistic nature of the assumption, this result may be of greater utility as a null model for future analyses than as an accurate assessment of the situation in usual feeding, but does suggest why the corpus quadrati is a relatively robust, reinforced structure.

The quadrate is nearly vertical in orientation, inclined slightly posteroventrally so the articular condyle lies slightly posterior to the squamosal articulation. The existence of an anteriorly-directed horizontal reaction at the condyle (h_B) depends largely on how closely the *M. pterygoideus anterior* reaction (h_{4A}) matches the horizontal component generated by the *M. pterygoideus anterior* (h_4). The horizontal components of the *M. adductor mandibulae externus* (h_2) and *M. adductor posterior* (h_3) are both small compared with h_4 and h_{4A} and will be neglected (they also operate in opposing directions and would hence probably nearly cancel). Judging from the model, h_{4a} is somewhat smaller than h_4 (were they equal the line of action of this muscle on the jaw would be vertical at its origin on the skull) and hence there is a positive h_B exerted upon the condyle. As this reaction is much smaller than the vertical reaction it seems plausible that the orientation of the quadrate does indeed reflect the vector sum of the reactions. It would seem that this is not necessarily so, the corpus quadrati could have been oriented in response to some other influence, and the reaction resisted by appropriate buttressing of the corpus. But this would presumably have been weaker than the situation obtaining. In fact the only substantial "buttress" is the lower temporal arch, that anteriorly reinforces the quadrate, the direction in which a buttress might be expected if the resistance force was directed as here proposed. Alternatively the quadrate could have been streptostylic and free to be moved to withstand resistance forces from several directions: this is consistent with the form of its dorsal articular surface (MOLNAR, 1991).

Similar inclination of the quadrate is seen in large theropod taxa (e.g., other tyrannosaurids, *Allosaurus* MARSH [1877], *Ceratosaurus* MARSH [1884], *Monolophosaurus* ZHAO & CURRIE [1993], *Sinraptor* CURRIE & ZHAO [1993], *Yangchuanosaurus* DONG, CHANG, LI & ZHOU [1978]) but not many smaller taxa (e.g., *Dromaeosaurus* MATTHEW & BROWN [1922], *Saurornithoides* OSBORN [1924], *Syntarsus* RAATH [1969], ornithomimosaurs), although oviraptorosaurs and *Avimimus* KURZANOV (1981) do show it.

Since it is shown in *Herrerasaurus* REIG (1963) (SERENO, 1995: photo on page 32) but not *Coelophysis* COPE (1889) or *Syntarsus* (COLBERT, 1989: fig. 40) it is not clear whether this is a plesiomorphic condition, especially as the large forms are not members of a monophyletic clade (HOLTZ, 1994; 1996). In some earlier forms (e.g., *Allosaurus* and *Ceratosaurus*) the slope is greater than in *T. rex*. If the quadrate orientation in these forms also reflects the direction of the reaction at the jaw joint, then the organization of the jaw adductors probably differed from that in *T. rex*.

Structure of space frame

In constructing his space frame representing the canine skull, BADOUX (1966a) used only triangular units. The space frame representing the *Tyrannosaurus* skull was constructed using quadrangles and other forms as well as triangles because I felt that using only triangles was an insufficiently accurate approximation. In several places, e.g. around the subtemporal fenestrae (Fig. 2B), or the supratemporal fenestrae (Fig. 2E), triangles could indeed have been used with little greater deviation from the actual structure. Only the set of four quadrangles around the orbit and infratemporal fenestrae (Fig. 2A) could not be replaced by triangular units without greatly deviating from the form of the skull, i.e. bars would have to be placed so as to pass through the orbit or a fenestra. Since fenestrae presumably cannot transmit forces, this would obscure the relationships of the fenestrae to force transmission within the skull. Hence while most of the *Tyrannosaurus* skull may be viewed as constructed so that the form would not have been distorted under such forces as were imposed (i.e., using triangular units), the temporal region might tend to have deformed, were it constructed of rodlike bars. It is, of course, not so constructed. These bars are broad in *Tyrannosaurus*, and hence the space frame approximation is not quite accurate. Interestingly, earlier forms, such as *Allosaurus*, *Ceratosaurus, Monolophosaurus, Sinraptor* and *Yangchuanosaurus*, had much thinner bars in the postorbital region. Hence it would seem that these bars in tyrannosaurs became more reinforced against structural deformation than in allosaurs and ceratosaurs.

Specific anatomical features related to biting stresses.

A portion of the *M. adductor mandibulae posterior* and possibly of the *M. pterygoideus posterior* may have attached to the nearly vertical plate formed by the pterygoid process of the quadrate and the quadrate process of the pterygoid. This plate attaches along its posterior edge to the main shaft of the quadrate, thus transferring applied forces to the quadrate member of the frame. The direction of the forces applied by these muscles was also nearly vertical, that is, nearly parallel to the surface of the plate. A force applied in this direction is less likely to deform the supporting structure, as the applied stress would be in the direction of the reinforcement, that is nearly co-planar with the pterygo-quadrate plate.

Similar considerations apply to the attachment of the adductors to the vertical supraoccipital crest. Both crest and plate are oriented so the surface of muscle attachment lies nearly parallel to the imposed forces, although the supraoccipital crest is considerably thicker than the pterygo-quadrate plate. These considerations may also apply to the infratemporal flange of the squamosal and quadratojugal to which part of the *M. adductor mandibulae externus* may have attached. In lateral view this is buttressed ventrally (in the direction of the imposed force) by the triangular form of the superior process of the quadratojugal, but sharply truncated dorsally. Deformation of the process would have been resisted by the narrow marginal bar along its anteroventral edge (clearly seen in MOLNAR, 1991: pl. 1, fig. 5).

SPACE FRAME ANALYSIS: STRESSES OF WEIGHT SUPPORT

Principles of the analysis

The skull may be considered a cantilever supported by the end of the cervical column. Using the same space frame approximation as previously, and introducing the effect of gravity and the supporting force applied by the epaxial musculature (Fig. 5), the stability of the frame may be examined. The weight will be considered to act at the center of gravity, which was determined from a two-dimensional projection of the skull to lie at about the anterior ends of the pterygoids, and will be considered to act at the transverse palatal bar. For simplicity the epaxial muscles will be assumed to act on the midline, about two-thirds of the way up the supraoccipital member. The most marked muscle and tendon scars on the posterior surface of the crest are just lateral to the midline at this region (cf. MOLNAR, 1991: pl. 7, fig. 1). All reactions would have been at the occipital condyle.

The statical indeterminacy for this condition may be easily determined to be positive as the variables m and j are unchanged from before, while $r = 17$ (the resistance of the prey, A, with components on each side of the skull, was removed, and the force of gravity, the epiaxial muscular supporting force and the two components at the occipital condyle, were added). As r is the only variable to change, and that being a increase of 2, the statical indeterminacy is

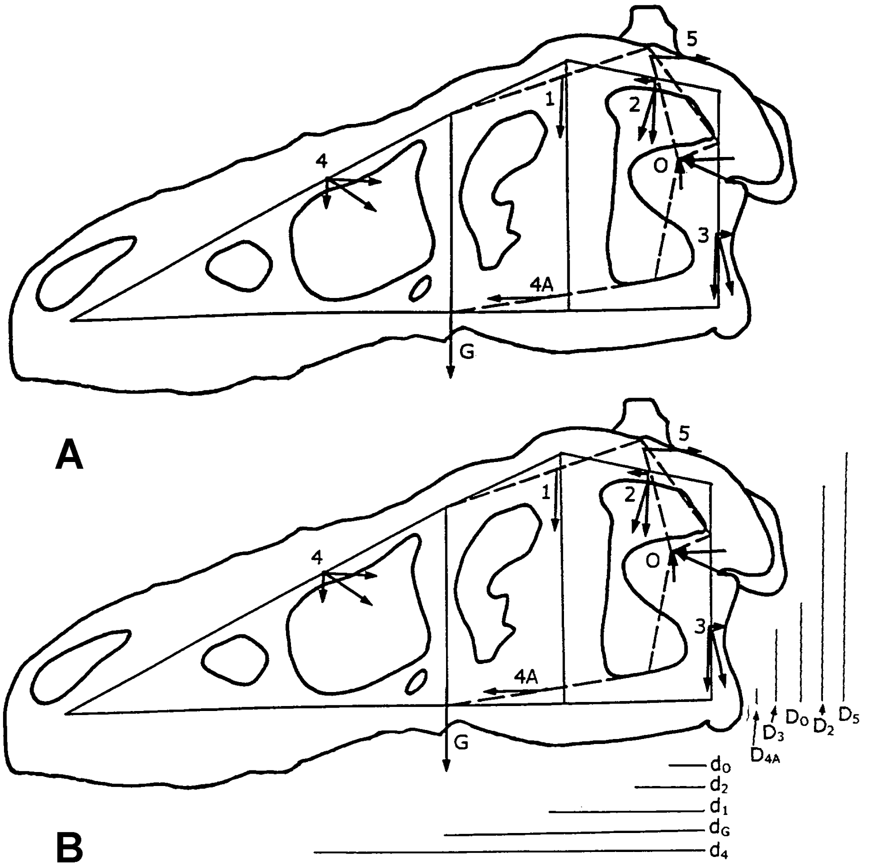

Fig. 5 - Loadings on the space frame used in the free body analyses of the structure under the force of gravity. **A** - Forces and reactions. **B** - Moments arms of the forces and reactions. Forces, reactions and moment arms as in Figure 4, with the addition of: 5 - force exerted by the cervico-occipital musculature; G - weight of skull; and O - reaction at the occipital condyle.

also increased by 2, to 87, still greater than zero. The frame is stable.

As the skull is a cantilever supported on the occipital condyle, all of the frame - hence all of the cranial skeleton - must be supported from the occipital face (and the broadly and firmly attached braincase). The details given in ADDENDUM III indicate that an anteriorly- (as well as an upwardly-) directed force was exerted upon the skull by the column, but probably of small magnitude. Hence the epaxial musculature must have exerted a force on the back of the skull greater than the weight of the head. If these muscles acted at an angle of less than 90° to the occipital face, then their moment arm was decreased and even more force must have been exerted to support the head. This presumably accounts for the large size of the muscle scars upon the posterior face of the supraoccipital crest and (together with the attachment of the *M. adductor mandibulae externus profundus)* for the existence of this crest.

Specific anatomical features related to weight support

The supraoccipital crest is oriented transversely to the direction of force of the epaxial musculature and so might tend to deform were it not strongly buttressed by the braincase, sagittal crest and *M. adductor mandibulae externus profundus,* which probably acted as a tensile reinforcement (and vice-versa when the adductor was acting). The weight of the jaw is borne principally by the braincase (via the *Mm. adductor mandibulae externus profundus* and *pseudotemporalis*), the nasal member (via the *M. pterygoideus anterior*) and the quadrate member (via the *M. pterygoideus posterior* and *M. adductor mandibulae posterior)* so that the preorbital and postorbital bars bore only the weight of themselves, the posterior palate, and adjacent soft structures.

The posterodorsal "corner" of the skull extends posteriorly behind the level of the occipital condyle in *T. rex* and other tyrannosaurids, and at least *Allosaurus, Monolophosaurus* and *Sinraptor* among the earlier forms. This "extension", in addition to increasing the area available for attachment of the *M. adductor mandibulae externus superficialis et medialis* and the *M. adductor mandibulae externus profundus,* also reduces the moment arms of these muscles with respect to the occipital condyle. This in turn reduced the torques applied by them to the skull by placing their lines of action closer to the occipital condyle, than if they were more anteriorly placed. Since these muscles attached to the jaws which were also supported (via the suspensorium) by the occipital condyle, presumably their torques would have been cancelled by that generated by the reaction at the quadrate condyles. Although the most of the adductors would have exerted a dorsally-directed force on the jaws when closed, the *M. pterygoideus anterior* was both large and strongly inclined anteriorly (cf. HORNER & LESSEM, 1993: 105 or FARLOW & MOLNAR, 1995: 38). This presumably produced the anteriorly-directed reaction at the jaw joint responsible for the cancelling this torque. Considering the skull and jaws together as a free body at equilibrium, of course, these torques could not have generated rotation as they were internal to the structure.

SPACE FRAME ANALYSIS: SIMULTANEOUS WEIGHT SUPPORT AND BITING

The idealized space frame has been shown to be stable under biting and gravitational stresses. Adding both of these together does not change the values of m and j, but r is now 22 (adding gravity and two components at the occipital condyle), so that $6(m - j) + r = 88 > O$, and so the frame is stable under the combined forces, as we would expect.

In actual biting and feeding, the forces exerted by the muscles on the skull would have varied in magnitude and direction, and there may have been added weight as portions of the prey were lifted. This weight increase would probably have been relatively small and of short duration and hence will be ignored. Most of the adductor forces would not have changed greatly in direction nor in magnitude except when the animal stopped feeding and had only to support the jaws. Then the magnitudes would have decreased. As the magnitudes do not explicitly enter into the analysis, this would not affect the results.

While feeding, mammalian carnivores and lizards (but apparently not oras - BUSBEY, 1995) often violently shake their prey. Such behavior may have been used by *T. rex*. This could have been done in several ways, by side-to-side movements of the head, or rotations of the head about a longitudinal axis (or, of course, some combination of these). The latter behavior would result in the application of torques to the skull. This could be analysed in terms of the space frame as the unilateral application of resistance to the maxillae and, as the prey was held by the jaws, application of forces to the contralateral jaws and hence to the contralateral side of the skull via the adductors and suspensorium (Fig. 6). Presumably the forces on the skull exerted by the ipsilateral adductors, and the resistance exerted on the contralateral maxilla are very much smaller (otherwise, of course, no torque would be exerted) and hence may be neglected. The space frame will be stable under these forces, of course, as may be seen from considering the statical indeterminacy. Since the number of forces and reactions has been reduced to 11 (Fig. 6) and nothing else has been

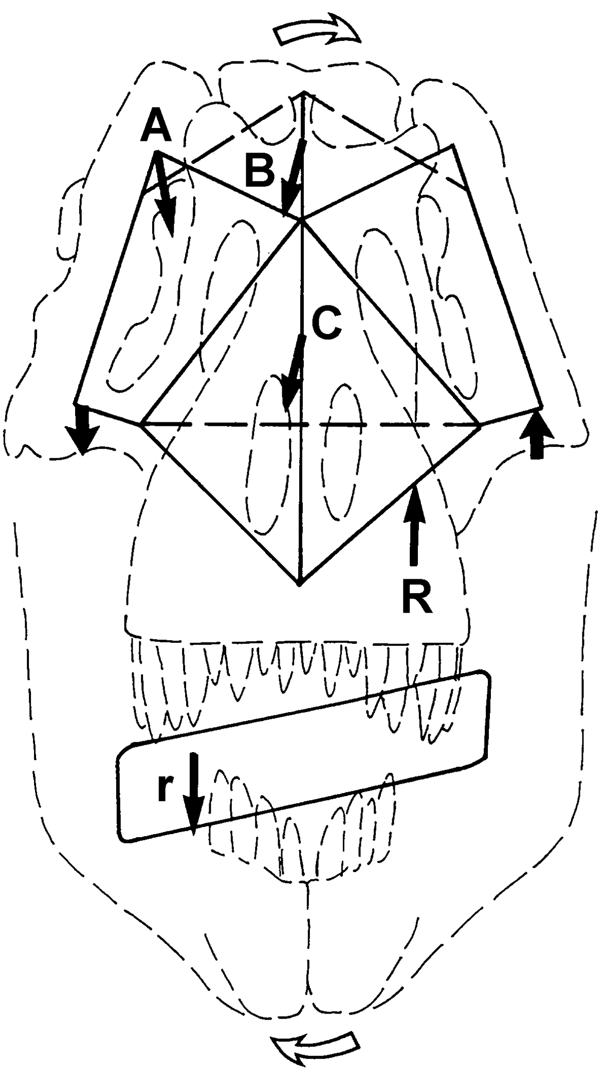

Fig. 6 - Forces and reactions on the jaws (dashed) and space frame (solid lines) for the skull (dashed) in rolling the head. Ideally, the number of forces (A, B and C) and reactions (R) exerted on the frame is reduced by half while nothing else is changed (r, reaction on the jaws). Open arrows indicate direction of motion of the head. Unlabelled arrows indicate forces and reactions at the craniomandibular joints from the inertia of the jaws: these (and r) do not enter into the analysis discussed in the text.

changed, the degree of statical indeterminacy for a rigid frame is 77, hence the frame is stable. Although a reassuring result, violent shaking of the head undoubtedly generated strong transient loadings which are not treated here, hence this result should not be used to infer that such shaking did occur.

FACTORS MILITATING AGAINST A RODLIKE STRUCTURE OF THE SKULL

Some theropod skulls approximate a structure of bars reasonably well - e.g. *Compsognathus longipes* WAGNER (1861)(OSTROM, 1978), *Ornitholestes hermanni* OSBORN (1903)(PAUL, 1988) and *Sinraptor dongi* (CURRIE & ZHAO, 1993) - but the skull of *T. rex* does not. This seems to be due, in part, to certain requirements for a functioning skull. In order to afford attachment sites for muscles, broad areas of bone must be provided (save for tendinous attachments) bars or struts often will not do. To support the central nervous structures a boxlike structure is needed, again bars are not sufficient. Hence, the skull must be a compromise between these (and probably other) factors. The brain and related structures are small with respect to the skull as a whole, and hence housed in a braincase which is small relative to the skull, and relative to the condition in mammals and birds. In addition, the braincase, particularly the dorsal portion, provides areas for attachment of some jaw adductors. The size of the jaw adductors implies a certain minimum area for their fleshy attachment, and a braincase large enough to afford this minimum area would seem to be approximately large enough to house the brain. This is not to imply that the size of the braincase is necessarily dictated by the size of the adductors or vice versa, but simply to point out the relationship of their sizes in large theropods.

Possibly the forces exerted on the skull would have been strong enough to fracture or deform the bones had the skull been constructed of the minimum number of simple bony bars arranged in the stable configuration. On the other hand, the skull did not function solely in feeding and the other factors (constraints) involved in skull design may well have necessitated departure from a design that resisted muscular and bite-reaction forces with minimal bony structure. Although the second possibility seems certain to have obtained, the first cannot be assessed without some indication of the relative strengths of the jaw adductors. However, *Monolophosaurus jiangi* ZHAO & CURRIE (1993) and *Yangchuanosaurus shangyouensis* DONG, CHANG, LI & ZHOU (1978) (DONG, ZHOU & ZHANG, 1983), have skulls that more closely approximate a Warren truss, which is composed entirely of triangular units, and hence could be approximated by a space truss (or frame) with fewer members. These forms differ from *T. rex* in being smaller and having relatively smaller adductor chambers. This suggests the hypothesis that the enlarged adductors of *T. rex* led to the strengthening of its skull.

The weight of a large skull is expected to be a factor in the deviation from a rod-like construction. Two of the taxa mentioned above are small theropods, and all are smaller than *T. rex*. The simple argument based on scaling indicates that weight should play a role. It is well known that weight increases as the cube of the linear dimension and muscle (and bone) strength only as the square. The resistance afforded by the prey to biting should not scale, as it depends on molecular and tissue structure and so would be, at least approximately, the same for small and large prey. Therefore with increased size, assuming a concomitant increase in cross-sectional area and hence strength of the muscles and bones, biting should be easier for a large predator, such as *Tyrannosaurus*. So biting stresses should not result in any relative increase in the size of the bony elements (other things being equal): increases in the size of (weight-bearing) bony elements should be due to the increased size and weight of the skull.

Thus the skull of *T. rex* probably lacks the rod-like construction of that of (some) smaller theropods because of i) the necessity for affording more extensive muscle attachment, and ii) supporting the relatively greater weight of a larger skull. These two factors probably interacted as the skull weighed more not only because of its larger size, but also because the adductors increased in size both absolutely as the head increased in size, and relatively as the adductor chambers expanded relative to the rest of the head.

Sensory structures were accommodated in regions that seem not to have been subject to any great stresses, either from biting or weight-support. The eyes were housed dorsally between the pre- and post-orbital bars (MOLNAR, 1991), neither of which was subject to great stress. The nasal capsule was anteriorly placed, under the nasals and between the bodies of the maxillae, where it would have been protected by these structures. The external ear was behind the skull in the otic notch and hence is not greatly involved in these design considerations of the skull.

TRAJECTORY ANALYSIS

Engineers may represent the compressive and tensile stresses of a beam by drawing trajectories. The tangents to these lines at each point represent the directions of the principle stresses at that point. The set of curves representing compressive stress is orthogonal to the set representing tensile stress. These curves may be determined mathematically (as explained in many structural mechanics texts, e.g. TIMOSHENKO & YOUNG, 1962), or they may be determined empirically (e.g. EVANS, 1957). Here neither was done, the lines were drawn by inspection and then certain implications of their hypothesized positions were tested.

In a cantilever, assuming its construction of homogeneous material of uniform strength, the trajectories run as two sets of roughly parabolic curves (Fig. 7A). The tensile trajectories extend along the top, curving downward at the free end, and the compressive trajectories along the bottom to curve upward at the free end. At some region between the upper and lower surfaces is a plane which will not change in length even if the beam is deformed under bending stress. This plane is the neutral surface (broken line in Fig. 7A). Further discussion of trajectorial theory may be found in structural mechanics texts, e.g. TIMOSHENKO & YOUNG (1962).

The application of trajectorial theory to skeletal structures is not entirely straightforward. The assumption of homogeneous material of uniform strength is not met as often as in engineering structures. Although the trajectories of a curved beam under vertical loading may reasonably well match the pattern of trabeculae in the head of a femur (cf. THOMASON, 1995: fig. 15.3) trabecular bone is not homogeneous in structure and so the theory cannot be applied to it. The theory may be used for midshaft cortical bone (THOMASON, 1995), and fractures in the cranial bones of LACM 23844 suggest that much or most of the cranial bone in *T. rex* was not trabecular, but more or less uniform in structure, at least to the unaided eye. Applying the theory to the skull as a whole, however, is perhaps intrepid. Although the skull of *T. rex* may (or may not) have been composed of material (bone) of more or less uniform strength and more or less uniform structure, the skull as a whole certainly was not a uniform, homogeneous structure. Therefore the trajectory analysis as done here can be only a first-order approximation to the situation in life. Nonetheless, unless the laws of physics were suspended, one may be certain that the skull was subject to tensile and compressive stresses and probably did have a neutral plane.

The trajectories were drawn on a picture of the skull by direct analogy with those of a simple cantilever beam, taking into account the construction of the skull. Since the trajectories must lie in the bone, they can only project through continuous struts or bars of bone (although these may consist of several elements in firm contact). If such continuous structures do not exist in the skull in regions where they would be expected from this method of analysis, then either this method is inapplicable or the tension or compression was transmitted through other tissues, not preserved.

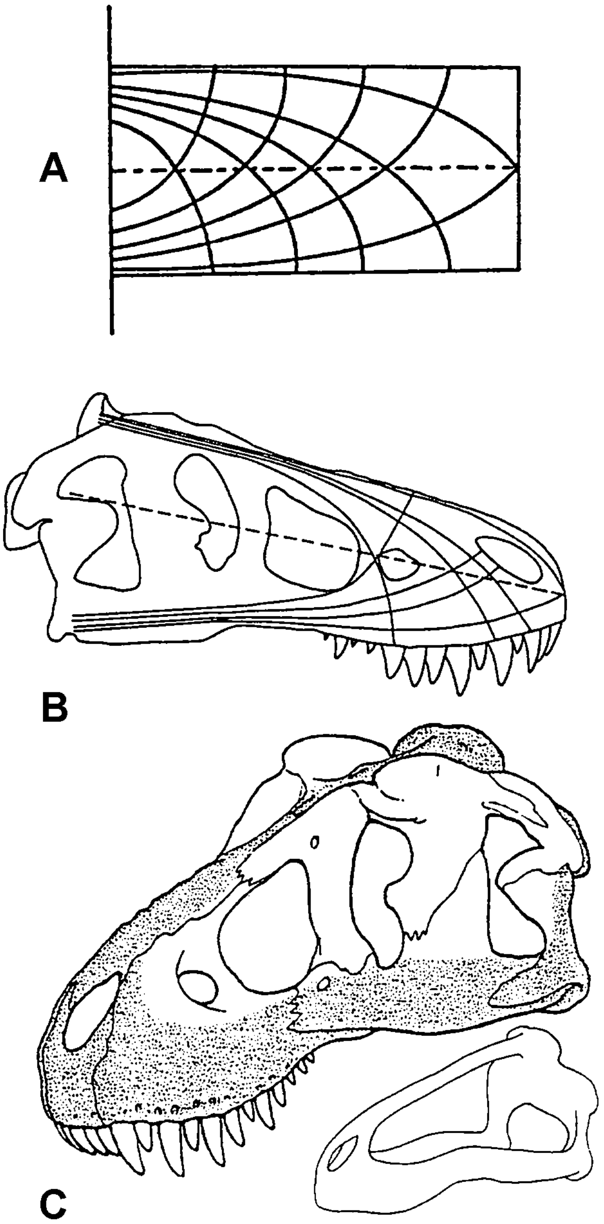

Fig. 7 - **A** - In a cantilever beam the stress trajectories are represented by two sets of roughly parabolic curves, grounded in the base. The tensile trajectories are above and the compressive below. **B** - Proposed approximation to the forms of the trajectories in the skull of *Tyrannosaurus rex* OSBORN (1905). **C** - Regions of the skull that would resist the tensile and compressive stresses, shown on the skull (stipple), and abstracted from the rest of the skull structure in the small image.

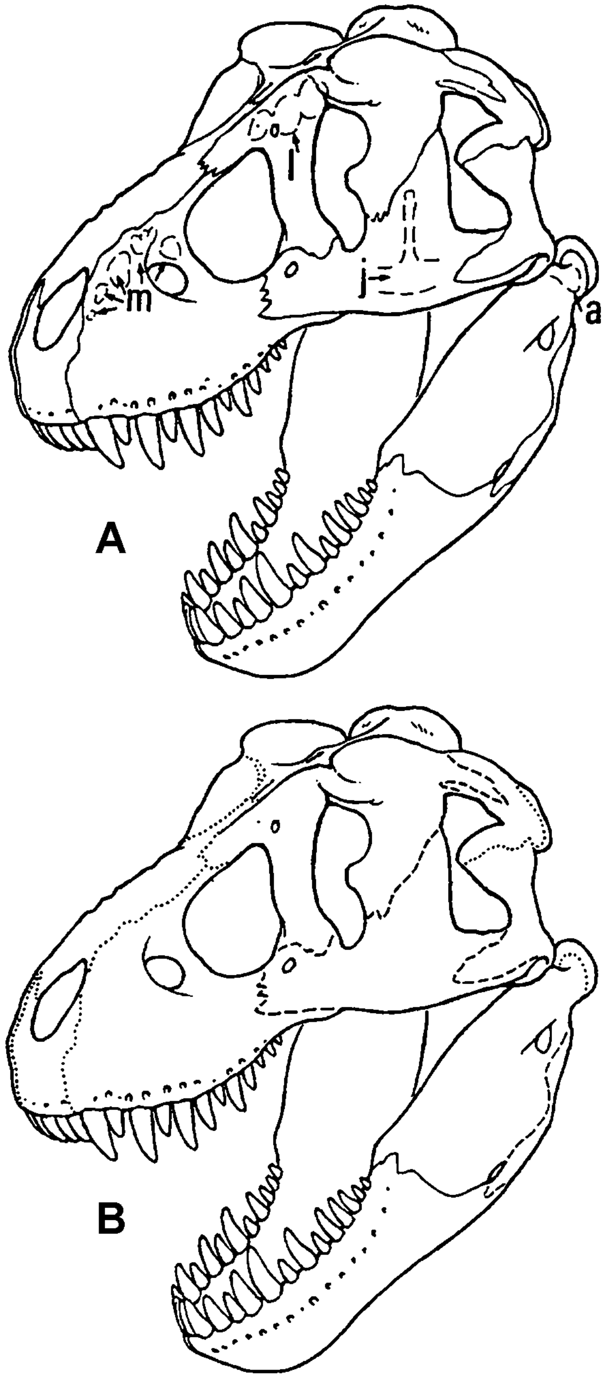

Fig. 8 - **A** - Positions of the sinuses in the skull of *Tyrannosaurus rex* OSBORN (1905), omitting those in the braincase and occiput, but showing that in the articular. a, Articular sinus; j, jugal sinus; l, lachrymal sinus; and m,maxillary sinuses. **B** - Positions of butt (dotted) and scarf (dashed) joints in the facial skeleton of *T. rex.* Although a scarf joint, the nasal-premaxillary joint is shown as a butt joint for the reasons given in the text.

Examining the skull in terms of tensile and compressive trajectories suggests that during “normal” conditions (i.e. subject to gravitational stress, but not those of feeding) the tensile stresses would have projected through the anterior bodies of the maxillae and along the nasals, frontals and parietals to the supraoccipital crest (Fig. 7B). The compressive stresses would have extended through the anterior bodies of the maxillae and posteriorly through the ventral portions of the maxillae and the jugals. The skull differs from the cantilever beam model in that the compressive trajectories are divided into two (symmetrical) groups, one on each side of the skull and separated by the palate, whereas the beam, of uniform structure, has a single set. In feeding, the positions of the tensile and compressive stresses would have been reversed, i.e. the compressive stresses would project through the maxillae, nasals and braincase elements and the tensile through the ventral maxillary regions and jugals, some of the palatal elements (the vomer) appearing too light and delicate to resist great stress. Reassuringly the skull does indeed have continuous bars of bone in the regions expected to be occupied by the tensile and compressive trajectories. The lateral fenestrae (infratemporal and antorbital) and orbits lie in the vicinity of the neutral surface (dashed line in Fig. 7B).

The nasals would have acted as a compressional member transmitting biting stresses to the braincase-occipital structure, and are rather heavily built among the theropods in general. They are strongly arched transversely and fused along the midline in tyrannosaurids. That portion of the maxilla over the anterior tooth row, where the greatest stresses from biting might be expected, is a solid plate and not the bar-like construction shown by the more posterior portions of the skull. The quadrate would have also acted as a compressional member, transmitting whatever stresses were generated by the reaction at the jaw joint to the squamosal and paroccipital process and thence to the braincase. The preorbital and postorbital bars do not seem likely, from these considerations, to have been subjected to sizeable stresses as they were removed from the regions to which biting stresses were applied (Fig. 7C).

However, the positions of the cranial openings obviously influenced the decisions made in drawing the trajectories. What evidence not used in placing the trajectories can be used to test their placement? We would expect that the stress-bearing elements would be solid, and not contain extensive sinuses that would weaken them. Most of the (known) sinuses (e.g., the lachrymal, quadrate, exoccipital, etc.) lie out of the regions of these trajectories (Fig. 8A), with the possible exception of the jugal chambers, which are of undetermined but presumably limited, extent. The maxillary chambers are laterally walled by thick bone and presumably would not weaken the maxillae.

We would also expect that the joints in the compressive member would be such that the bones abutted each other firmly, i.e. butt joints. Whereas those in other regions, particularly between elements in the region of the tensile trajectories, might be overlapping (or scarf) joints. (These kinds of joints are figured and described by HILDEBRAND, 1974). But if the trajectories were reversed in feeding from their pattern in support, which are to be taken as compressive and which tensile? Judging from the results of ERICKSON *et al.* (1996) the biting forces would seem to have been the stronger, so here the dorsal trajectories will be taken to be compressive and the ventral tensile.

Butt joints are found at the maxillo-nasal and naso-frontal contacts (Fig. 8B), the main joints in the proposed region of compressive stress (MOLNAR, 1991). The joints are not simple abutments, but have one element abutted against the other often with interlocking pegs and sockets (MOLNAR, 1991). The distribution of this kind of joint in the facial skeleton supports the trajectorial analysis. The region of the tensile trajectories shows overlapping joints, showing little or no abutment, at the maxillo-jugal, jugolachrymal, jugo-postorbital and jugo-quadratojugal contacts (MOLNAR, 1991).

If the distribution of these joints represents an adaptation to resisting strong biting stresses, ancestral or other taxa with weaker bites may show different patterns of joint architecture. *Baryonyx walkeri* CHARIG & MILNER (1986), for example, is suggested to have been piscivorous and therefore may be expected to have overlapping joints in the region limited to butt joints in *T. rex*. On the other hand, if the pattern is an inherited feature, a constraint, then it may be expected to be the same or very similar in that form.

FORCES INTERNAL TO THE SKULL

Internal forces in the skull may be analyzed by dividing it into two segments (cf. TAYLOR, 1992, who, however, used three segments). The anterior, snout segment would have borne the resistance forces from the bite point, while the posterior segment bore the chief part of the adductor forces and the reaction at the jaw joint (Fig. 9). The snout was subject to a dorsally-directed reaction (F) at the bite point, the posteroventrally-directed force from the *M. pterygoideus anterior* (P) and a ventrally-directed weight force (W) at the center of gravity. The compressive reaction (C) would have passed through the (snout portion of the) nasal-frontal-parietal member and the tensile reaction (T) through the lower marginal elements and palate. Finally, a vertical shearing force (S) would tend to shear the snout dorsally on the posterior section. If the bite point was on the maxilla, the forces would have been transmitted dorsally through the robust anterior body of the maxilla, to the nasals via the naso-maxillary butt joint. Tensile forces would have been resisted by the medially and laterally overlapping jugo-maxillary joint and the scarf joint between the palatine and pterygoid. If the bite point was on the premaxilla, there would have been the possibility of some small, transient motion of the premaxillae on the maxillae (MOLNAR, 1991), after which the force would have been transmitted via the nasal bar. The premaxillo-nasal joint is a scarf joint, but when both premaxillae are considered together the joint has the form of a wedge inserted between the anterior processes of the nasals. As the nasals were usually fused (MOLNAR, 1991), this would have acted as a butt joint, limiting the possible motion of the premaxillae and transmitting the forces to the nasals.

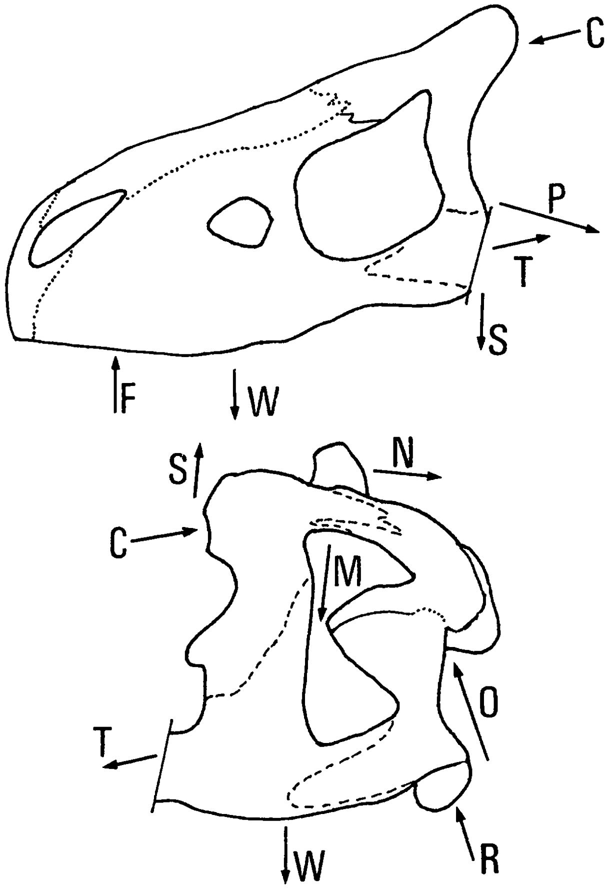

Fig. 9 - The skull of *Tyrannosaurus rex* OSBORN (1905) given as two free bodies, to analyze the internal forces and reactions. Butt joints dotted and scarf joints dashed. Abbreviations given in text.

The posterior part of the skull would have been subject to a largely dorsally-directed supporting force (O) at the occipital condyle and reaction forces (R) at the craniomandibular joints. The largely ventrally-directed weight force (W) and adductor forces (M) acting on the braincase and quadrate region and the largely posteriorly-directed muscular force (N) from the epaxial cervical musculature were also present. Tensile (T) and compressive (C) reactions and a shearing force (S) complemented those acting on the snout segment. The tensile reaction was resisted by the overlapping quadrate-quadratojugal and pterygo-quadrate joints while the compressive reaction was passed along to the cervical column through the fused joints of the braincase elements. The quadrate and quadratojugal were closely joined (MOLNAR, 1991) and formed a unit that would have resisted the oppositely directed reaction exerted at the jaw joint and muscular forces exerted on the braincase and upper temporal arch. This unit has a U-shaped section in the horizontal plane that would have resisted buckling under the resulting compressive stress.

STRUCTURAL ASPECTS OF THE MANDIBLE

GENERAL STRUCTURE

For purposes of description, the lower jaw of *Tyrannosaurus rex* may be conveniently divided into two parts: the anterior, tooth-bearing portion, consisting chiefly of the dentary, and the posterior portion having afforded the muscle attachments and articulation with the skull, and comprising the postdentary elements.

The anterior, dentigerous part of the dentary may be regarded as a solid bar, oval in cross-section. The major axis of this oval is vertical. The posterior portion of the mandible may be visualized as a "hoop" of bars supporting a thin plate of bone (composed of parts of the surangular and dentary) across them laterally, much as an embroidery hoop supports cloth (Fig. 10A-B) (but recognizing that the splenial also covered part of the "hoop" medially). The whole is oriented with the plate vertical. The upper portion of the "hoop" is formed by the dorsal, horizontal shelf of the surangular posteriorly, and the dorsoposterior bar of the dentary anteriorly. The lower portion is formed, sequentially from back to front, by the prearticular, angular and ventroposterior bar of the dentary. This portion, particularly the thin sheet of bone that forms the major portion of the surangular, afforded the chief area for attachment of the adductors onto the mandible.

STATIC ANALYSIS

Free body and space frame analyses

The mandibles, considered separately as free bodies, were subject to two classes of forces. Vertical forces were imposed by the adductors, pulling dorsally; and the resistance of the food, weight and the reactions at the jaw joints, both directed ventrally (Fig. 10C). Medially-directed forces were also imposed by the adductors, which had a weak medial component to their pull. So the mandibles may be considered as having had to resist three kinds of deformations: those resulting from the vertical forces alone, those resulting from the medial forces alone, and those resulting from both together, i.e. from im-

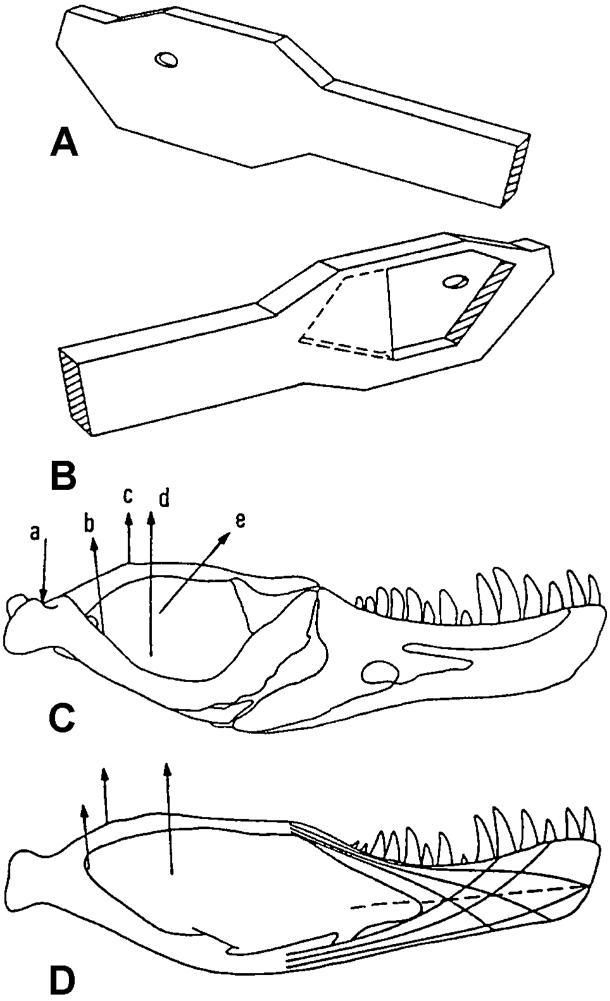

Fig. 10 - **A** - Block approximation to the right mandible of *Tyrannosaurus rex* OSBORN (1905), in lateral view. **B** -The same in medial view, showing the hoop-like structure of the posterior portion. **C** - Vertical forces were imposed upon the mandible, considered as a free-body, by the reaction at the jaw joint (a) and adductors (b-e). **D** - Proposed approximation to the forms of the trajectories in the mandible of *T. rex*. Lines of action of some of the adductors are shown in the posterior part of the mandible, which is considered as part of the base, so only the anterior portion may be considered as a cantilever. The neutral plane is dashed.

posed torques along the long axis of the mandible. These three classes of deformations will be treated with the assumption that the jaw was a rigid member, which is not quite accurate in view of the probable existence of an intramandibular joint, but sufficient for a first approximation.

BADOUX (1966b) presented a static mechanical analysis of the jaws of various mammals. He considered the ramus as a hollow, roughly rectangular shaft, and concluded that this was an example of maximum-minimum construction, as the rectangular bar was well-suited to resist imposed torsion, while its hollow condition conserved bone. Although not disputing these observations, one may perhaps better consider the mandibular ramus as being solid for there is no central chamber running along it in mammals or *T. rex*. The alveoli are normally occupied by teeth (roots), and the interalveolar volumes are occupied by the bony partitions between the alveoli, so it may be useful to consider it as a structure composed of a composite material (bone and dentine). The anterior part of the mandible of *T. rex* will be treated as if solid, which to a large extent it is.

The mandibular ramus of *T. rex* is oval in cross-section, the oval being oriented vertically with the widest portion toward the ventral border and with a longitudinal bar (the lingual bar) along the medial surface just above the middle (Fig. 11). The ramus may ideally be considered rectangular; a rectangular bar subjected to torque develops the greatest stress at the middles of the long (here vertical) sides, the region where the lingual bar is developed in *T. rex* (and some other theropods). This result is derived in many elementary structural engineering texts (e.g. MURPHY, 1946; CERNICA, 1966). The result is unchanged if the cross-section is considered an ellipse rather than a rectangle. For a vertically oriented ellipse, the major axis is vertical and thus the minor axis is horizontal. The stress, S_l, at the ends of the minor axis is,

$$S_l = (2T)/(\ ab^2)$$

where T is the imposed torque, a the major axis and b the minor axis. The derivation of this expression may be found in MURPHY (1946). The effect of the lingual bar is to increase the value of the minor axis, b. As this quantity (b) is represented in the expression by the reciprocal of the square, an increase in b decreases S_l, if the torque (T) is constant. So the lingual bar may be considered, at least in part, to resist strain resulting from torsion on the mandible. If so, one might expect more strongly developed lingual bars in forms with shallow rami, e.g. *Majungasaurus* LAVOCAT (1955). In fact a strongly developed bar seems to be present in *Majungasaurus crenatissimus* (DEPÉRET, 1896) as seen in LAVOCAT (1955: fig. 1D).

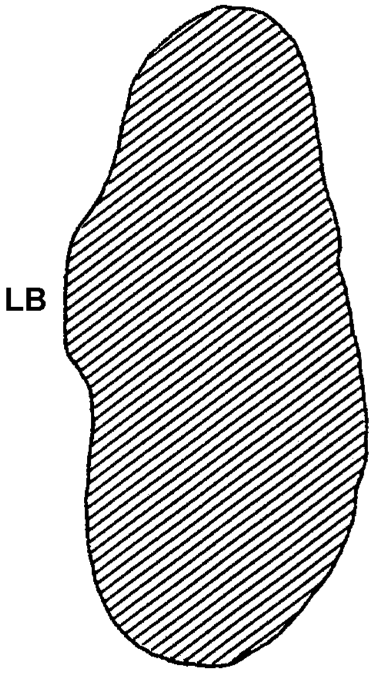

Fig. 11 - Cross-section of the left dentary ramus of *Tyrannosaurus rex* OSBORN (1905) (LACM 23844). Medial is to the left, LB indicates the lingual bar.

Considering the dentary as a cantilever, supported posteriorly by the adductors, vertical forces were applied through the teeth onto the ramus of the dentary. As shown in ADDENDUM IV, when the ramus is deep (in a vertical plane) it better resists these imposed stresses than if it were shallow.

The medially-directed forces exerted upon the mandibles cancelled one another if the mandibles are considered together, as the medially-directed force upon the right mandible is presumably equal, or approximately so, to that exerted upon the left mandible and oppositely directed. If each mandible is considered independently, the medially-directed forces are resisted by contact of the mandible with its opposite at the symphysis, and by the structure of the craniomandibular articulation (MOLNAR, 1991: 163). The ridge-and-groove structure of this articulation would have prevented any mediolateral motions here other than those associated with the opening and closing of the jaws.

Assuming that the jaws were rigid structures, however, may be an insufficient approximation in light of evidence for an intramandibular joint. Since this evidence remains unpublished, this aspect will not be treated here.

The forces of reaction at the jaw joint (and also those lateral forces imposed during the opening and closing of the jaws that resulted from the helical form of the articulation) were resisted by the articular. The articular has roughly the form of a tetrahedron and so may be represented by a tetrahedral space frame or truss (Fig. 12, 13). The tetrahedral form makes the frame and truss approximations equivalent because, since it consists entirely of triangular units, no rotation at the pivoted joints of the truss is possible. This structure may be considered as subject to three imposed forces: its weight, a reaction from the quadrate and a force from the adductors (transmitted by the other mandibular elements) and depressor together acting at all four of the joints (Fig. 13B). The weight of the articular would have been relatively small, in view of the large sinus, but possibly some of the weight of the more anterior portion of the mandible was also borne by the articular. Thus the number of components of reaction, r, is 6 (the two components acting at the anterior joint are co-linear and so are added); the number of joints, j, is 4; and the number of members, m, is 6. So the degree of statical indeterminacy is, $6(m - j) + r = 18 > 0$ and so the frame is, of course, stable under the imposed forces. The statical indeterminacy for the truss is 0, also stable. During opening or closing, when the articular was subject to lateral or medial force from the form of the articular surface, r would increase to 8, and the statical indeterminacies to 20 and 2 respectively. The tetrahedron is composed entirely of triangular elements and so it will in any case resist deformation. As the imposed stresses would have been resisted by the bars of the space truss, which were formed by the edges of the actual articular, material in the central region of the element would have played no role in resisting these imposed forces. And, as mentioned above, the articular is hollow, with a large central sinus chamber (MOLNAR, 1991). Although not an exact match, the form of the articular is the closest approach of any cranial structure to a model used in this analysis. The greatest departure from a tetahedron is that the posterior face is approximately semi-circular, rather than triangular. This match suggests that for the articular this analysis more completely captures the essential features of the design than for other cranial structures, which were also subject to the sometimes conflicting influences previously discussed.

Trajectory analysis

Like the skull, the mandible may be compared to a cantilever beam in terms of placement of tensile and compressive trajectories. Also like the skull, the bone of the mandible is not uniform in structure throughout so the comparison is only approximate. The portion behind the anterior margin of the Meckelian fossa, where the adductors attached, will be considered as the supporting base of the cantilever. So, unlike the skull, only part of the mandible can be reasonably analyzed as a cantilever. Also unlike the skull, the pattern of tensile and compressive trajec-

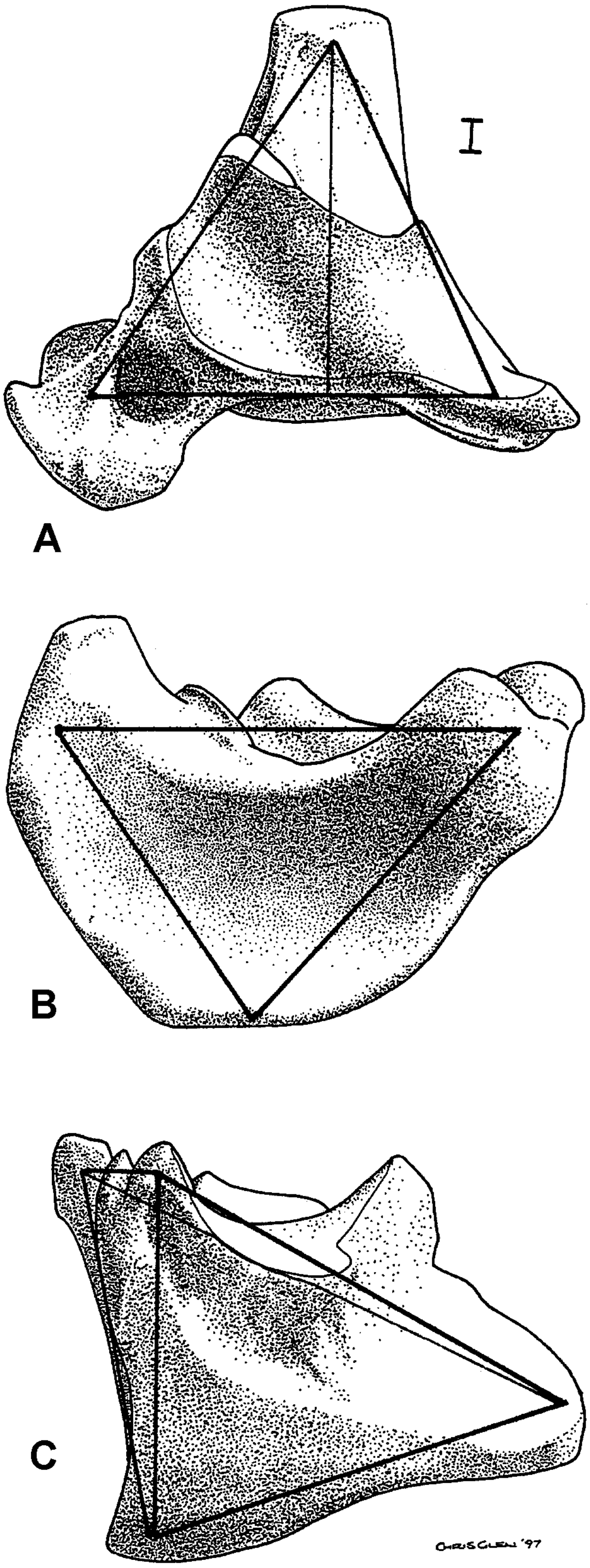

Fig. 12 - Proposed space frame approximation to the articular. **A** - Dorsal view. **B** - Posterior view. **C** - Medial view. Scale 1 cm.

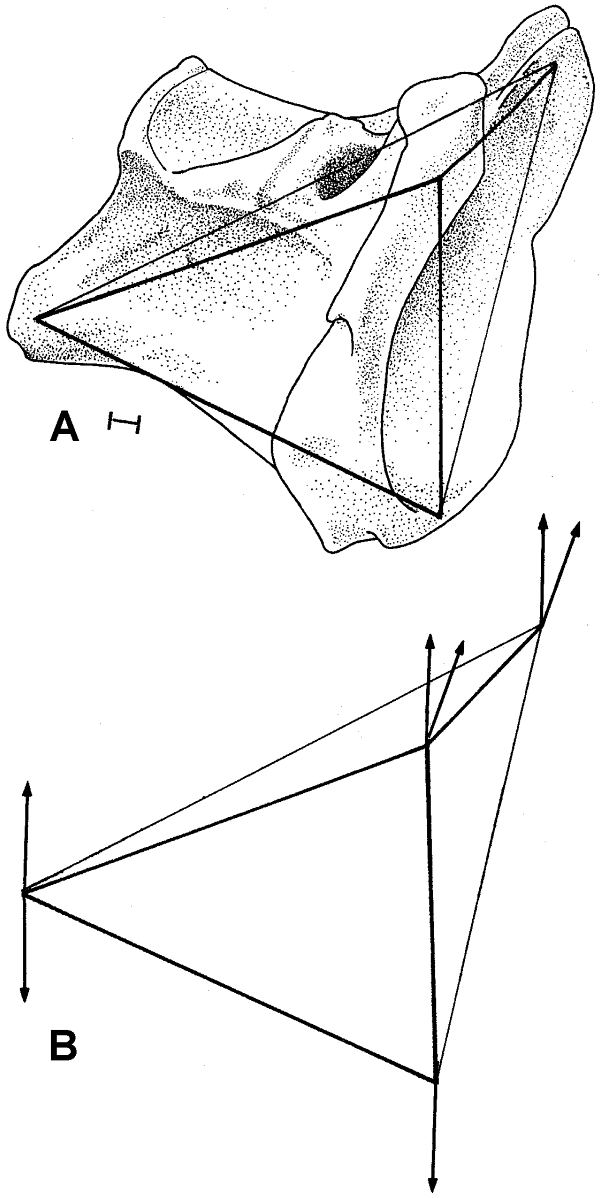

Fig. 13 - Proposed space frame approximation to the articular. **A** - Oblique view from lateral, behind and above. Scale 1 cm. **B** - Loadings on the frame used to calculate its degree of statical indeterminacy. At the front (left) the dorsally-directed load is from the adductors (exerted directly on the articular and via the more anterior mandibular elements) and the ventrally-directed load from the weight of the more anterior mandibular elements and part of that of the articular. The remainder of the weight of the articular is represented at the apex at the ventral rim of the posterior face. The upwardly-directed loads on the posterior face are from the joint capsule and the inclined loads from the *M. depressor mandibulae*. The loads are drawn as equal in ignorance of their relative strengths: almost certainly they were not equal.

tories would not have been different in weight support and biting. In both cases the tensile trajectories would occupy the dorsal and the compressive trajectories the ventral part of the mandible. The dentary remains approximately uniform in cross-section back to about the level of the tenth tooth. Posterior to this the mandible “splits” into dorsal and ventral marginal bars as previously described (see Fig. 10B and Molnar, 1991). These bars are joined by a thin sheet of the dentary laterally and by the thin splenial medially. These thin sheets of bone occupy the region near the neutral surface while the bars are marginal (dashed line in Fig. 10D), where the trajectories would be concentrated. To a first approximation (Fig. 10D) the tensile trajectories project back into the dorsal bar and the compressive trajectories extend into the ventral one. So the anterior part of the cantilever, the tooth-bearing ramus of the dentary, is analogous to a deep cantilever beam and the posterior portion shows a maximum-minimum construction with the dense bone concentrated in the regions of the greatest compressive and tensile stresses and the adductors attaching in the region of the neutral surface.

Taylor (1992) presented an analysis of the mandible of *Rhomaleosaurus zetlandicus* Phillips (in Anon.) in terms of bending moment and shear stress during biting. His analysis is essentially that of a double cantilever subject to three vertical forces applied at different positions. If the weight of the mandible is ignored, his analysis is directly applicable to *T. rex* as well. Taylor showed that the vertical bending moment gradually increases from the point of application of the bite force posteriorly to the region of adductor attachment. From there it decreases posteriorly to the point of application of the reaction force at the jaw joint. A difference between *Rhomaleosaurus* Seeley (1874) and *Tyrannosaurus* is that in the former that ratio of the length of the mandible (Taylor’s *b*) to the length of that portion in front of the muscle attachment (the cantilever part, Taylor’s *a*) is about 4:3, but in the latter it is about 3:2. This difference follows from the relatively more anterior portion of the muscular attachment in *Tyrannosaurus*, probably to support the weight of the mandible, negligible for a marine animal but not for a land-dwelling one.

Assuming a rectangular cross-section of the mandible, resistance to bending is proportional to the second moment of area, I, which in turn is proportional to the height (h) and width (w):

$$I = (h^3w)/6$$

From this equation, height is seen to be of particular importance in determining resistance to bending. The dentary of *T. rex*, although approximately oval in section as mentioned above, is not greatly different from rectangular. The form of the dentary, which maintains equal depth over its anterior half, but rapidly deepens posteriorly to about twice that depth thereby increasing resistance to bending by about eight times, is consistent with providing sufficient depth to counter the increasing bending moment.

TOOTH FORM AND BITE

TOOTH FORM

The existence of different tooth forms in theropods was first treated by STROMER (1934), who distinguished premaxillary from maxillary tooth forms in *Tyrannosaurus*. MADSEN (1976) was probably the first to distinguish different maxillary tooth forms, in *Allosaurus fragilis* MARSH (1877). However, in *T. rex* at least three tooth forms may be distinguished. These forms are distinct, but intergrade. Premaxillary teeth are D-shaped in cross-section, with both rows of serrations along the posterior face. One row lies along the posterolabial corner, and the other along the posterolingual. Hence these teeth are presumably not cutting or shearing teeth. They are oriented in the premaxilla with the rounded end anterior and the flattened end posterior. The “flat” posterior surface is not actually a plane surface but is slightly convex posteriorly. It is, however, noticeably flatter (has a much greater radius of curvature) than the anterior “face” of the tooth. The crowns of premaxillary teeth are, in general, about two-thirds to three-fourths as long as those of fully-erupted maxillary teeth. Premaxillary teeth presumably acted to grasp or hold the food, but as they lack any kind of cutting edge they could not have cut but only have torn rather inefficiently. Preliminary tests with the cast of a premaxillary tooth plunged into a styrofoam block showed that it is much easier for the crown to penetrate than to be dragged backwards in the direction of the flatter face.

The anterior maxillary teeth are larger, trenchant, recurved teeth. They are of lenticular cross-section over most of the blade, becoming quadrangular at the alveolus. [Thus, LAMBE's (1917b) supposed distinction between the maxillary teeth of *T. rex* and *Gorgosaurus libratus* LAMBE (1914) does not hold as OSBORN (1912) was presumably referring only to the blade when he described the teeth of *T. rex* as of lenticular cross-section.] The rows of serrations extend (roughly) down the anterior and posterior edges of the blades and thus, presumably, these teeth were used to shear the food. Preliminary tests with a cast of a mid-maxillary crown and styrofoam revealed that these crowns are much more easily dragged backwards through the block than premaxillary crowns.

The posterior maxillary teeth are similar in form to the anterior, but are smaller and relatively stouter in lateral view. These teeth are relatively less recurved along the posterior margin, the more extreme having a straight posterior margin. They are situated closer to the region of the muscle attachment to the jaws than the others and hence presumably were capable of exerting a greater force on the food. This is consistent with the stout form of the crowns.

The forms of the dentary teeth are similar to those of the upper teeth (OSBORN, 1912; MOLNAR, 1991). Only the anteriormost dentary tooth has the premaxillary tooth form, but it is somewhat smaller than the premaxillary teeth; teeth two through eight have the form of the anterior maxillary teeth. Posterior to the eighth tooth, the form gradually becomes like that of the posterior maxillary teeth. The change in form of the teeth of both upper and lower jaws is gradual.

TOOTH WEAR

Wear of three kinds can be seen in LACM 23844 (AMNH 5027 is not useable for such observation, as it is unclear whether some teeth may have had wear “touched up” for exhibition). Blunting of the tip, here termed “tip-rounding”, is found in LACM 23844, as in most theropods I have seen. This corresponds to the first type of wear discussed by ABLER (1992). This wear presumably results from contact of the teeth with the bones of the prey or possibly with the opposing tooth row. In LACM 23844 tip-rounding is seen on the maxillary and mid-dentary teeth.

A second type of wear, here called “faceting”, can also be found. In this condition a plane or nearly plane facet develops on the lingual or labial side of the tooth (but never on the anterior or posterior margin) near the tip. The worn surface is often continuous with that of tip-rounding. Faceting corresponds to the third type of wear discussed by ABLER (1992). I have also found this type of wear on many theropod teeth, although not as often as tip-rounding. As I have never observed facets on teeth opposing those with faceting, this kind of wear presumably does not arise from tooth to tooth contact, but rather from abrasion against the bones of the prey. Although if the rate of tooth replacement was high, it would have been possible for facets develop from tooth to tooth contact after which one of the teeth was shed, leaving a facet on one tooth but not its counterpart in the opposing tooth row. ABLER (1992, following Farlow) indicates that this kind of wear is found only on the lingual faces, suggesting that it does not result from tooth to tooth contact. Faceting is not present on the preserved teeth of LACM 23844.

The third type of wear is breakage. The fourth right premaxillary tooth of LACM 23844, has the appearance of having been broken, with a facet later

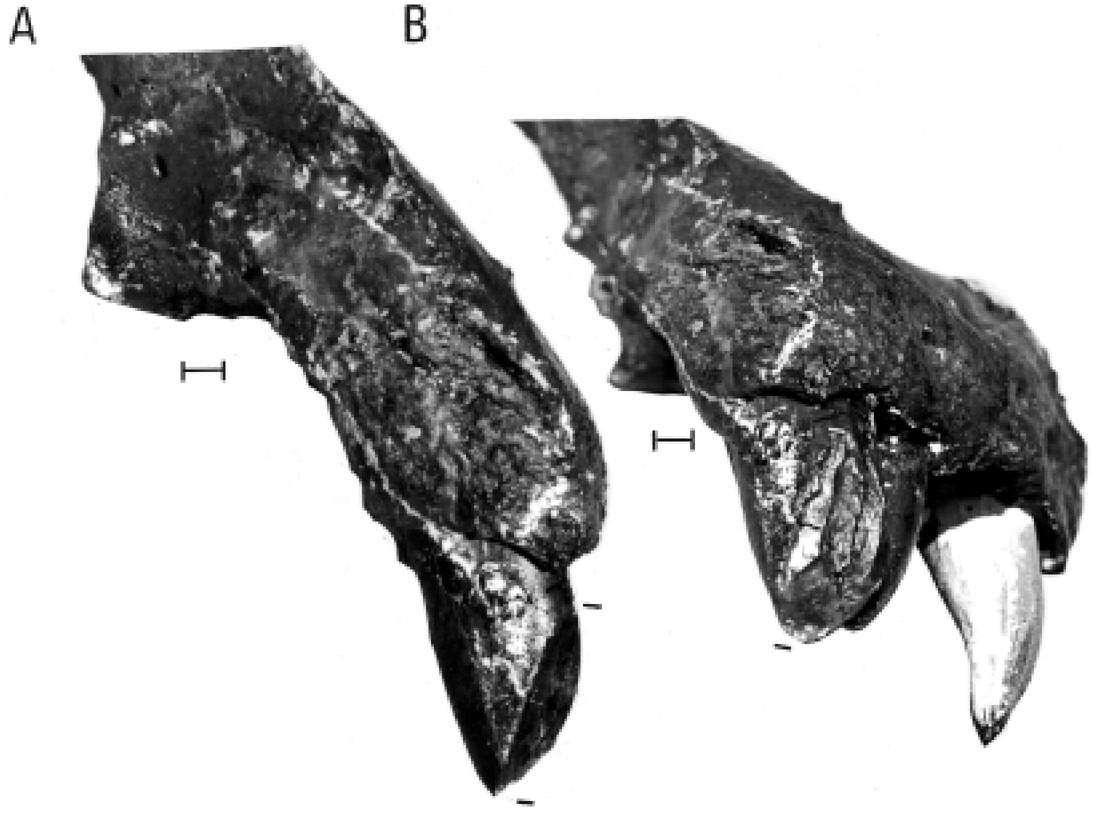

Fig. 14 - The fourth right premaxillary tooth of LACM 23844 (*Tyrannosaurus rex* OSBORN, 1905), showing a prominent wear facet (indicated by bars). **A** - Posterior view. **B** - Posterolateral-inferior oblique view, showing full extent of facet. The facet truncating the tooth is believed to have been worn after breakage of the crown. Scales 1 cm.

worn across the break (Fig. 14). This facet truncates the tooth, well below the tip to judge from the size of the cross-section. I assume that breakage was involved in view of the presumably frequent replacement of teeth, so it seems unlikely that so marked a facet could have been cut by wear alone. No other broken teeth have been reported in *T. rex*. This is the only broken tooth from a large theropod I have observed. However, JACOBSEN (1997) has reported that almost a third (29%) of a collection of presumably isolated tyrannosaurid teeth from the Dinosaur Park Formation were broken. This, in turn, suggests that broken teeth may have been preferentially shed.

A fourth type of tooth wear, the second type discussed by ABLER (1992), in which the serrations alone are worn off is commonly observed in gorgosaur teeth but has not (yet) been observed in *T. rex*. None of the kinds of wear observed clearly indicate any tooth to tooth contact.

CROWN RECURVATURE IN RELATION TO ROTATION ABOUT THE JAW JOINT

The teeth of both upper and lower jaws are recurved. Recurved teeth will most easily penetrate the prey if the direction in which they enter is approximately along the bisector of the angle formed by the anterior and posterior margins at the tip (Fig. 15A). This minimizes the cross-sectional area of the tooth perpendicular to the direction of penetration and so requires less energy to penetrate material of any given toughness than other tooth orientations.

Maxillary teeth three through nine of the right side of AMNH 5027 are so recurved that the bisector of the tips matches closely an arc drawn through the tooth, the radius of which is equal to the distance from tooth tip to center of the quadrate condyle (Fig. 15B). This was determined from Osborn's lateral view of the skull of AMNH 5027 (OSBORN, 1912: fig. 25). Insofar as can be determined from this figure, this condition also holds for maxillary tooth one but not for the eleventh or twelfth, for which this arc almost parallels the posterior margin rather than bisecting the tip. It has not been determined to obtain for the premaxillary teeth, but since their curvature does not differ greatly from that of the anteriormost maxillary tooth, it would seem likely.

This relation also obtains for the dentary teeth. In view of the possibility of rotation at the intramandibular joint, a second arc was drawn through these teeth, taking as the radius the distance from the tooth tip to the presumed center of rotation of the dentary-surangular joint (Fig. 15B). For the posterior dentary teeth the bisector of the tip lies more closely to this second arc, than for that drawn through the craniomandibular joint. Anteriorly of course, these two arcs come to match one another more closely, both roughly matching the bisector.

BITE

The recurved form of the teeth of *T. rex* allowed the teeth more easily to enter the prey when the jaw was widely open, as then the teeth would have been entering in the direction of the bisector of the angle at the crown, i.e. the direction of rotation of the jaw (Fig. 15A). The teeth may also have entered at an angle slightly posterior to this, since the posterior edge of the maxillary and most dentary teeth seems sharp enough to have sliced into the prey. The bisectors of the crown angles of the upper and lower teeth become parallel to one another when the jaws are open to an angle of about 40 (which is a reasonable maximal angle consistent with the unpublished reconstructed muscular mechanics). With the jaws open to this angle a sphere or cylinder 0.4 m in diameter (measured from the AMNH 5027 cast skull) could have been accommodated between the tips of the teeth, and a bite could have been taken from an even larger convex body. From such a large convex body, the premaxillary and anterior dentary teeth would have caught and held the flesh (as mentioned previously since these teeth do not have a posterior cutting edge, they would tend to grasp, rather than slice through, the prey), which would then have been pinched into the mouth. This portion could then have been sliced off by the shearing of the maxillary and central and posterior dentary teeth. ABLER (1992) has suggested that although tyrannosaurid teeth of this form could inflict "credible slashes in meat", they were probably primarily used for gripping. So the chunk of food was perhaps removed by pulling and tearing.

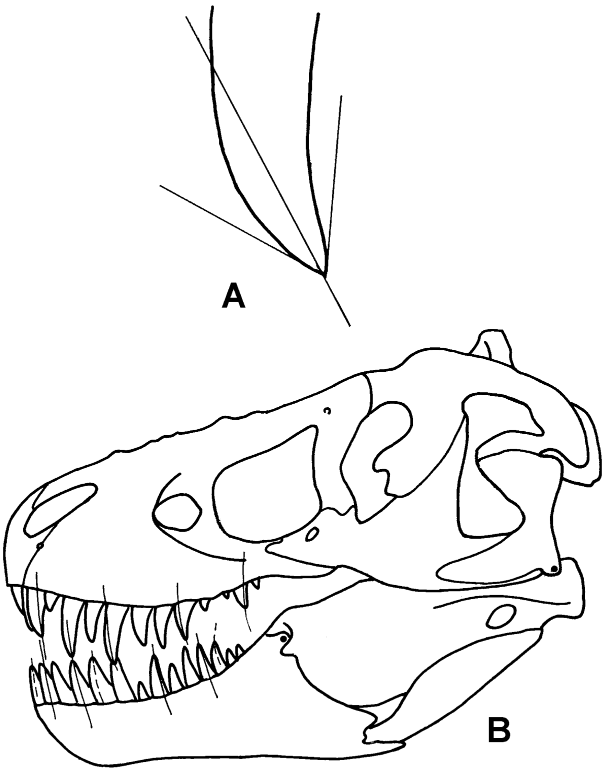

Fig. 15 - **A** - The bisector of the angle formed by the tangents to the anterior and posterior margins at the tip of a recurved (maxillary) tooth. **B** - Maxillary teeth three through nine of the right side of AMNH 5027 are so recurved that the bisectors of the tips match (solid) arcs drawn through the teeth, the radii of which equal the distances from the tooth tips to the center of the quadrate condyle. The dashed arcs, for the dentary teeth, are those with centers at the dentary-surangular joint.

DISCUSSION, WITH SPECULATION

Oras (*Varanus komodoensis*) kill their smaller prey by attacking the neck (AUFFENBERG, 1972) and presumably cutting the carotids or jugulars or possibly the spinal cord. The hadrosaur *Anatotitan* CHAPMAN & BRETT-SURMAN (1990) is found in beds contemporaneous with those yielding *Tyrannosaurus*, and in even large hadrosaurs the neck was rather narrow. This may be seen on several of the mounted specimens, for example, *Anatotitan copei* (LULL & WRIGHT, 1942: pl. 15) and *Corythosaurus casuarius* BROWN [specimens previously referred to *C. excavatus* GILMORE (1923), (LULL & WRIGHT, 1942: pl. 28) and *C. intermedius* PARKS (1923), (GLUT, 1972: 55)]. Measurements made of three modern reptiles [*Alligator mississippiensis* DAUDIN (1801)*, Iguana iguana* LINNAEUS (1758) and *Ctenosaura pectinata* WIEGMANN (1834)] indicate that the maximum width of the neck at the level of the second to fourth cervicals is about 2.5 times the width of the corresponding cervical centrum. This approximates the width of the neck in hadrosaurs as independently reconstructed by PAUL (1987). Assuming that this relation also held for hadrosaurs where, if anything, the neck may have been relatively thinner than in the living forms examined, the neck of *Edmontosaurus regalis* LAMBE (1917a) would be about 30 cm in width, as the cervical centrum figured by LAMBE

(1920: fig. 30) is approximately 12 cm in transverse diameter. The transverse diameter of the fourth cervical of LACM 23502, a specimen of *Edmontosaurus* sp. from the Hell Creek Fm. (length estimated at 8.5 m), is 5.2 cm indicating a neck width of approximately 13 cm. *Edmontosaurus regalis* occurs in the Horseshoe Canyon Fm. (LULL & WRIGHT, 1942) and has also been reported in the Hell Creek (ROHRER & KONIZESKI, 1960; ROHRER, 1961), so it was a contemporary of *Tyrannosaurus*. *Edmontosaurus* LAMBE (1917a) is one of the larger hadrosaurs (estimated length, 9-12 m), so that the gape possible in a *Tyrannosaurus* the size of the AMNH 5027 individual was great enough to accommodate the neck of even a fairly large hadrosaur (e.g. *Edmontosaurus*). Thus it was possible for *Tyrannosaurus* to attack and kill a hadrosaur by grasping the neck and cutting the carotids or jugulars or spinal cord. Since *Tyrannosaurus* (at c. 14 m) is larger than most, if not all, of the known contemporaneous hadrosaurs of the Alberta-Montana-Wyoming region, it is not difficult to conceive that *Tyrannosaurus* attacked the hadrosaur from above. Morris (pers. comm., 1972) points out, however, that hadrosaurs (probably mostly *Edmontosaurus*), while occurring in this region in the Hell Creek Fm., are rare, and ceratopsians are more common. An attack from above to the neck of a ceratopsian would seem to have been less effective because of the large parietal-squamosal frill developed in conjunction with increased power of the bite (OSTROM, 1964); hence other methods of attack may have been used for ceratopsians. AUFFENBERG (1972) reports that oras also dispatch prey by inflicting deep septic wounds and then waiting for the prey to become weakened by infection. Such an approach is also quite possible for tyrannosaurs, although its use would seem difficult, if not impossible, to verify. Even so, ABLER (1992) has suggested that meat lodged in the serrations of tyrannosaurid teeth - as his experiments showed it does - would doubtless have supported colonies of bacteria, which could have infected the wounds.

The large cats seem not to dispatch prey by breaking the neck, but rather by suffocation or strangulation (SCHALLER, 1969), although the neck may be broken in the struggle (COWIE, 1966). The strangulation or suffocation is apparently accomplished by holding closed the nostrils and mouth, or the trachea of the prey (SCHALLER, 1972). Such a method would also be possible for a *Tyrannosaurus* attacking a hadrosaur or other ornithopod, as the mouth of the *Tyrannosaurus* is quite large enough to grasp the snout and jaws of a hadrosaur or smaller ornithopod. Shaking of the prey would obviously be possible for such small forms as *Thescelosaurus* GILMORE (1913) but the shaking of a 3 or 4 (metric) ton hadrosaur (COLBERT, 1962) taxes the imagination. This is especially so since attacking by strangulation or slicing of the main vessels of the neck would be a less expensive mode of obtaining prey. Holtz (pers. comm., 1997) suggested that the same effect might be achieved by biting the snout of the prey animal and crushing it, and so cutting off the airway. He notes that no known specimens show the damage that might be expected from such an attack, but the skull of an animal so attacked might have been sufficiently damaged as to became disarticulated or broken in the process of burial and preservation. Examination of broken and disarticulated ornithopod and ceratopsian skulls for this kind of damage might well be in order.

I have postulated in this paper that certain portions of the skull of *Tyrannosaurus rex* function partly to resist tensile stress. Although it was commonly supposed that bone acts to resist tensile stresses (e.g., YOUNG, 1957; BADOUX, 1966a; TAYLOR, 1992), OXNARD (1971) argued that bony elements are rarely if ever subjected to tensile stresses and that their chief supportive function is resistance to compressive stresses. Oxnard uses as examples the forces exerted upon the arm bones of brachiating primates and argues convincingly that in such cases there are indeed no tensile stresses on the bones themselves.

However, such cases as the skull or mandibles where bony elements or structures may be considered as cantilevers are not discussed. In the vertebral column, of course, the tensile resistance is supplied by the epaxial musculature. There seems, however, to have been no “epi-cranial” or “epi-mandibular” musculature to resist tensile stresses for the skull or mandibles. Hence it is likely that bone in such situations does indeed resist tensile stress.

SUMMARY

The analyses in this paper have allowed elucidation of some functional aspects of the form of certain individual elements of the skull and jaws of *Tyrannosaurus rex* as well as of these structures as a whole. The plane frame analysis of the snout is consistent with the interpretation that the lateral compression of the snout - also marked in other large theropods and the baurusuchid and pristichampsine crocodilians - was correlated with the application of strong vertically-directed forces on the teeth and is consistent with the work of BUSBEY (1995) and ERICKSON *et al.* (1996).

The skull, analyzed as a space frame, was found to have been stable under the modelled forces imposed during feeding and in support. This is not surprising as one would tend to believe *a priori* that the skull structure must have been stable under forces normally imposed. However, the postorbital region of the skull seems less stable than the rest since it

can reasonably be approximated only by quadrangular units which tend to deform by rotation at the joints. Thus this region would have required reinforcement which was provided by the widening of the postorbital bar and the deepening of the posterior ramus of the jugal. The orientation of the quadrate is consistent with a role in resisting the modelled dorsoanteriorly-directed reaction at the craniomandibular joint.

The quadrate bar and the dorsal elements of the skull, the parietals, frontals, nasals, as well as the maxillae and premaxillae, and the braincase-occipital complex seem to represent the regions of the skull subjected to the greater stresses. These are subjected to stresses in feeding as well as in just supporting the weight of the head. The position of the compressive and tensile trajectories as proposed here is supported by i, the existence of continuous bars of bone in the appropriate regions, ii, location of the sinuses outside of these regions, and iii, distribution of butt and scarf joints, so that the former are found in regions interpreted as resisting compressive stresses during biting, and the latter in regions resisting tensile stresses. The major lateral openings of the skull, the orbit, the antorbital fenestra and the infratemporal fenestra, are all in the vicinity of the neutral surface of the skull, in areas of little stress. Perhaps it is better to look at the positioning of the members of the space frame rather than at the positioning of the fenestrae *per se*. A quadrate bar is necessary to resist the reaction forces of the mandible on the skull, so also is the main body of the jugal which forms the suborbital and jugal bars (these bars are designated in Fig. 2), as these resist compressive stress in the support of the head. Preorbital and postorbital bars are presumably necessary for the support and protection of the eye, as well as to resist torsional stress. In the large areas between these bars there is no obvious necessity for bone, and it is here that there are the large openings. It is interesting in this connection that the orbit itself is somewhat larger than one might *a priori* expect to house just an eyeball. The supratemporal fenestrae are lateral to the nasal-frontal-parietal bar, the region of resistance to compressive stress in biting, and tensile stress in head support, again in an area of reduced stress. This does not imply that the location of the fenestrae can be explained in terms of the structure of the space frame, for the space frame was constructed using knowledge of the location of the fenestrae, and furthermore they could have been occupied by thin sheets of bone. However, it does seem that, although the members could be rearranged or some perhaps removed, fenestrae will tend to occur, at least in large forms, in areas not exposed to great stress (cf. FOX, 1964; FRAZETTA, 1968). Similarly, the more extensive sinus chambers seem to be placed outside of regions of great stress. Those of the quadrate and the maxilla occupy a relatively small volume of these elements, unlike, for example, the lachrymal, where a large portion of the horizontal ramus is occupied by chambers. The large sinus chambers lie outside the main regions of compressive stress (the maxilla-nasal-frontal-parietal line), instead being found in the lachrymals, jugals, ectopterygoids, and basisphenoid, although there is the fairly large chamber of the articular which, however, has relatively the thickest walls and is of approximately tetrahedral form. The corpus quadrati lies behind the sinus chambers of the quadrate, which are in the base of the pterygoid process (cf. MOLNAR, 1991: fig. 7), and is of relatively small cross-sectional area, about 400 mm^2 near the minimum. However, the stress is no doubt also resisted by the closely articulated quadratojugal, which is thickened along its posterior margin.

The existence of the prominent supraoccipital crest of tyrannosaurs can probably be correlated with support of the head which, when large, needs a large posterior surface for the attachment of the supporting epaxial muscles.

The lingual bar of the dentary may be explained, at least in part, as an adaptation to reduce the maximum torque on the anterior portions of the mandibles, while the great depth of the dentary [as compared to earlier theropods, e.g. *Allosaurus, Ceratosaurus, Proceratosaurus* VON HUENE (1926), etc.] may be thought of as an adaptation to reducing the maximum bending strain in this portion of the mandible. The posterior "splitting" of the dentary seems an example of the reduction of bone where it is not needed, this being at the neutral surface, and hence bearing less compressive or tensile stress than the dorsal and ventral margins. The jaw adductors would exert a force more or less parallel to the plane of the surangular, which thus needs only reinforcement along its dorsal edge.

The teeth are differentiable into three different classes of form, which grade one into the other. These are the premaxillary form, the anterior maxillary form, and the posterior maxillary form. The premaxillary form seems to be associable with a grasping function, while the maxillary forms would seem to have been more shearing teeth (although, judging from the work of Abler, with some grasping function as well). Tooth wear is present, but in no case is it clearly attributable to tooth to tooth contact. Instead it would seem that the teeth were worn (and perhaps even broken) during their contact with the food. The wearing of teeth, which presumably were being relatively rapidly replaced, would imply forceful contact with (presumably) the bones of the prey animals. The curvature of the teeth roughly matches the circular arcs of radius equal to the distance from the tooth tip to the craniomandibular joint.

The jaws of *T. rex* could open widely enough to grasp the neck of most contemporaneous hadrosaurs, so that cutting of the blood supply to the head, or closing of the trachea, or even (considering the large size of the jaw adductors) breaking the spinal column of the hadrosaurs would seemingly have been possible. A different method of attack would have had to be utilized for armored forms as ankylosaurs and ceratopsians. There is no indication from the cranial osteology that *T. rex* could not have been an active predator.

The main hypothesis being tested by this analysis is whether or not the skull is constructed so that the major stresses are resisted by bony tissue. In his study of *Rhomaleosaurus*, TAYLOR (1992) assumed that the cranial form was optimized to resist the forces impressed in feeding. This assumption is not really necessary. If the cranial form matches (to some reasonable extent) expectations derived from engineering-type analyses based on these assumption, we have evidence that the form is (to that extent) optimized to resist those forces. For example, the trajectory analysis of the *Tyrannosaurus* skull suggests that a bar composed of the premaxillae, nasals, frontals and other, more posterior braincase-occipital elements resisted compressive stresses imposed during feeding. This structure is made up of robust elements resulting in a solid bony construction from the nares to the occiput. This matches expectations derived from the analysis: if, on the other hand, the nasals were interrupted by a fenestra (for attachment of the anterior pterygoid muscles perhaps) then the structure would be unexpected. Other hypotheses regarding the cranial form could then be entertained, that the stresses were not predominantly resisted by osseous tissues, say, or that feeding was not a major influence on cranial structure.

ACKNOWLEDGMENTS

I am very grateful to the following for their assistance with various aspects of this study: the late E.C. Olson (University of California, Los Angeles), P.P. Vaughn, F. Crescitelli, N.G. Lane and Jane Ann Robinson (all then at UCLA), R. Long (then at University of California, Berkeley), B.J.K. Molnar, W.J. Morris (then at Occidental College), M.J. Odano, T. Downs and D. Whistler (all then at LACM), A.R.I. Cruickshank (Leicester City Museum) and Y. Tomida (National Science Museum, Tokyo). B.P. Pérez-Moreno, T.R. Holtz and A.R.I. Cruickshank provided helpful comments on the ms, and Holtz provided the observation on the rarity of secondarily palates among theropods and suggested an alternative killing strategy. S. Sachs (Düsseldorf) kindly (and promptly) translated the abstract. The artwork was done by Laurie Beirne, Christopher L. Glen and the author.

COLLECTION ABBREVIATIONS

AMNH - American Museum of Natural History, New York; LACM - Natural History Museum of Los Angeles County, Los Angeles; MOR - Museum of the Rockies, Bozeman.

ADDENDUM I

Calculation of statical indeterminacy for the space frame and truss.

The degree of statical indeterminacy is given by the formula $6m + r - 6j$ for a frame and $m + r – 3j$ for a truss (AU, 1963), where m is the number of members (struts), j, the number of joints, and r, the number of components of reaction. The first may be rewritten: $6(m - j) + r$. If this term is greater than or equal to zero, then the structure is stable under the forces imposed. In this case, $m = 29$, $j = 18$, $r = 19$ thus, $6(m - j) + r = 85>0$, hence the frame, the rigid structure, is stable under these forces. For the truss, $m + r – 3j = -6<0$, so the pin-connected structure is not stable. This is the first approximation mentioned in the text and illustrated in Fig. 4. If the components are applied at the joints, their total number is 21. For the truss, $m + r – 3j = -12$. For these analyses the reactions are assumed to all act in the sagittal and parasagittal planes. Although a reasonable approximation, certainly there would have been small components in the transverse plane as well. Addition of these to the formulae would increase r, and so not affect the statical indeterminacy for the space frame. If each of the muscles exerted force with a transverse component, r would increase to 33, $m + r – 3j = 6>0$ and the truss would also be stable.

ADDENDUM II

Estimation of whether the moment about the point of application of resistance or the jaw joint was the greater.

From the free-body diagram of Figure 5A it may be seen that if the moment about the quadrate condyles ($\mathbf{M_B}$) is zero, i.e. $M_B = 0$, then, $h_3D_3 + h_4D_4 - h_{4a}D_{4a} - h_2D_2 + V_Ad_A - V_4d_4 - v_ld_l - V_2d_2 = 0$, where the h terms represent the horizontal components of the forces, the v terms the vertical components, the d terms the horizontal distances (or moment arms) and the D terms, the vertical moment arms. Forces resulting in a clockwise torque are taken to be positive. Isolating the reaction at the maxilla, $v_Ad_A = h_{4a}D_{4a} + h_2D_2 + v_4d_4 + v_ld_l + v_2d_2 - h_3D_3 - V_4d_4$. Similarly for the moment about the maxilla $\mathbf{M_A}$, $M_A = 0$, which may be written, $v_Bd_A = h_3D_3 + h_4D_4 + v_4(d_A - d_4) + v_l(d_A - d_1) + v_2(d_A - d_2) - v_3d_A - h_{4a}D_{4a} - h_2D_2$.

Dividing these and, since the actual value of the fraction is not of interest but only whether the numerator or the denominator is greater, dropping equal terms from the numerator and denominator, gives: $(v_ld_l + v_2d_2 + v_4d_4 - h_3D_3)/[v_l (d_A-d_1) + v_2(d_A -d_2) + v_3d_A + v_4(d_A -d_4) - h_2D_2 + h_3D_3]$.

For comparison it may be noted (from Fig. 5A), $d_A - d_1 > d_1$ hence, $v_l (d_A - d_1) > v_ld_l$ and $d_A - d_2 > d_2$ hence, $v_2 (d_A - d_2) > v_2d_2$. Now however, $d_A - d_4 < d_4$ hence $v_4 (d_A - d_4) < v_4d_4$. From Figure 5A it appears that $|v_l (d_A - d_1) + v_2(d_A - d_2)|$ is sufficiently larger than $v_ld_l + v_2d_2$ to more than offset this difference. Also from this figure it appears that $|v_3d_A + h_3D_3 - h_2D_2| > |-h_3D_3|$ as $|v_3d_A|$ seems larger than $|h_2D_2|$. Hence v_B was probably greater than v_A, and the force of resistance at the condyle would be greater than that applied at the maxillae, if the forces exerted by the muscles were all roughly equal.

ADDENDUM III

Supportive forces exerted on the skull by the epaxial musculature.

Referring to Figure 5B, since the body is in equilibrium, $F_x = 0$ and the horizontal components must be balanced (that is $h_3 + h_4 + h_5 = h_2 + h_{4a} + h_0$).

Therefore, if $h_0 = 0$, then $h_3 + h_4 + h_5 = h_2 + h_{4a}$, now h_2 is approximately equal to h_3, but h_{4a} is certainly less than h_0, hence less than $h_4 + h_5$. So a net posteriorly-directed force is exerted on the skull by the musculature which must be resisted by the cervical column. But if the jaw adductors are merely supporting the weight of the jaws, their components (h_2, h_3 and h_4) and reaction (h_{4a}) would presumably be relatively small, so this horizontal force would also be small. Taking the moments, M_0, around the occipital condyle, and neglecting the vertical components of the muscle forces which are merely supporting the weight of the jaws which is less than v_g (probably much less, unlike the situation of the horizontal components), and also the horizontal components of the jaw muscles which must cancel when the jaws are at rest, $v_gd_g = h_5(D_5 - D_0)$. As d_g is greater than $(D_5 - D_0)$ so h_5 must exceed v_g. Hence the epaxial musculature must exert a force upon the back of the skull greater than the weight of the head.

ADDENDUM IV

Comparison of resistance to torsion of the tyrannosaur and crocodilian dentary, considered as cantilever beams.

If the dentary is approximated by a symmetrical rectangular beam, then the maximum bending stress is given by,

$$= (Mc)/I$$

M is the bending moment, c one-half of the depth of the beam, and I the moment of inertia of the cross-sectional area. For a rectangle, the moment of inertia of the cross-sectional area, I_r, is

$$I_r = (Bh^3)/12$$

(these equations are derived in elementary texts dealing with structural mechanics, e.g. DEN HARTOG, 1949; CARPINTIERI, 1997). The height of the beam is h (note that h = 2c), while B is the width. The dentary of *T. rex* is considerably deeper than those of crocodilians, for example. This greater depth reduces the bending stress resulting from a given moment. This may be shown as follows: compare a rectangular beam with a square beam (to represent the crocodilian dentary). For the square beam, the moment of inertia of the cross-sectional area, I_s, is,

$$I_s = B^4/12$$

as for a square h = B. The maximum bending stress for the rectangular beam $_r$ is thus,

$$_r = (Mc)/[(Bh^3)/12]$$

while that for the square beam $_s$ is,

$$_s = (Mc)/(B^4/12)$$

To compare, one is divided into the other,

$$_r/\ _s = [Mc/(Bh^3/12)]/[Mc/(B^4/12)]$$

As h is greater than B by definition, so h^3 is greater than B^3. Thus also $_s$ is greater than $_r$, so that in part at least, a deep jaw may be considered an adaptation to reducing the maximum bending moment upon the dentary.

REFERENCES

ABLER, W.L. (1992) - The serrated teeth of tyrannosaurid dinosaurs and biting structures in other animals. *Paleobiology*, **18**: 161-183.

ANONYMOUS (1854) - Report of the council of the Yorkshire Philosophical Society. *Ann. Rept. Yorkshire Phil. Soc.*, 1852: 7-8.

AU, T. (1963) - *Elementary Structural Mechanics.* Prentice-Hall, Englewood Cliffs, 521 pp.

AUFFENBERG, W. (1972) - Komodo dragons. *Nat. Hist.*, **81**(4): 52-59.

AUFFENBERG, W. (1981) - *The Behavioral Ecology of the Komodo Monitor.* University Presses of Florida, Gainesville, 406 pp.

BADOUX, D.M. (1964) - Lines of action of masticatory forces in domesticated dogs. *Acta Morphol. Neerl.-Scand.*, **5**: 347-360.

BADOUX, D.M. (1966a) - Framed structures in the mammalian skull. *Acta Morphol. Neerl.-Scand.*, **6**: 239-250.

BADOUX, D.M. (1966b) - Statics of the mandible. *Acta Morphol. Neerl.-Scand.*, **6**: 251-256.

BUSBEY, A.B. (1995) - The structural consequences of skull flattening in crocodilians *in* THOMASON, J. (Ed.), *Functional Morphology in Vertebrate Paleontology*, Cambridge University Press, Cambridge, pp. 173-192.

CARPINTIERI, A. (1997) - *Structural mechanics, a unified approach.* Chapman & Hall, London, 761 pp.

CERNICA, J.N. (1966) - *Strength of Materials*. Holt, Rienhart & Winston, New York, 450 pp.

CHAPMAN, R.E. & BRETT-SURMAN, M.K. (1990) - Morphometric observations on hadrosaurid ornithopods, *in* CARPENTER, K. & CURRIE, P.J. (Eds.), *Dinosaur Systematics, approaches and perspectives*, Cambridge University Press, Cambridge, pp. 163-177.

CHARIG, A.J. & MILNER, A.C. (1986) - *Baryonyx*, a remarkable new theropod dinosaur. *Nature*, **324**: 359-361.

COLBERT, E.H. (1962) - The weights of dinosaurs. *Am. Museum Novit.*, **1900**: 1-16.

COLBERT, E.H. (1989) - The Triassic dinosaur *Coelophysis*. *Museum North. Ariz. Bull.*, **57**: 1-160.

COPE, E.D. (1887) - The dinosaur genus *Coelurus*. *Am. Naturalist*, **21**: 367-369.

COPE, E.D. (1889) - On a new genus of Triassic Dinosauria. *Am. Naturalist*, **23**: 626.

COWIE, M. (1966) - *The African Lion*. Golden Press, New York, 96 pp.

CURRIE, P.J. & ZHAO X. (1993) - A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Can. J. Earth Sci.*, **30**: 2037-2081.

DAUDIN, F.M. (1801) - *Histoire Naturelle, Générale et Particulière des reptiles; ouvrage fasiant suit à l'Histoire naturell général et particulière, composée par Leclerc de Buffon; et rédigee par C. S. Sonnini, membre de plusieurs sociétés savantes*. F. Dufart, Paris, **2**, 432 pp.

DEPÉRET, C. (1896) - Note sur les dinosauriens sauropodes et théropodes du Crétacé supérieur de Madagascar. *Bull. Soc. Géol. France*, **24**(3): 176-196.

DONG Z.; CHANG Y.; LI X. & ZHOU Y. (1978) - Note on a new carnosaur (*Yangchuanosaurus shangyouensis* gen. et sp. nov.) from the Jurassic of Yangchuan District, Sichuan Province. *Kexue Tongbao*, **23**: 298-302. (In Chinese)

DONG Z.; ZHOU S. & ZHANG Y. (1983) - The dinosaurian remains from Sichuan Basin, China. *Palaeontol. Sinica*, ser. C, **162**: 1-145.

ERICKSON, G.M.; VAN KIRK, S.D.; SU, J.; LEVENSTON, M.E.; CALER, W.E. & CARTER, D.R. (1996) - Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones. *Nature*, **382**: 706-708.

EVANS, F.G. (1957) - *Stress and Strain in Bones*. Charles C. Thomas Publisher, Springfield, 245 pp.

FARLOW, J.O. & MOLNAR, R.E. (1995) - *The Great Hunters*. Franklin Watts, New York, 64 pp.

FARLOW, J.O.; SMITH, M.B. & ROBINSON, J.M. (1995) - Body mass, bone "strength indicator", and cursorial potential of *Tyrannosaurus rex*. *J. Vertebr. Paleontol.*, **15**: 713-725.

FOX, R.C. (1964) - The adductor muscles of the jaw in some primitive reptiles. *Univ. Kansas Publ. Museum Nat. Hist.*, **12**: 657-680.

FRAZETTA, T.H. (1968) - Adaptive problems and possibilities in the temporal fenestration of tetrapod skulls. *J. Morph.*, **125**: 145-158.

GILMORE, C.W. (1913) - A new dinosaur from the Lance Formation of Wyoming. *Smithsonian Misc. Coll.*, **61**: 1-5.

GILMORE, C.W. (1923) - A new species of *Corythosaurus*, with notes on other Belly River Dinosauria. *Can. Fld-Nat.*, **37**: 1-9.

GLUT, D.F. (1972) - *The Dinosaur Dictionary*. The Citadel Press, Secaucus, 218 pp.

HARTOG, J.P. DEN (1949) - *Strength of Materials*. McGraw-Hill, New York, 323 pp.

HILDEBRAND, M. (1974) - *Analysis of Vertebrate Structure*. John Wiley & Sons, New York, 710 pp.

HOLTZ, T.R. JR. (1994) - The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *J. Paleontol.*, **68**: 1100-1117.

HOLTZ, T.R. JR. (1996) - Phylogenetic taxonomy of the Coelurosauria (Dinosauria: Theropoda). *J. Paleontol.*, **70**: 536-538.

HORNER, J.R. & LESSEM, D. (1993) - *The Complete T. rex*. Simon & Schuster, New York, 239 pp.

HUENE, F. VON (1926) - On several new and unknown reptiles of the order Saurischia from England and France. *Ann. Mag. Nat. Hist.*, **17**(9): 473-489.

JACOBSEN, A.R. (1997) - Wear patterns of tyrannosaurid teeth: an indication of biting strategy. *J. Vertebr. Paleontol.*, **16**: 43A.

JENKINS, I. (1997a) - Finite element analysis of skull dynamics in a Permian synapsid (mammal-like reptile). *J. Morph.*, **232**: 271.

JENKINS, I. (1997b) - Constructional morphology of the gorgonopsid skull: adaptive pathways among a Permian predator. *J. Morph.*, **232**: 271.

KURZANOV, S.M. (1981) - O neobichnikh teropodakh iz verkhnego Mela MNR. *Sovm. Sov.-Mong. Palaeontol. Eksped., Trudy*, **15**: 39-50.

LAMBE, L.M. (1914) - On a new genus and species of carnivorous dinosaur from the Belly River Formation of Alberta with a description of the skull of *Stephanosaurus marginatus* from the same horizon. *Ottawa Nat.*, **28**: 13-20.

LAMBE, L.M. (1917a) - A new genus and species of crestless hadrosaur from the Edmonton Formation of Alberta. *Ottawa Nat.*, **31**: 65-73.

LAMBE, L.M. (1917b) - The Cretaceous theropodous dinosaur *Gorgosaurus*. *Geol. Surv. Can. Mem.*, **100**: 1-84.

LAMBE, L.M. (1920) - The hadrosaur *Edmontosaurus* from the Upper Cretaceous of Alberta. *Geol. Surv. Can. Mem.*, **120**: 1-79.

LAVOCAT, R. (1955). Sur une portion de mandibule de théropode provenant du Crétacé supérieur de Madagascar. *Bull. Museum Hist. Nat., Paris*, Sér. 2, **27**: 256-259.

LINNAEUS, C. (1758) – *Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, specues cum characteribus, differentiis, synonymis, locis.* (10th edition) Laurentii Salvii, Holmiae, 824 pp.

LULL, R.S. & WRIGHT, N.E. (1942) - Hadrosaurian dinosaurs of North America. *Geol. Soc. America, Spec. Paper*, **40**: 1-242.

MADSEN, J.H.JR. (1976) - *Allosaurus fragilis*; a revised osteology. *Utah Geol. Mineral Surv. Bull.*, **109**: 1-163.

MARSH, O.C. (1877) - Notice of some new dinosaurian reptiles from the Jurassic Formation. *Am. J. Sci.*, **14**(3): 514-516.

MARSH, O.C. (1884)- Principle characters of American Jurassic dinosaurs. Pt. VIII. The order Theropoda. *Am. J. Sci.*, **27**(3): 329-340.

MATTHEW, W.D. & BROWN, B. (1922) - The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Am. Museum Nat. History Bull.*, **46**: 367-385.

MOLNAR, R.E. (1991) - The cranial morphology of *Tyrannosaurus rex*. *Palaeontographica, A*, **217**: 137-176.

MURPHY, G. (1946) - *Advanced Mechanics of Materials*. McGraw-Hill Book Co., Inc., New York, 307 pp.

NEWMAN, B.H. (1970) - Stance and gait in the flesh-eating dinosaur *Tyrannosaurus*. *Biol. J. Linn.*, **2**: 119-123.

OSBORN, H.F. (1903) - *Ornitholestes hermanni*, a new compsognathoid dinosaur from the Upper Jurassic. *Am. Museum Nat. History Bull.*, **19**: 459-464.

OSBORN, H.F. (1905) - *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Am. Museum Nat. History Bull.*, **21**: 259-265.

OSBORN, H.F. (1912) - Crania of *Tyrannosaurus* and *Allosaurus*. *Am. Museum Nat. History Mem.*, (n.s.) **1**: 1-30.

Osborn, H.F. (1924) - Three new Theropoda, *Protoceratops* zone, central Mongolia. *Am. Museum Novit.*, **144**: 1-12.

Ostrom, J.H. (1964) - A functional analysis of the jaw mechanics in the dinosaur *Triceratops. Postilla*, **88**: 1-35.

Ostrom, J.H. (1978) - The osteology of *Compsognathus longipes* Wagner. *Zitteliana*, **4**: 73-118.

Ouwens, P.A. (1912) - On a large *Varanus* species from the island of Komodo. *Bull. Jard. Bot. Buitenzorg*, **2**: 1-3.

Oxnard, C.E. (1971) - Tensile forces in skeletal structures. *J. Morph.*, **134**: 425-436.

Parks, W.A. (1923) - *Corythosaurus intermedius*, a new species of trachodont dinosaur. *Univ. Toronto Stud. Geol. Ser.*, **13**: 1-32.

Paul, G.S. (1987) - The science and art of restoring the life appearance of dinosaurs and their relatives. A rigorous how-to guide, *in* Czerkas, S.J. & Olson, E.C. (Eds.), *Dinosaurs. Past and Present*, **2**, Natural History Museum of Los Angeles County & University of Washington Press, Seattle, pp. 4-49.

Paul, G.S. (1988) - The small predatory dinosaurs of the mid-Mesozoic: the horned theropods of the Morrison and Great Oolite - *Ornitholestes* and *Proceratosaurus* - and the sickle-claw theropods of the Cloverly, Djadokhta and Judith River - *Deinonychus, Velociraptor* and *Saurornitholestes. Hunteria*, **2**: 1-9.

Raath, M. (1969) - A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. *Arnold. (Zim.)*, **4**: 1-25.

Reig, O. (1963) - La presencia de dinosaurios saurisquios en los “Estratos de Ischagualasto” (Mesotriásico superior) de las provincias de San Juan y La Rioja (Republica Argentina). *Ameghiniana*, **3**: 3-20.

Rohrer, W.L. (1961) - On the occurrence of *Edmontosaurus* in the Hell Creek Formation of Wyoming. *J. Paleontol.*, **35**: 230.

Rohrer, W.L. & Konizeski, R. (1960.) - On the occurrence of *Edmontosaurus* in the Hell Creek Formation of Montana. *J. Paleontol.*, **34**: 464-466.

Russell, D.A. (1970) - Tyrannosaurs from the Late Cretaceous of western Canada. *Nat. Museum Nat. Sci. Publ. Palaeontol.*, **1**: 1-34.

Schaller, G.B. (1969) - Life with the king of beasts. *Natl. Geograph.*, **135**: 494-519.

Schaller, G.B. (1972) - Predators of the Serengeti: Part 1. The social carnivore. *Nat. Hist.*, **81**(2): 38-49.

Seeley, H.G. (1874) - Note on some of the generic modifications of the plesiosaurian pectoral arch. *Quart. J. Geol. Soc. London*, **30**: 436-449.

Sereno, P.C. (1995) - Roots of the family tree. *Nat. Hist.*, **104**(6):30-32.

Stromer, E. (1934) - Die Zähne des *Compsognathus* und Bemerkungen über das Gebiss der Theropoda. *Centralbl. Miner.*, Abt. B, **1934**: 74-85.

Taylor, M.A. (1992) - Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. *Phil. Trans. Roy. Soc. London,* **335**: 247-280.

Thomason, J.J. (1995) - To what extent can the mechanical environment of a bone be inferred from its internal architecture?, *in* Thomason, J. (Ed.), *Functional Morphology in Vertebrate Paleontology*, Cambridge University Press, Cambridge, pp. 249-263.

Timoshenko, S. & Young, D.H. (1962) - *Elements of the Strength of Materials.* (4th edition) D. Van Nostrand Co., Inc., Princeton, 377 pp.

Wagner, A. (1861) - Neue Beiträge zur Kenntnis der urweltlichen Fauna des lithographischen Schiefers. V. *Compsognathus longipes* Wagn. *Abhandl. Bayer. Akad. Wiss.*, **9**: 30-38.

Wiegmann, A.F.A. (1834) - *Herpetologia Mexicana: seu descriptio amphibiorum Novae Hispaniae pars prima saurorum species.* C. G. Luderitz, Berlin, 54 pp.

Yamazaki, N. (1995) - Approaches from biomechanics, *in* NHK Special Program Team (Ed.), *This is the Dinosaur!: new aspects of dinosaurs based on the scientific approach*, Shinchousa, Tokyo, pp. 98-125. (In Japanese).

Young, J.Z. (1957) - *The Life of Mammals.* Oxford Univ. Press, Oxford, 820 pp.

Zhao X. & Currie, P.J. (1993) - A large crested theropod from the Jurassic of Xinjiang, People’s Republic of China. *Can. J. Earth Sci.*, **30**: 2027-2036.