

THE CRANIAL MORPHOLOGY OF *TYRANNOSAURUS REX*

BY

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With 15 plates and 9 figures in the text

Zusammenfassung

Tyrannosaurus rex war ein großer, räuberischer Theropode, der die Rocky Mountains Region von Nord-Amerika während der jüngsten Kreidezeit (Maastrichtium) bewohnte. Frühere Arbeiten über diese Form sind mit einer Ausnahme rein beschreibend. Die vorliegende Studie richtet sich auf die Morphologie des Schädels und der Kiefer, insbesondere auf die Beschreibung individueller Elemente.

Bestimmte charakteristische Merkmale des Schädels von *T. rex* stehen mit seiner ernährungsmäßigen Entwicklung in Zusammenhang. Die Adduktorkammer wurde vergrößert. Dies zeigt sich in der transversalen Ausdehnung der Postorbitalregion, in der vergrößerten Supratemporalgrube und in einer vertieften postdentalen Hälfte des Kiefers. Das System des cranialen Sinus war ebenfalls ausgeprägter als in weniger abgeleiteten Theropoden.

Das Vorkommen einer wohlausgebildeten postorbitalen Rauigkeit bei einigen Stücken, die indessen bei anderen unterdrückt ist, könnte einen Sexualdimorphismus darstellen. Ein Stück, MOR 008, kann ein älteres Individuum sein: es zeigt eine extreme Entwicklung der nasalen Rauigkeit und eine erhöhte Häufigkeit von Verwachsungen cranialer Elemente.

Schlüsselwörter: Tyrannosauridae — *Tyrannosaurus rex* — Maastrichtium — Nordamerika — Asien.

Abstract

Tyrannosaurus rex was a large, raptorial theropod that inhabited the Rocky Mountains region of North America during uppermost Cretaceous (Maastrichtian) times. Previous work on this form, with one exception, has been completely descriptive. This study focuses on the morphology of the skull and jaws, especially on the description of the individual elements.

Certain characteristic features of the *T. rex* skull are related to its trophic development. The adductor chamber was enlarged, which is reflected in the transverse expansion of the postorbital region, an enlarged supratemporal fossa and a deepened postdentary moiety of the jaw. The system of cranial sinuses was also more extensive than in less derived theropods.

The existence of a well-developed postorbital rugosity in some specimens, although it is subdued in others suggests sexual dimorphism in that structure. One specimen, MOR 008, may represent an elderly individual: it exhibits extreme development of the nasal rugosity and an increased frequency of fusions of cranial elements.

Key words: Tyrannosauridae — *Tyrannosaurus rex* — Maastrichtian — North America — Asia.

Introduction

Tyrannosaurus is a genus of large, bipedal theropod dinosaur familiar from its inclusion in nearly every book on fossil animals. Thus a general introduction is unnecessary. Fossils of *Tyrannosaurus* have been found in North American rocks of Maastrichtian age (latest Cretaceous) in Alberta (RUSSELL 1970), Montana (OSBORN 1905), Wyoming (OSBORN 1905, 1912), South Dakota (BJORK 1982), and New Mexico (GILLETTE, WOLBERG & HUNT 1986).

The type species is *Tyrannosaurus rex* OSBORN (1905). Six other species have been referred to this genus. *Tyrannosaurus amplius* (MARSH 1892; reference by KUHN 1937) is based on the crown of a premaxillary tooth (YPM 269)

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that is now referred to *Aublysodon mirandus* (MOLNAR & CARPENTER 1989). The second species, *Tyrannosaurus bataar* MALEEV (1955 a), from Mongolia, was synonymized with *Tarbosaurus efremovi* by ROZHDESTVENSKY (1965), which then became *Tarbosaurus bataar*. In 1905, OSBORN described an incomplete theropod from the Lance Formation of Wyoming: *Dynamosaurus imperiosus*. This he himself (1906) assigned to the genus *Tyrannosaurus* as *T. imperiosus*. It is indistinguishable from *T. rex*.

In addition to the three nominate North American species, three species have been reported from China. *Tyrannosaurus lanpingensis* YEH (1975), a nomen nudum, is based on isolated teeth from the Upper Chingshing Formation of Lanping, Yünnan. These teeth are of Lower Cretaceous age and probably derive from a non-tyrannosaurid theropod (DONG, personal communication, 1986). *Tyrannosaurus turpanensis* ZHAI, ZHANG & TONG (1978), also a nomen nudum, is based on isolated teeth from the Subashi Formation of the Turpan Basin, Xinjiang. It is probably referable to *Tarbosaurus* (DONG, personal communication, 1986). *Tyrannosaurus luanchuanensis* DONG (1979) is based on teeth and bone fragments from the Qiuba Formation (TONG & Wang 1980), Luanchuan County, Henan. These teeth are very large and thus are consistent in size with those of *Tyrannosaurus*. HU (1973) described and figured (Plate 10, Figure 1) a first? metatarsal from the Wangshi Formation of Shandong that he assigned to "*Tyrannosaurus* cf. *rex*". This metatarsal may represent *Tyrannosaurus* or *Tarbosaurus*. These forms seem referable to *Tarbosaurus* (CURRIE, pers. comm., 1990).

Tyrannosaurids all date from the late Cretaceous (Campanian and Maastrichtian) of Canada, the United States, Mongolia and China. *Tyrannosaurus* (= *Dynamosaurus* = *Manospondylus*), along with the related genera *Albertosaurus* (= ? *Deinodon*, = ? *Gorgosaurus*), *Alectrosaurus*, *Alioramus*, *Chingkankousaurus* (= ? *Tarbosaurus*), *Daspletosaurus*, *Nanotyrannus* and *Tarbosaurus*, constitutes the family Tyrannosauridae. The genus *Gorgosaurus* has been used by BAKKER, WILLIAMS & CURRIE (1988) and CURRIE (1987), as the type skull is crushed and incomplete and hence difficult to compare with other specimens (BAKKER, WILLIAMS & CURRIE 1988). Here it is regarded as a synonym of *Albertosaurus* for convenience, not as a reliable statement of taxonomic affinity. *Manospondylus gigas* (COPE 1892) is here considered a probable synonym of *T. rex* following OSBORN (1916). *Chingkankousaurus fragilis* is based on an incomplete right scapula (YOUNG 1958). This was recognised as a tyrannosaurid only by WHITE (1973). The scapular blade is much narrower with respect to its length than in such genera as *Allosaurus* and *Ceratosaurus* and is similar to those of the tyrannosaurids, especially *Albertosaurus*. Thus it is here considered a tyrannosaurid.

In spite of its familiarity there is no complete study of the osteology of *Tyrannosaurus*, which has received little attention (with the exception of NEWMAN, 1970) since OSBORN's last paper on it in 1916. A discussion of the cranial sinus chambers and their significance to the relationships of theropods and birds has appeared (MOLNAR 1985) and a new generic diagnosis has been given by BAKKER, WILLIAMS & CURRIE (1988). But there has been little functional analysis in spite of the likely importance of this species in the terrestrial ecology of the latest Cretaceous, just prior to the widespread extinctions.

The use of term "carnosaur" here follows the proposed usage of MOLNAR, KURZANOV & DONG (1990). The term "suture" is used in the anatomical sense, as an immobile interlocking junction, rather than simply as any contact between two bones. Collection designations are: AMNH, American Museum of Natural History (New York City); BM(NH), British Museum (Natural History) (London); CM, Carnegie Museum (Pittsburgh); CMNH, Cleveland Museum of Natural History (Cleveland); FMNH, Chicago Field Museum of Natural History (Chicago); IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, (Beijing); LACM, Los Angeles County Museum of Natural History, (Los Angeles); MMS, Minnesota Museum of Science (St. Paul); MOR, Museum of the Rockies (Bozeman); OMNH, Museum of the University of Oklahoma (Norman); NMC, National Museum of Natural History (Ottawa); NMMNH, New Mexico Museum of Natural History (Albuquerque); OUM, Oxford University Museum (Oxford); PIN, Palaeontological Institute of the Academy of Sciences of the U.S.S.R. (Moscow); SDSM, Museum of Geology, South Dakota School of Mines and Technology (Rapid City); TMM, Texas Memorial Museum (Austin); TMP, Tyrrell Museum of Palaeontology (Drumheller); UCM, University of Colorado Museum (Boulder); UCMP, Museum of Paleontology, University of California (Berkeley); UNM, University of New Mexico Museum (Albuquerque); USNM, National Museum of Natural History (Washington); UUV, University of Utah (Salt Lake City); YPM, Peabody Museum of Natural History, Yale University (New Haven).

Material: The following specimens were examined: *Tyrannosaurus rex*, AMNH 5027, AMNH 5029, AMNH 5117, BM(NH) 7994, CM 1400, LACM 23844, MOR 008, SDSM 12047, TMP P81.6.1, TMP P81.12.1, UCMP 118742; *Tyrannosaurus* sp., MMS 51-2004, TMM 41436-1; *Albertosaurus libratus*, AMNH 5336, AMNH 5346, TMP P85.62.1;

Albertosaurus megagracilis, LACM 23845 (holotype); *Albertosaurus sarcophagus*, NMC 5600 (holotype); *Nanotyrannus lancensis*, CMNH 7541 (holotype); *Tarbosaurus bataar*, AMNH 6794 (cast); *Acrocantiosaurus atokensis*, MUO 8-0-S9 (holotype, postorbital only seen); *Allosaurus fragilis*, AMNH 600, CM 11844, CM 21726, LACM unnumbered, UUVF 3, UUVF 5583, UUVF 5961, UUVF 6000, plus the following specimens collected by Dr. J.H. MADSEN, 2154, 5582, 71-1, 71-3, 71-151, A1-1(CR), Q-6, Q-19, X31'; *Ceratosaurus nasicornis*, USNM 4735 (holotype); ? *Ceratosaurus* sp., CM 21704; ? *Daspletosaurus* sp., OMNH unnumbered; *Dilophosaurus wetherilli*, UCMP 37302 (holotype), plus other specimens at the time unregistered; *Dromaeosaurus albertensis*, AMNH 5356 (holotype); *Eustreptospondylus oxoniensis*, OUM J13558 (holotype); *Indosaurus raptorius*, AMNH 1753, AMNH 1955; and *Megalosaurus bucklandi*, OUM J13506 (holotype), OUM J13505 and OUM J29813.

The genus *Tyrannosaurus* is known from twenty specimens, with a further ten probably referable. Of these twenty fourteen are referred to *T. rex*, and the remainder to *T.* sp. — these are:

Tyrannosaurus rex

CM 9380 (formerly AMNH 973), the holotype. Consists of skull and jaw elements, cervical, dorsals, sacrals, gastralia, right humerus, femora and tibiae. From the Hell Creek Formation, near Jordan, Dawson Co., Montana. Described by OSBORN (1905, 1906, 1912, 1916).

AMNH 5005. Cranial fragments and fibula. From the Hell Creek Fm. at Crooked Creek, Montana. This specimen could not be located in 1971.

AMNH 5027. Skull, jaws, shoulder girdles, pelves, cervicals, dorsals, sacrals and a few caudals. From the Hell Creek Fm. near Jordan, Dawson Co., Montana. Described by OSBORN (1912, 1916).

AMNH 5117. Braincase, including occiput: "postfrontal" (i. e. postorbital), pterygoid and hyoid were also catalogued, but were not found in 1971. From the Lance Fm. of Converse Co., Wyoming. Described by OSBORN (1912).

AMNH 5881. Femur, tibia, fibula and phalanges. No stratigraphic or locality data given. Could not be found in 1971. Described by OSBORN (1906).

BM(NH) R7994 (formerly AMNH 5866). Dentaries, cervicals, dorsals, and incomplete pelvis and femur: palatines also listed, but were not seen in 1985. From the Lance Fm. of Weston Co., Wyoming. Described by OSBORN (1905, 1906). Holotype of *Dynamosaurus imperiosus* OSBORN (1905).

CM 9379 (formerly AMNH 5029). Braincase, including occiput and artificial endocranial cast: splenial, articular and prearticular were also catalogued, but were not found in 1971 (at the AMNH). From the basal sandstone of the Hell Creek Fm., near Jordan, Dawson Co., Montana. Described by OSBORN (1912).

LACM 23844. Jaws and incomplete skull, cervicals, dorsals, caudals, shoulder girdle, ribs, incomplete ischia and femur, fibula, incomplete metatarsus. From the Hell Creek Fm. of Jordan, Dawson Co., Montana.

MOR 008. Incomplete skull. From the Hell Creek Fm.(?) near Custer, Montana.

SDSM 12047. Skull and jaws, and c. 40% of the postcranial skeleton. From the Hell Creek Formation, reportedly low in the section, of Butte Co., South Dakota. Reported by BJORK (1982).

TMP P81.6.1. Skull and jaws and c. 30% of the postcranial skeleton. From the Willow Creek Formation of Alberta.

TMP P81.12.1. Postorbital and much of the postcranial skeleton. From the Scollard Formation, near Huxley, Alberta.

TMP PC 82.50.11. Large right maxilla.

UCMP 118742. Maxilla. From the Hell Creek Formation of Montana.

UCMP 131583. Maxilla and dentaries. From the Hell Creek Formation of Montana.

Tyrannosaurus sp.

AMNH 3982. Two dorsal centra, the holotype of *Manospondylus gigas*. One centrum was reported lost by OSBORN (1916). From an unspecified horizon, presumably the Hell Creek Formation, South Dakota. Described by COPE (1892) and discussed and figured by OSBORN (1916).

CM 1400. Cranial and jaw fragments, ischial fragments, ribs and chevrons. From the Lance Formation of Snyder Creek, Niobrara Co., Wyoming. CM 9401, a fragmentary lachrymal, may pertain to this specimen.

MMS 51-2004. Anterior portion of braincase. From the Lance Formation(?) of northwestern South Dakota.

NMMNH P-1013-1. Dentary, prearticular, articular, teeth, chevron. From the McRae Formation near Kettle Top Butte, New Mexico. Described by GILLETTE, WOLBERG & HUNT (1986).

USNM 6183. Femur, tibia and fibula. From the Lance Formation(?) of Alkali Creek, Niobrara Co., Wyoming.

LAWSON (1976) described a maxilla (TMM 41436-1), from the Maastrichtian Tornillo Gr. of Brewster Co., Texas, as pertaining to a juvenile *T. rex*. His grounds for this were the general proportions of the maxilla, a narrow bar separating the maxillary from the antorbital fenestra, and evidence that the size of the maxillary fenestra decreased with growth in *T. rex* relative to maxillary length. Because the maxillary fenestra of TMM 41436-1 is large, this implies that it would decrease in relative size with growth in *T. rex*, but increase in, e. g., *Albertosaurus libratus* (LAWSON 1976), and hence in this specimen would come to resemble that of an adult *T. rex*. Although it may be doubted that the bar separating the maxillary from the antorbital fenestra is particularly narrow in *T. rex*, the proportions of the maxilla are as expected from growth trends in modern crocodylians.

The following specimens may also pertain to *Tyrannosaurus*: AMNH 1011, an incomplete tooth from the Hell Creek Fm. of Montana; AMNH 5020, right fourth metatarsal from the Hell Creek Fm. near Lismas, Montana; AMNH 5021, pedal phalanx from the Hell Creek Fm. near Lismas, Montana; AMNH 5044, caudals from the Hell Creek Fm. at Sand Creek, Montana; CM 244, a phalanx from the Lance Fm. of Lance Creek, Wyoming; IVPP unnumbered specimen, a metatarsal from the Wangshi Fm. of Shandong, China (HU 1973); NMC 9554, an incomplete cervical from the Scollard Fm. near Huxley, Alberta (RUSSELL 1970); NMC 9950 (now part of TMP 81.12.1), pedal phalanx from the Scollard Fm. near Huxley, Alberta (RUSSELL 1970); UCM 38804, partial tooth from the Laramie Fm. of Weld Co., Colorado; UNM FKK-076, tooth from the Naashoibito Fm. San Juan Basin, New Mexico; and USNM 2110, right fourth metatarsal from the Lance Fm. of Converse Co., Wyoming (GILMORE 1920); USNM 8064, right ilium from the Lance Fm. (?) of Alkali Creek, Niobrara Co., Wyoming. There are many other isolated teeth referred to *T. sp.* not listed here.

Description

Introduction

The skull and jaws of *Tyrannosaurus rex* were figured and described by OSBORN (1906, 1912). In the first of these papers he discussed the incomplete skull and jaws of the holotype (CM 9380, previously AMNH 973) but figured the elements only in lateral view, as part of a reconstruction of the skull. His later paper (1912) described additional material; AMNH 5027, AMNH 5029 (now CM 9379) and AMNH 5117. The first of these is a nearly complete articulated skull with jaws (in addition to the axial skeleton), the other two consist only of braincases. In that paper all of the elements present are figured in articulation except for the maxilla (which is also figured separately), hence the internal surfaces of the elements are neither figured nor described.

Since 1912, three reasonably complete skulls of *T. rex* have been recovered which add greatly to our knowledge of the cranial elements. In 1967, an incomplete but articulated skull and jaw was collected by Dr. WILLIAM MACMANNIS of Montana State University and brought to the Museum of the Rockies (Bozeman, Montana). This skull (MOR 008) was apparently eroded approximately to the midline prior to discovery and thus exposed the medial surfaces of many of the cranial elements. This skull has recently been disarticulated and completely prepared by Dr. JOHN HORNER. An incomplete skull and skeleton was discovered in 1968 by Mr. HARLEY GARBANI for the Los Angeles County Museum of Natural History, and recovered by a field crew under the direction of Dr. J. R. MACDONALD. The skull of this specimen (LACM 23844) consists of almost complete, but disarticulated, elements. In 1981 Dr. PHILLIP BJORK collected a third, complete and articulated skull and associated partial skeleton, which is now at the South Dakota School of Mines in Rapid City. There are two further specimens at the Tyrrell Museum, Drumheller, Alberta: one (TMP P81.12.1), on display, consists of much of the postcranial skeleton, but of the skull only a postorbital, and the other (TMP P81.6.1) has a reasonably complete skull currently under preparation. Most recently mandibular elements and a chevron reportedly from *T. rex* have been described from the McRae Formation of New Mexico (GILLETTE, WOLBERG & HUNT 1986). An almost complete skeleton was recently collected by the Museum of the Rockies.

The skull of LACM 23844 was discovered disarticulated, and that of MOR 008 has been disarticulated in preparation. These have provided the opportunity to study the morphology of the individual cranial bones. When originally found that of MOR 008 was eroded to the midline, so the internal relationships of the elements could be observed. The two articulated skulls studied, AMNH 5027 and SDSM 12047, have both undergone shearing and some crushing. The skull of AMNH 5027 has been sheared such that the right side has been displaced dorsally relative to the left, and vertically stretched posteriorly, so that the squamosal has become separated from the quadratojugal and the post-orbital slightly separated from the jugal. That of SDSM 12047 has been sheared in the opposite sense, and crushed at least on the left side.

A complete description of the cranial elements is neither feasible nor desirable as most have been well described by OSBORN. Therefore the elements will be described principally with regard to five aspects: description of elements and of surfaces of elements not previously observable; features or structures that have not been previously treated (e.g. cranial sinuses); individual variation; features relating to the reconstruction of the cranial musculature, and; features relating to joint form. This study in its original form was part of the requirements for the degree of Ph. D. at the University of California, Los Angeles. It is intended that the present publication form the basis for a functional study of the skull of *T. rex* in preparation, hence the inclusion of features related to joint form and muscle reconstruction. The teeth will be discussed in that study. Variation is treated in some detail in order to facilitate recognition of variable features in other taxa, and to assist in distinguishing between the kinds of features that vary and those that indicate taxonomic difference (cf. MOLNAR 1990). Comparison with *Allosaurus fragilis* is emphasized, because this is a well-known form, monographed by MADSEN (1976) and GILMORE (1920). Comparison with other tyrannosaurids is desirable, but little detailed cranial osteology is yet available (except for MALEEV 1974). Because comparison with other tyrannosaurids relates to the distinguishing features of *Tyrannosaurus* it will be largely treated in the discussion. This study depends primarily on four specimens: AMNH 5027, LACM 23844, MOR 008 and SDSM 12047.

Because of variant usage in the literature it is advisable to consider the nomenclature relating to the cranial fenestrae. The term fenestra will here be used to refer only to the actual aperture. The excavation that often surrounds the aperture (as e.g. for the antorbital fenestra) will be termed the recess or fossa. Thus the antorbital fenestra will be described as laying in the antorbital fossa.

Little reference is made here to circulatory or central nervous structures. These have been treated by OSBORN (1912), and as little new material of the braincase has become available since that time (and that material has yet to be completely prepared and reassembled), they are not included. Detailed measurements of the elements are not presented as it was felt that too many elements were crushed or too incomplete for significant measurements to be made.

Osteology

Premaxilla (Fig. 1, Pl. 1): The premaxilla of *T. rex* has the form of a low, trapezoidal prism set on end (the tooth-bearing surface). It was figured in lateral, dorsal and ventral aspects by OSBORN (1912, Pls. 1 and 2 and Fig. 6). The body is surmounted by a prominent recurved nasal process anteriorly and a less prominent, flattened maxillary process posteriorly. It contacts only two other elements, the maxilla posteriorly and the nasal dorsoposteriorly (but see 'vomer'). The nasal process reaches back to the nasal, forming the dorsal margin of the naris, and the maxillary process forms the ventral margin. The premaxilla of *Tyrannosaurus rex* is much like that of *Allosaurus fragilis* with the anterior margin rising perpendicularly from the ventral border, and in this feature it differs from those of *Megalosaurus hesperis* (WALDMAN 1974) and *Eustreptospondylus oxoniensis*. The premaxilla bears four compressed teeth.

Premaxillae are well-preserved in AMNH 5027 and LACM 23844, missing from SDSM 12047 and not yet prepared on MOR 008. The following description is based on LACM 23844.

A dorsoventrally elongate foramen, opening into the oral cavity just below the palate, lays on the maxilla-premaxilla contact. The walls of this channel are smooth, and occupy one-third of the area of the maxillary contact surface of the premaxilla (Fig. 1). The corresponding face of the maxilla is too poorly preserved for the channel to be traced. Six or seven large foramina are set into the external surface of this bone. Three are aligned parallel to, and just above, the ventral margin and the others lay dorsal to them.

The palatal surface of the premaxilla bears a ridge along its medial border. When both premaxillae are articulated these ridges contribute to the formation of a single ridge along the symphysis which extends posteriorly to the anterior apex of the vomer. This ridge separates the tooth depressions of left side of the premaxillary part of the palate from those of the right.

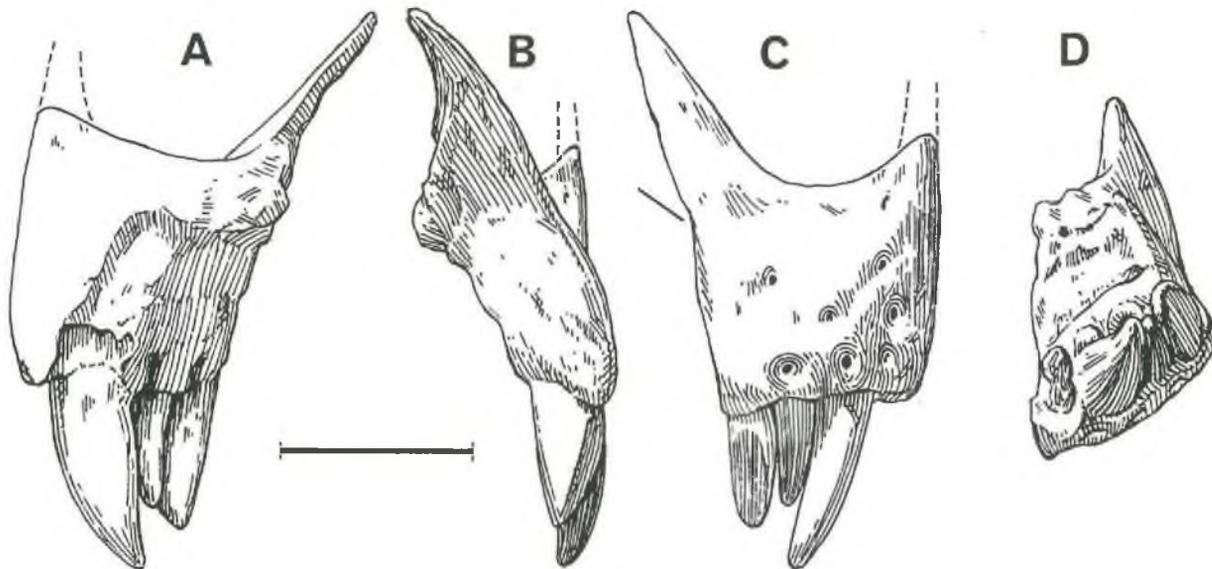


Fig. 1. *Tyrannosaurus rex* OSBORN, LACM 23844, right premaxilla. — A. Medial view. B. Posterior view. C. Lateral view. D. Ventral view. Dotted lines indicate broken nasal process. 0.3×.

Maxilla (Pl. 2): Described by OSBORN (1906) and later figured (OSBORN 1912, Pl. 1 and Figs. 22 and 23) the maxilla of *T. rex* agrees in general form with those of the other well-known species of large theropods. The maxilla is roughly triangular with the apex directed forward: it is deeply emarginate from behind. This emargination forms the antorbital fenestra, anterior to which is the maxillary (previously termed the second antorbital) fenestra. Both fenestrae are set in a distinct common fossa that is more pronounced than in e.g. *Albertosaurus*. The floor of this fossa is inset from the general surface level by 2 to 3 cm. The maxillae are well-preserved in AMNH 5027, LACM 2384, SDSM 12047 and UCMP 118742. The maxillae contact the premaxillae anteriorly, the nasal dorsally, and behind the nasal the lachrymal meets the upper arm of the maxilla above the antorbital fenestra, and medially the shelf-like palatal process joints the vomer anteriorly and palatine posteriorly.

The maxilla of LACM 23844 bears a small foramen along the ventral margin of the antorbital fossa between the maxillary and antorbital fenestrae. This foramen is not found in the maxillae of AMNH 5027 or CM 9380, but opens on the posterior margin of the maxillary fenestra in UCMP 118742. The maxillary fenestra varies in form. In AMNH 5027 it is (roughly) trapezoidal in outline (on the left side) as it is in SDSM 12047 and UCMP 118742, but in CM 9380 it is oval (almost triangular), and in LACM 23844 it is triangular. It is intermediate in form on the right side of AMNH 5027.

The sculpture of the maxilla terminates abruptly at the edge of the antorbital fossa. TMP P81.6.1 is unique in that the maxilla bears no discernible sculpture. A series of prominent foramina parallels the ventral margin.

The maxillae of AMNH 5027 and SDSM 12047 exhibit, just behind the 12th tooth, a sharp lateral flexure of 30° to the long axis. However, in the maxillae of LACM 23844, this flexure is both more subdued, of only 10°, and more anterior, at the 9th tooth. The maxillary flexure is doubtless related to that of the jugal, which together form of the postorbital expansion of the skull: this feature is treated in the discussion.

The maxillae of LACM 23844 and UCMP 118742 bear along their dorsal (nasal) margins a series of chambers — one small and three large — separated by incomplete partitions. The extent and form of these chambers is shown in Fig. 2. Their development varies: in LACM 23844, the third from the front is largest, but in UCMP 118742 the second is largest. A small foramen on the medial face of the maxilla of CM 9380 (OSBORN 1912, Fig. 23), just

posterodorsal to the maxillary fenestra, apparently communicates with these chambers. A foramen on the lateral face at this position is figured by OSBORN (1912, Fig. 22) in this specimen, which is not present in AMNH 5017, LACM 23844 or SDSM 12047. The dorsal portion of the bar separating the maxillary from the antorbital fenestra houses a large triangular chamber apparently not connected to the other four.

In AMNH 5027, CM 9380 and SDSM 12047 (on the right side) the maxilla bears 12 alveoli but in LACM 23844, and possibly on the left is SDSM 12047, it has only 11 alveoli. In anterior view the teeth incline slightly laterally as they do in the Komodo dragon, *Varanus komodoensis*.

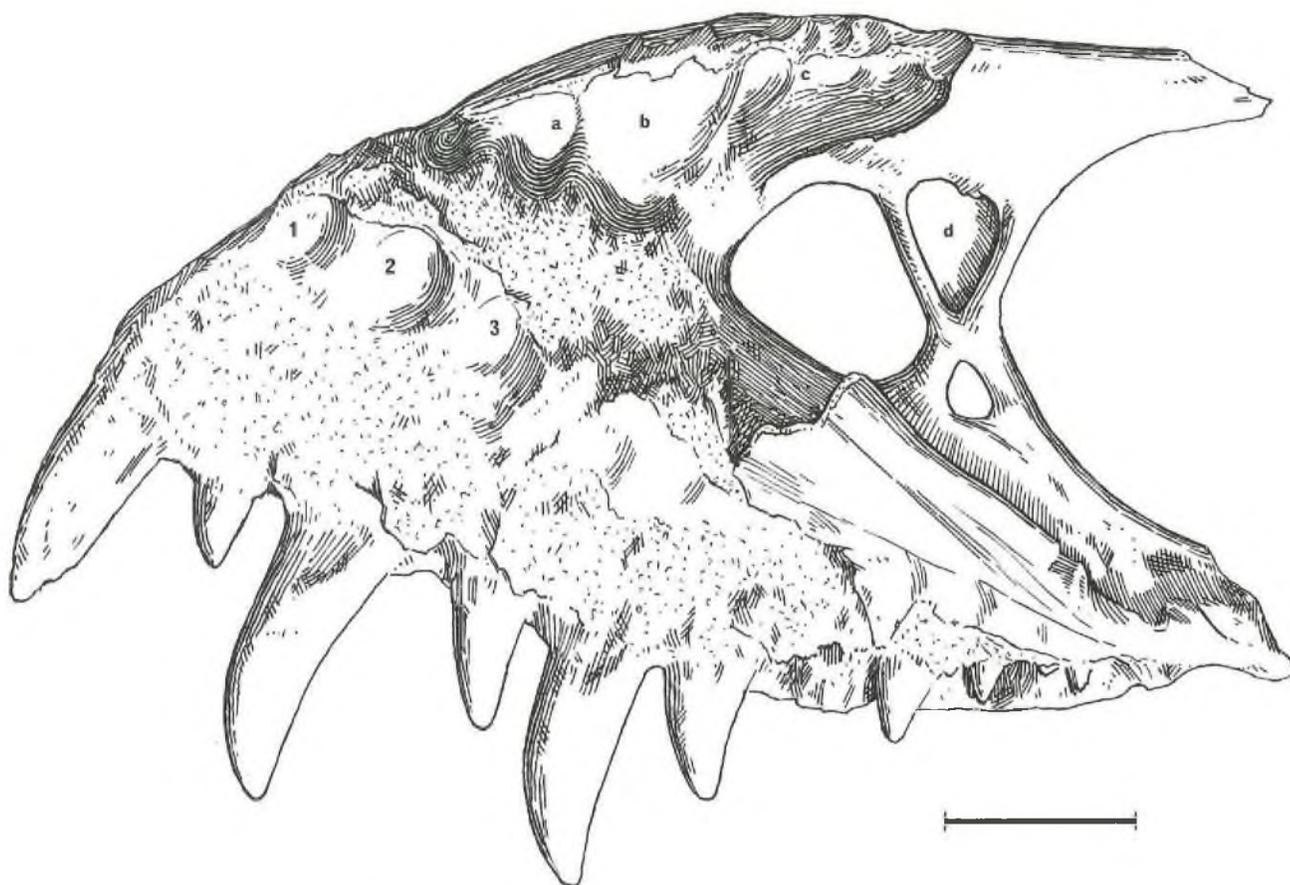


Fig. 2. *Tyrannosaurus rex* OSBORN, LACM 23844, right maxilla represented diagrammatically in medial view. — The exposed sinus chambers may be seen just anterodorsal (a, b and c; the anteriormost is not lettered) and posterodorsal (d) to the maxillary fenestra. The presumed tooth impressions (1, 2 and 3) may also be seen anteriorly, just below the broken palatal process. 0.3x.

The medial (palatal) shelf of the maxilla had a long contact with the palatine. In LACM 23844 and UCMP 118742 the palatal process of the maxilla is relatively more dorsal in position, c. 130% further from the ventral margin than in AMNH 5027 and CM 9380. Although SDSM 12047 exhibits some distortion this process appears to be in a position comparable to that of AMNH 5027, rather than to that of LACM 23844. The medial face of the maxilla bears a number of shallow depressions like those found in the palate of alligatorids. The depressions are assumed to have accommodated the tooth crowns when the mouth was closed, as in alligatorids. The anteriormost is in the palatal part of the premaxilla, and is followed posteriorly by three in the maxilla, decreasing in size posteriorly. These five are large and distinct. The impressions fade out at the mid-portion of the maxilla but become noticeable again posteriorly as three smaller, shallow, confluent depressions that together form a longitudinal groove. These impressions are clear in AMNH 5027, LACM 23844 and UCMP 118742, and the anterior impressions may be seen in OSBORN's figure (1912, Fig. 23) of the maxilla of CM 9380 but impressions were not seen on SDSM 12047. The spacing of the anterior five impressions matches the spacing of the five anterior dentary crowns.

Lachrymal (Pl. 1): The lachrymal has a form like that of the letter "L" inverted, with its lower ramus forming the dorsal part of the preorbital bar. It meets the nearly horizontal upper ramus at an angle of 60°. Along almost the entire length of its upper ramus, the lachrymal joins medially with the nasal and it contacts the maxilla at its anterior termination. It meets the prefrontal and the frontal posteriorly and, apparently, the ethmoid medially along the upper portion of the descending ramus. The jugal contacts the ventral termination of the descending ramus. The inflated, roughly cylindrical upper ramus shows no indication of having borne a lachrymal horn as in earlier large theropods, such as *Allosaurus fragilis*, *Ceratosaurus nasicornis* and *Yangchuanosaurus shangyouensis*. The lachrymal is figured by OSBORN (1912, Pls. 1 and 2) in both lateral and dorsal aspects, in articulation with the other cranial elements. This description relies heavily on LACM 23844; less so on AMNH 5027, MOR 008 and SDSM 12047.

The horizontal ramus of the lachrymal is extensively excavated into a series of at least three chambers (Fig. 3). The small lateral foramen opens into the central of these. The descending ramus is flat, thin and presumably solid; medially it bears a prominent, oblique, slightly curved ridge extending from posterodorsal to anteroventral. A smaller chamber located just lateral to the top of this ridge opens broadly anteriorly and communicates posteriorly with the orbit via a narrow canal (0.04 cm in diameter in MOR 008). Its location and relationships suggest that this canal accommodated the lachrymal duct, and the chamber possibly a nasal sinus.

As on the maxillae the surface sculpture terminates abruptly, marking the dorsal border of the antorbital fossa. This fossa does not extend onto the descending ramus. No sculpture is apparent on the lachrymal of TMP P81.6.1.

Nasals: The general form and appearance of the nasals is shown by OSBORN (1912, Pls. 1 and 2). The nasals resemble those of *Albertosaurus libratus* but are more rugose in most specimens. Anteriorly the nasal touches the premaxilla both above and below the external naris. Laterally, over most of its length, it joints the maxilla and, posteriorly, the anterior ramus of the lachrymal. Tapering posteriorly, the nasals are strongly constricted between the lachrymals and posteriorly have only restricted contact with the frontals. A small contact with the prefrontals may have existed immediately lateral to the junction with the frontals, but this cannot be verified on any known specimen.

The nasals are strongly arched in transverse section, and have a dorsal surface that is usually strongly rugose at the midline. These rugosities are absent in TMP P81.6.1, and less pronounced in LACM 23844 and SDSM 12047 than in AMNH 5027. They are most emphatically developed in MOR 008, where prominent cusps are present (Pl. 3). This specimen also shows several well-developed foramina (to 1 cm in diameter). The dorsal surface is distinctly depressed at the level of the anteriormost contact with the lachrymals. There is no indication of internal chambers.

The premaxillary processes of the nasals of LACM 23844 are broken just anterior to the nasal symphysis, however sufficient remains to indicate that they were oval, nearly cylindrical rods like those of MOR 008, but unlike the flattened premaxillary processes of AMNH 5027.

Postorbital (Pl. 4): The postorbital, in articulation, is figured by OSBORN (1912, Pl. 1): it is preserved in AMNH 5027, LACM 23844, MOR 008, SDSM 12047 and TMP P81.12.1. Essentially a flat, broad, vertical plate it is, in its upper portion mildly concave internally and convex externally. The postorbital of *T. rex* is much broader than in the earlier *Allosaurus fragilis*, *Ceratosaurus nasicornis* and *Yangchuanosaurus shangyouensis*. It is even slightly broader than in *Alectrosaurus olseni*: it is matched in broadness, however, by that of the unrelated *Carnotaurus sastrei*. This vertical plate sweeps forward ventrally in a gentle curve, to give to the orbit the so-called keyhole shape characteristic of *T. rex*. The postorbital meets the frontal, and posteriorly adjacent to it the laterosphenoid, joined anteromedially along its upper margin. Posteriorly it is embraced by the squamosal and ventrally touches with the jugal. The external surface has very low relief, with a rugosity of varying development situated dorsoposteriorly adjacent to the orbit. Crescentic roughened areas of low relief are found here in other tyrannosaurids as well as rugosities in *Allosaurus fragilis* (MADSEN 1976) and the sauropod *Camarasaurus* (MADSEN, personal communication, 1972).

Just below the dorsal margin the smoothly curved flange, extending anteromedially to contact the frontals, forms the anterolateral margin of the supratemporal fenestra. Judging from comparison with living crocodylians this area forms part of the area of origin of the *M. adductor mandibulae externus profundus*.

The lateral face of the anteroventral portion of the plate-like body is distinctly depressed "into" the orbit and set off from the remainder of the lateral face by a slope. In AMNH 5027, LACM 23844 and TMP P81.12.1 this depressed segment bears an anteroventrally directed process that projects into the orbit. Such a process has not been found in any other tyrannosaurid, and is not preserved in either MOR 008 or SDSM 12047.

Because there is considerable, systematic variation in the form of the postorbital rugosity it is interesting to con-

sider this structure in some detail. This rugosity is least developed in LACM 23844 and most exaggerated in MOR 008: the sequence of increasing prominence is LACM 23844, TMP P81.12.1, SDSM 12047, AMNH 5027, MOR 008.

The postorbital of LACM 23844 bears a low roughened area (Pl. 4), rather than an actual rugosity. This is more or less linear in form, extending from the centre of the dorsal margin ventrally, and curving gently anteriorly at its ventral termination. It fades into parallel ridges posteriorly. Just in front of this rugose "line" is a smooth area, with tubercles at the dorsal margin of the element. Just above the dorsal margin of the orbit is a short groove anteriorly, rimmed both above and below by tubercles.

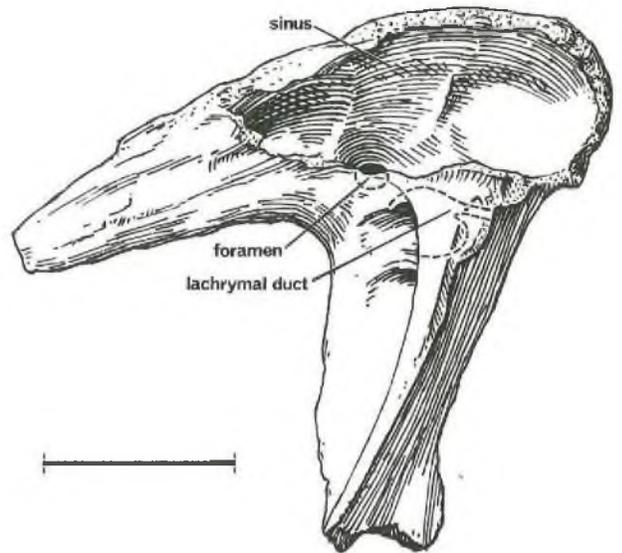


Fig. 3. *Tyrannosaurus rex* OSBORN, LACM 23844, right lachrymal represented diagrammatically in medial view. — The upper sinus chambers are exposed, and the chamber in the descending ramus is indicated by dotted lines. The position of the lateral foramen is also indicated in dotted line. 0.3x.

A rugosity is present in TMP P18.12.1 in the form of a crescent open anteriorly. Prominent, roughly hemispherical, upper and lower excrescences are linked by a less prominent rugose ridge. The anterior, supraorbital portion of the postorbital is rugose, but without the projecting eave-like flange found in SDSM 12047, AMNH 5027 and MOR 008.

In SDSM 12047 only the left postorbital rugosity is exposed: it is oval, with a narrow sulcus posteriorly continuous with the smooth lateral face of this bone. The upper limb of the rugosity is low and elongate, much as in AMNH 5027, and the also elongate lower limb extends posteriorly for an equal distance. Slightly overhanging the orbit, this lower limb bears ventrally a flat face rimmed by a narrow groove bounded both above and below by lines of tubercles. The rugosity fades anteriorly into the sculpture of the posterior portion of the lachrymal.

The rugosity of AMNH 5027 is more emphatic, and apparently better developed (or better preserved) on the left. It exhibits the basically crescentic pattern found in SDSM 12047 with a central sulcus, floored by smooth bone, open behind. This sulcus is more broadly open than in SDSM 12047. The lower limb is a bulbous, almost hemispherical structure that overhangs the orbit: not elongate as in SDSM 12047. The flat ventral face over the orbit is edged by a narrow groove, in turn rimmed by the lines of tubercles as is SDSM 12047. The upper limb is low and anteroposteriorly elongate, extending along the dorsal margin of the postorbital: it is rugose externally, but smooth medially. Anteriorly there is a deep notch or groove between the rugosity and the lachrymal, not seen on any other specimen.

The rugosity of MOR 008 (Pl. 4) shows similarities to those of SDSM 12047 and AMNH 5027. This rugosity extends over almost the entire dorsal portion of the postorbital. The orbit is overshadowed by the flat, ventral surface of an eave-like projection. This projection is edged by a groove, lined both above and below by a row of tubercles, as in both AMNH 5027 and SDSM 12047. Its dorsal surface slopes, more or less smoothly, back to the dorsal margin of the element, much as an awning slopes back to the roof of a building. A dorsal branch of the rugosity extends posteriorly along the dorsal margin of the postorbital, paralleled by an elongate ventral branch (at the level of the ventral margin of the squamosal process). These branches are separated by a smooth-floored sulcus, open posteriorly.

The rugosities of SDSM 12047, AMNH 5027 and MOR 008 share two characteristic features: above the orbit is a groove rimmed on both sides by tubercles, and the rugosity is formed like a crescent open posteriorly. LACM 23844 also shares the tubercle-edged groove. TMP P81.12.1 shares with the other tyrannosaurids a rugosity formed like a crescent open forwards.

Squamosal (Pl. 2): This element is completely preserved in CM 9380 (where it is incorporated into the reconstructed skull and thus is not available for examination) and in SDSM 12047. It is described and figured by OSBORN (1906, Fig. 1). The disarticulated squamosal of MOR 008 lacks only the ventral (quadratojugal) process, but in AMNH 5027 the dorsal margins are missing from both sides. No squamosals were found with LACM 23844 and the element mounted in that position in the reconstructed skull is in fact the ectopterygoid. This came about by mistake that was recognized too late to be corrected. This description relies principally on MOR 008 and SDSM 12047.

Viewed from above the squamosal is quadrate in form, and the anterior margin is deeply embayed into a smooth curve, laying between the elongate anterolateral and anteromedial processes. This anterior moiety of the body, approximately in the horizontal plane, lays above the lateral temporal fenestra and posteriorly becomes a plate, orientated in a parasagittal plane, that arcs back and downward from its contact with the postorbital to meet the upper termination of the quadrate. In dorsal aspect this posterior part of the body appears as a short posterior projection (Pl. 2). The dorsal face of the anterior part is flat, but the ventral is broadly concave, forming a wide inverted trough. Laterally this portion of the body embraces the squamosal process of the postorbital, and medially it contacts the exoccipital-opisthotic.

From the posterior part of the body, where it meets the quadrate, a thin, deep quadratojugal process extends forward along the top of the quadratojugal. Medially the anterior portion of the body comes into contact with the supraoccipital crest of the parietal. This anterior portion of the body of the squamosal is hollow, with a large sinus chamber that opens both via a posteriorly-directed canal, and through a fenestra in the posterolateral region of the ventral face.

In lateral view the squamosal is shaped like the letter "V" laying on its side. The body forms the upper leg of the "V", and the quadratojugal process the lower. The dorsal part of the lateral temporal fenestra is largely encompassed within this "V". At the apex of the "V" a smooth surface extends posteriorly from the margin of the fenestra onto the lateral face of the squamosal (Pl. 5). A similar feature may be seen on the quadratojugal. This smooth surface is set off posteriorly from the roughened external surface of the bone by a distinct low, obtuse ridge in MOR 008 and in AMNH 5027. Comparison with the living crocodylians suggests that this is part of the area of origin of the *M. adductor mandibulae externus superficialis et medialis*.

The nearly complete skulls of *Albertosaurus libratus* (AMNH 5434) and *Daspletosaurus torosus* (RUSSELL 1970, Fig. 7) show the dorsal face of the squamosal posteriorly bounding the supratemporal fenestra. This shelf is placed behind the level of the supraoccipital crest. The articulated skulls of *T. rex* (AMNH 5027 and SDSM 12047) seem to show this surface laying mostly anterior to the level of that crest. However the preservation of both skulls makes a firm conclusion impossible, and the form of the isolated squamosal of MOR 008 suggests a similar position to those of the earlier tyrannosaurids.

Jugal (Pl. 3): The jugal is described and figured by OSBORN (1912, Pls. 1 and 2): it consists of a long, deep, laterally compressed body surmounted by a prominent triangular ascending process meeting the postorbital. This element is similar in form to that of *Allosaurus fragilis*. Anteriorly it touches the maxilla, and posteriorly embraces the ventral process of the quadratojugal. The ectopterygoid joins with the ventral margin of the jugal just behind the maxillary junction. AMNH 5027, LACM 23844 and SDSM 12047 retain well-preserved jugals. The jugals of LACM 23844 differ from those of AMNH 5027 and the right of SDSM 12047 in that the marked inward flexure of the anterior moiety is absent. In other words, the jugals of LACM 23844 are almost straight in ventral aspect. In AMNH 5027 and at least on the left side of SDSM 12047 the anterior one-third of the body of the jugal is inclined at 60° to the remainder. On the left side of SDSM 12047 the flexure is of 45° to 50° and at the level of the ventral jugal rugosity. The significance of this is explored in the discussion.

A large foramen on the lateral surface of the maxillary process of the jugal marks the anterior extremity of a large chamber in the body of the jugal. During preparation the left jugal of LACM 23844 was accidentally broken vertically through the anterior portion of the ascending process. This revealed a closed chamber leading dorsally into the ascending process from the central chamber in the body of the jugal. The ascending channel terminates dorsally

in a slight expansion just dorsal to the ventral extremity of the postorbital contact (Fig. 4). At the centre of the base of the postorbital process, on the medial face, a small foramen opens via a channel 0.8 cm in diameter into what is presumably the central portion of this chamber. Roughly opposite this foramen, on the lateral face of the left jugal of LACM 23844, is another small foramen with an acutely pointed flange behind. This foramen is absent from AMNH 5027, but opens into the sinus chamber in LACM 23844.

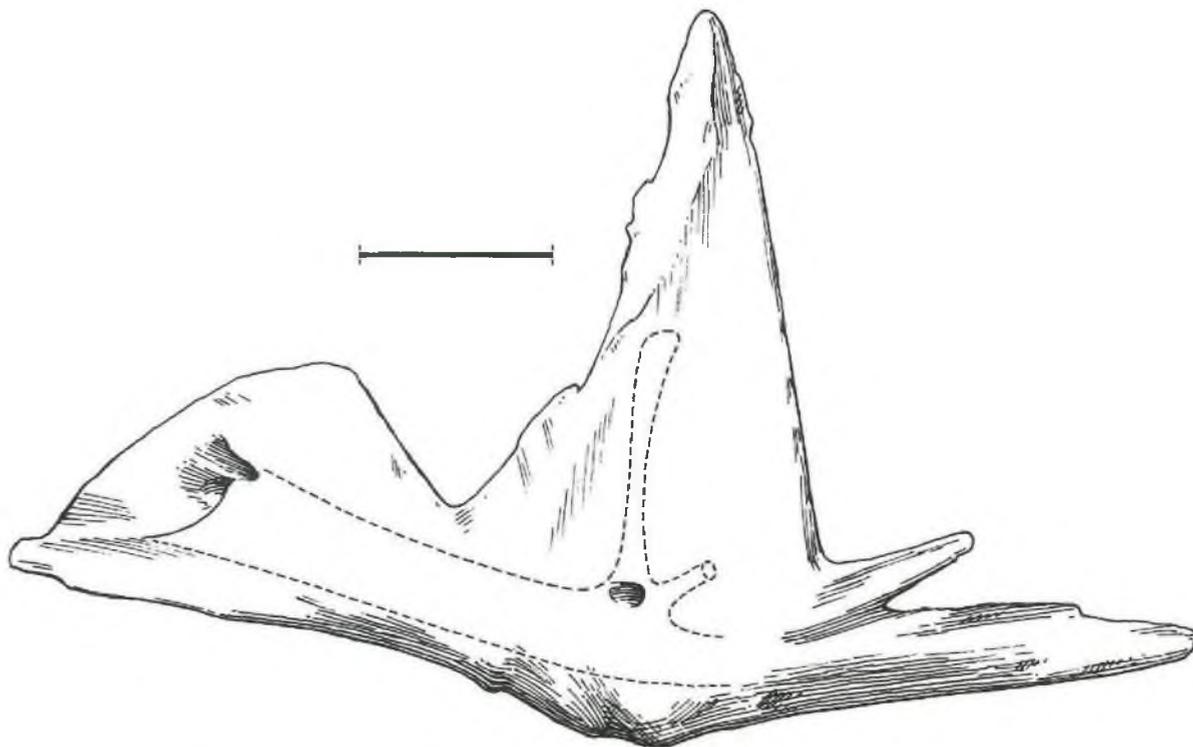


Fig. 4. *Tyrannosaurus rex* OSBORN, LACM 23844, left jugal in lateral view. — The presumed extent of the internal chambers is shown in dotted line. The medial foramen also so indicated, at the end of the short passage directed posterodorsally from the area of the lateral foramen. 0.3X.

Both jugals of LACM 23844 and of SDSM 12047 show marked rugosities along the ventral margin beneath the postorbital process. These rugose areas differ in detail. In LACM 23844 the central of these consist of a depressed, roughly circular area facing ventrolaterally, with two projections ventrally and slightly medially just behind the circular region. This rugosity is less marked on the right jugal. The left jugal of SDSM 12047 (the surface of the right is not sufficiently well exposed) bears anteroposteriorly orientated linear projections at this location. The left jugal of LACM 23844 also shows rugose areas on the lateral face, just below the orbit (not preserved on the right).

Quadratojugal (Pl. 1): The quadratojugal is figured in articulation by OSBORN (1912, Pl. 1). This element, quite different in form in *Tyrannosaurus* from those of non-tyrannosaurids, is basically a laterally compressed vertical shaft from which two processes project anteriorly; the jugal process below and squamosal process above. A third, smaller process extends medially around the quadrate to which the quadratojugal is rigidly attached. The jugal process reaches forward to contact the jugal. The squamosal process is deeply concave laterally. Because its dorsal margin is very thin, seemingly no articulation with the squamosal existed. The left quadratojugal of LACM 23844 is complete as are the right of MOR 008 and the left of SDSM 12047, but neither of AMNH 5027 is complete.

The anterior margin of the quadratojugal, that bounds the posterior extension of the ventral part of the lateral temporal fenestra, bears a smooth surface that extends back from the fenestra for 2.5–4 cm. There is a similar feature on the squamosal. This smooth surface is bounded posteriorly by an abrupt rim (Pl. 1), bearing rugosities in MOR 008. This surface may have afforded attachment for part of the external mandibular adductor. Similar, but less marked, features are found in the other tyrannosaurids and *Allosaurus fragilis* (AMNH 600).

The quadratojugal of LACM 23844 has an oval rugosity on the lateral surface of the vertical isthmus. This consists of marked protuberances at the top and bottom, with low crescentic ridges between. This area is not preserved in AMNH 5027, and such a structure is not found in any of the other specimens, although there is a broad, shallow concavity at this position in MOR 008. Such a rugosity is not present in *Allosaurus fragilis*, but is reported in *Ornithosuchus longidens* (WALKER 1964). It resembles a tendon scar, but no tendon known to me attaches to the lateral face of the quadratojugal.

Vomer (Fig. 5): The vomer is figured only in ventral view in situ by OSBORN (1912, Fig. 6), and so here will be treated in more detail than elements more completely described and figured by OSBORN. The vomer of AMNH 5027 is complete and preserved in articulation, and that of MOR 008 lacks the anterior portion (the rhomboid plate). That of LACM 23844 is represented by two pieces, not sharing a contact. This description is based largely on the vomers of LACM 23844 and MOR 008.

The vomer may be divided into two portions, the anterior rhomboid plate (described by OSBORN) and a posterior, laterally compressed stem (Fig. 5). The stem is bifurcate, composed of two plates closely appressed on the midline, much as in *Allosaurus fragilis* (MADSEN 1976) and *Megalosaurus hesperis* (WALDMAN 1974) thus confirming Waldman's identification. The division between these plates apparently extends further forward dorsally than ventrally. The stem deepens posteriorly (at least as far as preserved in MOR 008). In lateral aspect the ventral margin is slightly concave ventrally, but the dorsal margin is nearly straight, but with an abrupt drop in level near the centre. The rhomboid plate is thin and concave ventrally; it is much broader than in *Allosaurus fragilis* (MADSEN 1976).

The ventral margin of the left branch of the stem in LACM 23844 bears two circular pits which resemble alveoli, but (if so) retain no traces of teeth — no such feature could be found in MOR 008.

The vomer is met extensively, both laterally and dorsally, by the palatal process of the maxilla: it may reach far enough forward to contact the premaxilla, but this is unclear. The posterior stem of the vomer was overlapped laterally by either the anterior, vomerine process of the pterygoid or the medial margin of the palatine (or both). No specimen is sufficiently well-preserved and exposed to allow confidence regarding these contacts.

The rhomboid plate is approximately twice as large in AMNH 5027 (24 cm long) as in LACM 23844 (12 cm long). It is not inconceivable that this part of the vomer actually derives from the specimen of *Albertosaurus megagracilis* (LACM 23845) found adjacent to LACM 23844. But this seems unlikely because the cranial elements of LACM 23844, although disarticulated, were associated in a relatively small area. Pending the discovery of further complete vomers of either *Albertosaurus* or *Tyrannosaurus* this vomer is considered, albeit tentatively, to pertain to *T. rex*.

Palatine (Pl. 6): This element is figured in place by OSBORN (1912, Fig. 6), and is preserved in AMNH 5027, MOR 008 and SDSM 12047. In both AMNH 5027 and SDSM 12047 only the ventral surface is exposed. The palatine is an inflated, trapezoidal element with a planar ventral face (Pl. 5). The long base of the trapezoid, extended by short anterior and posterior processes, contacts the maxilla. Thus the palatine of *T. rex* is quite different in form from those of *Albertosaurus libratus* and *Daspletosaurus torosus*, which are basically V-shaped (figured by RUSSELL 1970). The short medial edge of the trapezoid met either the pterygoid or vomer (or both). As in both *Albertosaurus sarcophagus* and *Daspletosaurus torosus* (RUSSELL, personal communication, 1985) the palatine of MOR 008 is extensively excavated, with the thin dorsal and ventral walls reinforced by central transverse internal ridges. The palatines of MOR 008 and SDSM 12047 exhibit no ventral foramen as in *Albertosaurus* and *Daspletosaurus*, possibly because of their incompleteness, although one was figured by OSBORN (1912, Fig. 6) in AMNH 5027.

The anteromedial margin of the palatine, bounding the internal naris, is deeply embayed. The posterior margin is smoothly rounded and emarginate from behind in SDSM 12047. This posterior margin is not in contact with the pterygoid wing of the ectopterygoid in this specimen, nor in AMNH 5027, but seemingly a fenestra opens in the palate between the palatine and ectopterygoid (OSBORN 1912). It is not clear, due to the distortion of the specimens, whether the anterior process of the ectopterygoid contacted this margin: it does not in *Daspletosaurus torosus* (RUSSELL 1970). There is some indication in SDSM 12047 that the internal chamber may have opened posteriorly just dorsal to the posterior margin.

Ectopterygoid (Transversal — Pl. 7): Among the elements of LACM 23844 is an incomplete left ectopterygoid, another is preserved in articulation in AMNH 5027, and MOR 008 retains both ectopterygoids. SDSM 12047 shows the anterior part (at least) of the left. Ectopterygoids are figured in situ in the skull of the AMNH 5027 by OSBORN (1912, Fig. 6). This description is drawn largely from MOR 008.

The ectopterygoid, although relatively larger, resembles that of *Daspletosaurus torosus* (RUSSELL 1970, Fig. 9) and is in form like a triskelion with one limb (the medial) almost entirely removed (Pl. 7). It has an anterolateral, posterolateral and truncate medial arm. The abbreviate medial limb extends from the central body of the ectopterygoid to overlap dorsally the palatal plate of the pterygoid. This process is a thin horizontal flange, flaring slightly toward its medial margin. The anterolateral limb contacts the jugal, and the posterolateral limb forms (in conjunction with the ectopterygoid process of the pterygoid) the "pterygoid wing". The jugal limb, complete only in SDSM 12047, tapers smoothly toward its distal termination. The posterolateral pterygoid limb is connected dorsally to the posterior portion of the medial process by a web of bone, roofing a fenestra of moderate size.

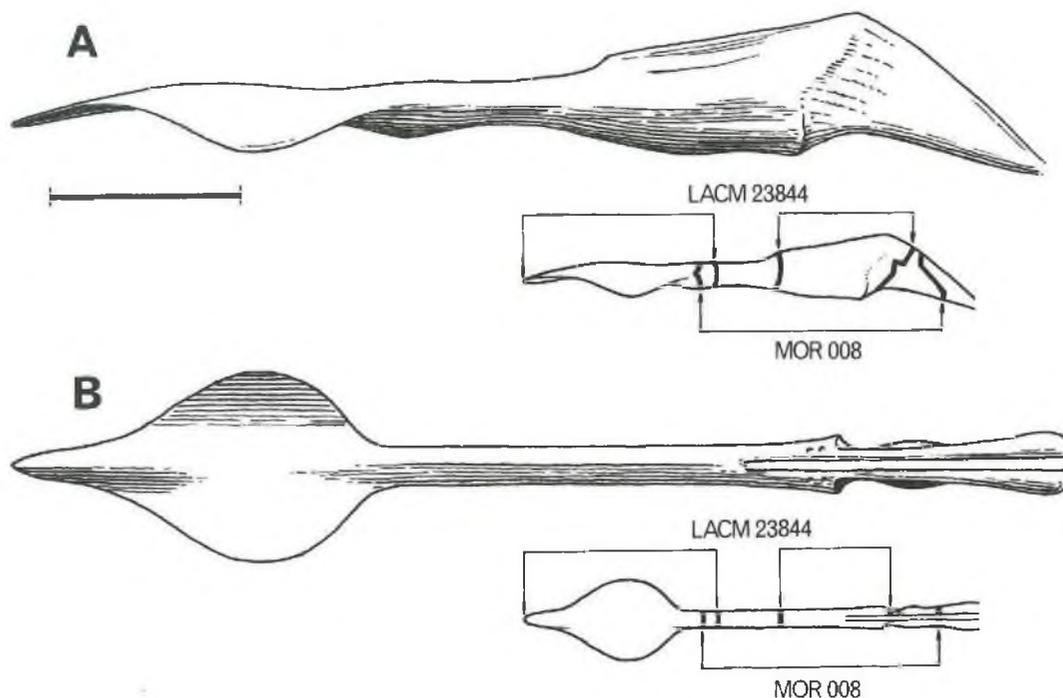


Fig. 5. *Tyrannosaurus rex* OSBORN, reconstruction of the vomer. — A. Left lateral view. B. Ventral view. The extreme posterior portion is unknown. The insets indicate which parts of the reconstruction are based on LACM 23844 and which on MOR 008. Scale bar 10 cm.

The greater portion of the pterygoid limb is occupied by a set of (at least) three interconnecting chambers, opening posteroventrally, presumably into the oral cavity. Such vacuities are common among theropods, and have been described for *Allosaurus fragilis* (MADSEN 1976), *Daspletosaurus torosus* (RUSSELL 1970), *Deinonychus antirrhopus* (OSTROM 1969), *Dromaeosaurus albertensis* (COLBERT & RUSSELL 1969), *Garudimimus brevipes* (BARSBOLD 1983), *Nanotyrannus lancensis* (GILMORE 1946), *Saurornithoides junior* (BARSBOLD 1983), *Saurornitholestes langstoni* (SUES 1978) and *Tarbosaurus bataar* (MALEEV 1974) as well as for *T. rex*. The functional significance is unknown: *Albertosaurus libratus* has only a small vacuity (RUSSELL 1970) and they are absent from *Ceratosaurus nasicornis*, ornithomimids and oviraptorosaurs. The medial chamber of the ectopterygoid of LACM 23844 is the largest, occupying the central region of the medial half of the pterygoid limb, and extending anteriorly for an unknown distance into the pterygoid ramus. The distal chamber is the next largest and occupies the distal region of the limb. The central chamber is the smallest: it is broadly connected with the distal chamber beneath a bridge of bone but seemingly not with the medial chamber. The chambers open posteriorly via a broad aperture in the pterygoid limb.

The surface of these chambers is smooth, as is most of the external surface of this element. The surface of the anteroventral part of the pterygoid limb is roughened (in LACM 23844 but not in MOR 008 or SDSM 12047), to an extent comparable to the rugosities of the external surface of the skull.

Pterygoid (Fig. 6, Pl. 8): Of the pterygoids only the palatal surfaces are exposed in SDSM 12047 and AMNH 5027 (OSBORN 1912, Fig. 6), hence this element has been less adequately described than most others. It is poorly

known among theropods in general and is figured in isolation only for *Tarbosaurus bataar* (MALEEV 1974) and *Allosaurus fragilis* (MADSEN 1976). The pterygoid of *T. rex* is generally similar to the pterygoids of those two taxa. Among the elements of LACM 23844 is an incomplete left (and fragmentary right) pterygoid, and MOR 008 showed an almost complete right pterygoid in place prepared from the medial side, and now removed.

The pterygoid is composed of two major components: a horizontal, flat palatal plate and a flat, plate-like, vertical quadrate process (Fig. 6). A thin, flat ectopterygoid process extends laterally, and a vomerine process anteriorly from the palatal moiety of the pterygoid. The palatal plate makes contact anteriorly with the vomer and palatine, posteriorly with the basisphenoid, and laterally and dorsally with the ectopterygoid. The quadrate process rises from the palatal plate just anterior to the basisphenoid contact and is orientated vertically in the skull, moderately inclined to the sagittal plane. The quadrate processes of LACM 23844, MOR 008 and SDSM 12047 are thin and rather delicate, but that of CM 1400 is robust (as in *Albertosaurus megagracilis*: MOLNAR 1980). Apparently the thickness of this process is subject to individual variation (or CM 1400 may be incorrectly identified).

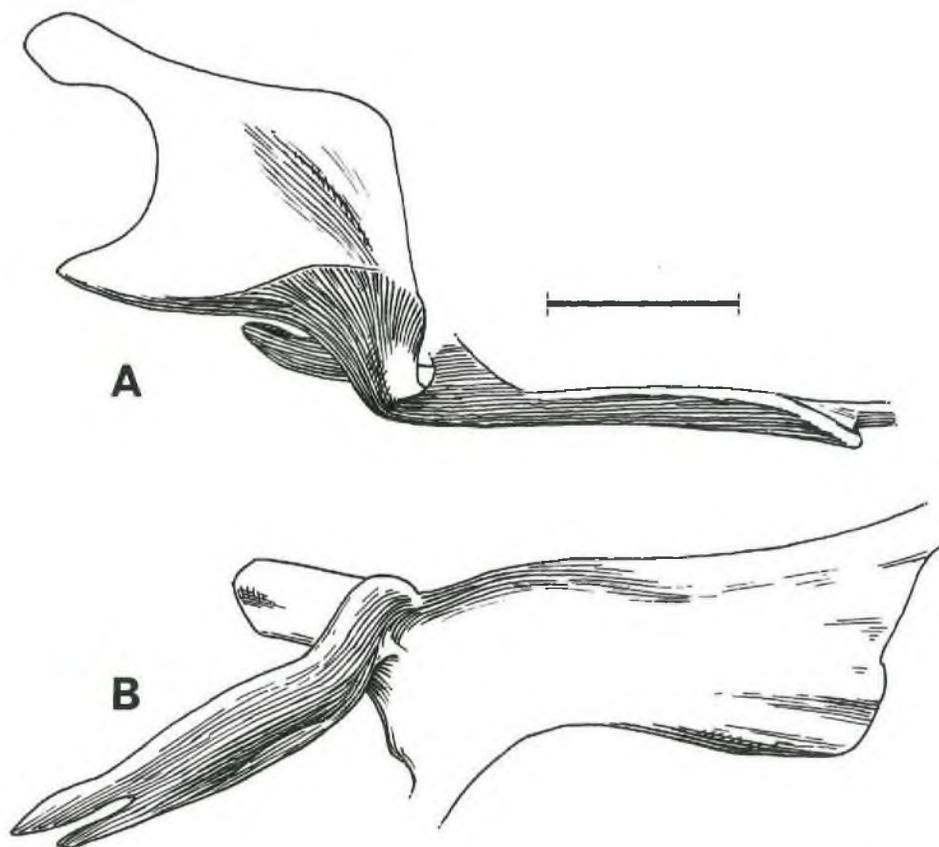


Fig. 6. *Tyrannosaurus rex* OSBORN, reconstruction of the right pterygoid. — A. Lateral view. B. Dorsal view. Based on LACM 23844 and MOR 008. The extent and form of the anterior and lateral processes are unknown. Scale bar 10 cm.

The medial face of the quadrate process is flat and almost featureless, and the external face is mildly convex. The posterior edge of the quadrate process is concave, so that dorsal and ventral marginal processes extend posteriorly. There is a slight bounding ridge laying somewhat posterior to the dorsal of these two processes on the medial surface of the quadrate.

A small process extends posteriorly from the posterior margin of the palatal plate, just behind the root of the quadrate process, and makes contact with the basiptyergoid process of the basisphenoid. This contact remains in articulation in SDSM 12047. On the medial surface of the pterygoid process of the quadrate there is a roughened sub-circular area just anteromedial to the basiptyergoid contact (Pl. 8). MOR 008 in addition exhibits a set of at least four helical ridges extending from anterodorsal to posteroventral just medial to this marking along the anterior margin

of this process (again as in *Allosaurus fragilis*). These features may mark the attachment of the *M. levator pterygoideus*. The remainder of the medial surface of this process is smooth.

Epipterygoid (Pl. 9): Visible in the left antorbital fenestra of AMNH 5027 (OSBORN 1912, Pl. 1) is an inflated rodlike element that OSBORN (1912) labelled an ectopterygoid. This element bears little resemblance to an ectopterygoid and both ectopterygoids are visible. Thus this element is not an ectopterygoid: it has for many years been labelled “epipterygoid”, and this seems correct. (OSBORN’s label may have been the result of a typographical error rather than an incorrect identification.) The epipterygoid of AMNH 5027 must have been displaced anteriorly about one-half meter from its *in vivo* position to be visible, and in addition has been rotated by 90° so that its lateral face now looks anteriorly. MOR 008 exhibited the ventralmost portion of the right epipterygoid apparently *in situ*, in contact with the dorsal margin of the quadrate process of the pterygoid (Pl. 9).

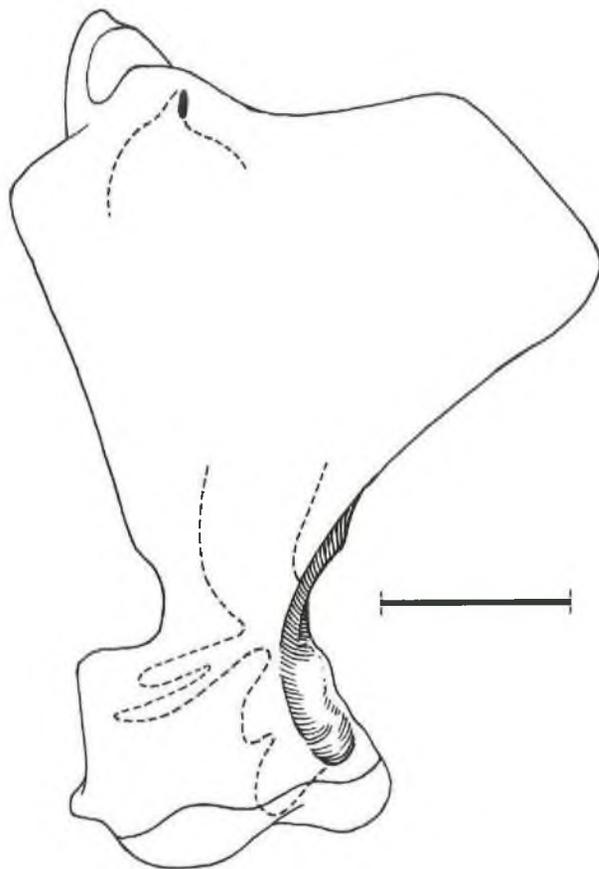


Fig. 7. *Tyrannosaurus rex* OSBORN, diagram of right quadrate in anterolateral view. — Based largely on I.ACM 23844, but also on MOR 008. The known extent and positions of the internal chambers are indicated by dotted lines. 0.3x.

Epipterygoids have been described, for post-Triassic theropods, only for *Albertosaurus sarcophagus* (LAMBE 1904, given as *Dryptosaurus incrassatus*), *Allosaurus fragilis* (MADSEN 1976), *Ceratosaurus nasicornis* (HAY 1908) and *Dromaeosaurus albertensis* (COLBERT & RUSSELL 1969): a possible epipterygoid has been reported in *Compsognathus longipes* (OSTROM 1978). Ventrally the epipterygoid contacts the anterodorsal margin of the pterygoid and dorsally the anteroventral face of the laterosphenoid (at least in *D. albertensis* and *A. fragilis*; the dorsal end is not preserved in *C. nasicornis* and is not in place in *A. sarcophagus*). A shallow concavity on the laterosphenoid of *T. rex*, which might mark the dorsal articulation of the epipterygoid, will be further discussed in the section on the braincase.

The epipterygoid of MOR 008 is flattened mediolaterally and has a slightly roughened contact surface for the pterygoid. This surface is bounded dorsally by a distinct curved angulation or rim. The form of the epipterygoid cannot be completely determined from the portions visible in either AMNH 5027 or MOR 008. There is an upper strongly convex bar, wider (transversely) than long, and a ventral flattened subcircular plate, visible in AMNH 5027 (OSBORN 1912, Fig. 3). The pterygoid articular portion in MOR 008 apparently corresponds to this subcircular plate,

which faces anteriorly as the element is now orientated in AMNH 5027. The dorsal bar resembles the epipterygoid of *Albertosaurus sarcophagus* as figured by LAMBE (1904). He describes this element as a "conico-cylindrical bone" (LAMBE 1904, p. 14), a description fitting the upper portion of the epipterygoid of AMNH 5027: the lower portion of the epipterygoid was not exposed on that specimen of *A. sarcophagus*.

Quadrate (Pl. 10): The quadrate of *T. rex* resembles those of other theropods such as *Albertosaurus* and *Allosaurus*. In form it is a vertical bar, flaring broadly both medially and laterally at the condyle, and supporting medially the plate-like pterygoid process. This process extends forward to widely overlap the corresponding quadrate process of the pterygoid. In addition, the quadrate dorsally meets the squamosal, laterally the quadratojugal, and ventrally the articular. The condyle is divided by a helical depression — as described by GILMORE, 1920, for *Allosaurus fragilis*.

The deep, flat, smoothly surfaced pterygoid process extends anteriorly and slightly medially, and is markedly concave on the medial face in LACM 23844. SDSM 12047 shows a concave roughening (on the left side) at this position. A large foramen lays at the medial edge of the anterior face of the quadrate just above the condyle as in other tyrannosaurids. The foramen connects to the chambers within the quadrate. In *Allosaurus* there is a distinct depression at this position, but no foramen.

The ventral portion of the quadrate contains two chambers (MOLNAR 1985) revealed in LACM 23844 and MOR 008, the smaller lateral to the larger. It is with the larger of these (c. 9 cm in height in MOR 008) that the foramen communicates (Fig. 7). A canal extends dorsally into the pterygoid process and is of undetermined extent, although it is clear that a passage, presumably this one, extends to just below the dorsal termination of this element. Two channels (in LACM 23844 and at least one in MOR 008) extend into the lateral process which articulates with the quadratojugal.

The dorsal portion of the quadrate is topped by a roughly saddle-shaped articular surface for the squamosal: this is further described in the section on joints.

Braincase: All braincases of *Tyrannosaurus* examined (AMNH 5029, AMNH 5117, MOR 008 and MMS 51-2004) have the elements firmly articulated. The AMNH specimens were described by OSBORN (1912). The contacts all are sutural, allowing no motion between these elements. Little improvement upon the observations of OSBORN (1912) regarding the ethmoid elements and parasphenoid has been made, so these will not be extensively discussed. The nomenclature of the braincase elements used by MADSEN (1976) is followed here.

The frontal (Pl. 8) is a moderately thick plate, trapezoidal in dorsal view and declined posteriorly where it is invaded by the supratemporal fossa. This fossa occupies about two-thirds of the dorsal surface of the frontal, leaving only a small anterior triangle directly underlying the integument. This is quite distinct from both *Albertosaurus* and *Daspletosaurus*, where the supratemporal recess occupies only the posterior half of the dorsal face of the frontal (cf. CURRIE 1987). The frontal is almost entirely surrounded by contacts with other elements: the nasal, prefrontal and lachrymal anteriorly, the postorbital laterally and the parietal posteriorly. Ventrally it meets the ethmoid and laterosphenoid. Each frontal is about one-half as thick (dorsoventrally) as broad and is invaded below, along its medial margin, by the endocranial cavity.

The fused parietals (Pl. 8) join in a sharp, but rounded sagittal ridge, sloping on either side into the supratemporal recesses which sharply constrict them in dorsal view. Anteriorly the parietal slopes upwards to meet the frontal surface of the supratemporal fossa at a sharp flexure. Posteriorly it rises proud of the skull roof, to spread laterally in the prominent supraoccipital crest. This reaches almost to the squamosal on either side, as recognised by OSBORN (1912). Ventrally the parietal contacts the laterosphenoid, proötic and exoccipital-opisthotic.

The ethmoid of AMNH 5117 (Pl. 11) is a trough-shaped bone underlying the frontals and posterior extremities of the nasals, and reaching posteriorly to the parasphenoid. Anteriorly it is subdivided by a thin median septum, that divided the two olfactory nerves. It shows no indication of a lateral contact with the lachrymal, as suggested by the medial articular surface of that of LACM 23844, and hence is either incomplete in AMNH 5117, or less extensively ossified than that (unfortunately not found) of LACM 23844.

The laterosphenoid ("orbitosphenoid" of OSBORN: Pl. 11) is a dorsoventrally elongate element, broader above — between frontal and proötic — than below, along the basisphenoid. The upper portion is triradiate, with a small process extending medially to the parasphenoid, a robust lateral postorbital process, and a thick posterior extension reaching the proötic. This description relies on AMNH 5117. The laterosphenoid reaches the frontal and parietal above, the postorbital laterally, the proötic and exoccipital-opisthotic behind, the parasphenoid in front and the

basisphenoid below. The posterior face of the postorbital process forms part of the anterior surface of the channel leading to the adductor chamber. A dorsoventrally elongate concavity (Pl. 11), lays anteroventral to this process. It is bounded anteriorly and posteriorly by sharp ridges, the anterior of which is interrupted by the foramen for the fourth cranial nerve.

OSBORN (1912) states that the laterosphenoid also bears foramina for the second, third and fifth cranial nerves, although in his Fig. 8 he clearly illustrates the second cranial nerve as exiting through the parasphenoid (there given as “?presphenoid”) the third as exiting at the parasphenoid-laterosphenoid junction, and the maxillary and mandibular branches of the fifth as exiting at the laterosphenoid-proötic junction. Although the precise relationships of certain foramina of AMNH 5117 are obscured by the fusion of the braincase, that of the second cranial nerve appears to lay on the parasphenoid. The foramen for the third cranial nerve lays lateral to that for the second on the anterior face of the laterosphenoid. The foramen of the fourth cranial nerve, as mentioned previously, lays on the sharp edge at the meeting of the anterior and lateral faces of the laterosphenoid, and is posterior and slightly ventral to that for the third cranial nerve. The relationships of these foramina in other carnosaurs is treated in the discussion. The ophthalmic branch (N. ophthalmicus profundus) of the trigeminal exits through the laterosphenoid on its posterior aspect, posteroventral to that of the fourth cranial nerve, but the foramen for the remaining two branches of the trigeminal appears to lay on the laterosphenoid-proötic contact (as illustrated by OSBORN).

The elongate proötic extends from a sigmoid laterosphenoid contact in front to the V-shaped junction with the exoccipital-opisthotic behind and from the parietal above to the exoccipital-opisthotic below. Seen in lateral view it is backed by the exoccipital-opisthotic: presumably — as no disarticulated braincases were available for study this has not been confirmed. That of AMNH 5117 shows a broad, shallow concavity on the lateral surface extending from immediately above the foramen ovale and fading out over the fenestra ovalis (Pl. 11). This concavity is anteriorly delimited by a ridge which becomes indistinct posteriorly which, to judge from its location, may mark the origin of the levator of the pterygoid. The proötic roofs the foramen ovale.

As in *Allosaurus fragilis* (MADSEN 1976) the exoccipital and opisthotic have never been observed separately in *T. rex*, thus following MADSEN the term “exoccipital-opisthotic” is used here. The exoccipital-opisthotic has roughly the form of a rectangular plate, and extends laterally and slightly posteriorly from the foramen magnum, supraoccipital and basioccipital to form the paroccipital process. It reaches the supraoccipital crest of the parietal above, and has a buttress below contacting the basisphenoidal region in a gentle curve. The paroccipital processes are not declined as they are *A. fragilis*. The exoccipital-opisthotic is anteriorly overlapped by the proötic. The seventh cranial nerve exits from the anterior face of this element near its junction with the laterosphenoid, and the fenestra ovalis lays on the border of the exoccipital-opisthotic with the proötic.

The exoccipital-opisthotic of AMNH 5117, completely preserved only on the right side, shows that this element contained at least one sinus chamber, as reported by RUSSELL (1970). The posterior surface of the right exoccipital-opisthotic has been crushed forward, collapsing into the chamber and thus revealing its existence (Pl. 7). The left exoccipital-opisthotic has been broken through this chamber. The chamber occupies the dorsolateral portion of the exoccipital-opisthotic, and is greatest in its mediolateral dimension and shortest in its anteroposterior dimension, apparently having the form of a very flattened ellipsoid. It extends from beneath the supraoccipital crest laterally to almost the tip of the paroccipital process.

The distal tip of the exoccipital-opisthotic bears a flat, dorsoventrally elongate facet, wide at the top and narrowing ventrally. This facet is set off by an obtuse angulation from the rest of the posterior face of the element. The anatomy of the living crocodylians suggests that this is probably the area of origin of the *M. depressor mandibulae*.

The basioccipital (Pl. 7) forms the occipital condyle of *T. rex*: presumably there was also some contribution from the exoccipital-opisthotic, but fusion of the braincase obscures the extent of this. The condyle is reniform in shape and dorsoventrally compressed. The basioccipital continues ventral to the condyle as a triangular plate, apex upward, appressed to the posterior face of the basisphenoid. Each lateral edge of this plate meets the buttress from the exoccipital-opisthotic. The basioccipital tubera are placed at the ventrolateral angles of this plate.

The supraoccipital (Pl. 7) stands appressed to the posterior face of the supraoccipital crest of the parietals. Its sutural contacts may be seen on AMNH 5117: it sends a triangular process laterally between the parietal and the exoccipital-opisthotic, as in *Allosaurus fragilis* but more extensive. A less extensive process projects dorsolaterally along this crest, above the lateral process. Ventrally it is fused with the exoccipital-opisthotic. In *A. fragilis* (MADSEN 1976) the supraoccipital stands dorsally along the midline to form a prominent wedge-shaped block (the supraoccipital

wedge of BAKKER, WILLIAMS & CURRIE 1988). Such a block is present in *T. rex*, but seems not a part of the supraoccipital, from which it is separated by a suture in both AMNH 5029 and AMNH 5117. If this interpretation is correct, the supraoccipital is of quite different form in *T. rex* than in *A. fragilis*.

The basisphenoid (Pl. 7) projects ventrally as a transverse plate bounded above by the basioccipital, exoccipital-opisthotic, proötic and laterosphenoid. At each ventrolateral angle of this plate is the short, stout basisphenoid process, bearing the basipterygoid articulation. The posterior face of this plate bears two fossae but there is no ventral basicranial fontanelle, although this is well-developed in *Allosaurus fragilis* (MADSEN 1976, Fig. 14) and less prominent in *Albertosaurus libratus* (RUSSELL 1970, Fig. 4). Instead, as observed by OSBORN (1912) and BAKKER, WILLIAMS & CURRIE (1988), the basisphenoid extends ventrally as a thick plate only slightly inclined to the plane of the posterior face of the basioccipital.

At the contact of the laterosphenoid with the basisphenoid, well above the basipterygoid process, is the elongate opening identified by OSBORN (1912) as that of the internal carotid artery (Pl. 11). This foramen is overlain by a distinct slot, open ventrolaterally, in the margin of the laterosphenoid. The basisphenoid of *T. rex* and other tyrannosaurids also contains a set of sinus chambers: the recessus basisphenoideus of OSBORN (1912), asserted to be homologous to the sinus sphenoidalis of mammals by MOODIE (1915). These presumably open through a relatively large pair of apertures, set side by side on the posterior surface of the basisphenoid, just ventral to its contact with the basioccipital. These chambers are described in detail for *Albertosaurus* by RUSSELL (1970). In both *Albertosaurus* and *Tyrannosaurus* the canal for the internal carotid lays in close proximity to the central chamber of the basisphenoid. Indeed, in the sectioned braincase of *T. rex*, AMNH 5029, the carotid canal actually opens into this sinus chamber, becoming a groove in the anterior part of the lateral wall (OSBORN 1912, Pl. 3). A similar condition has been reported in the primitive crocodylian, *Sphenosuchus acutus* (WALKER 1972).

The anterior face of the basisphenoid plate exhibits a depressed area in the form of an isocles triangle, with the apex directed upwards (Pl. 9). In AMNH 5117, adjacent to the lateral edges of this depression are two anteriorly-projecting laminae, joined above. By analogy with the situation in *Allosaurus fragilis* (MADSEN 1976) I take these to be the ventral laminae of the parasphenoid, although in AMNH 5117 they no longer exhibit a connection with the body of the parasphenoid. This seems to have been broken away since the publication of OSBORN (1912), where it is clearly shown in his Figs. 7 and 8. Above, flooring the anterior portion of the endocranial cavity lays the plate-like body of the parasphenoid. It joins the ethmoid anteriorly, the frontal laterally and the laterosphenoid behind, and lays in the horizontal plane.

Dentary (Pl. 12): The dentary is an elongate, laterally compressed tooth-bearing bar, with its ventral margin at the symphysis curving up abruptly from below to the tooth-bearing edge. Posteriorly the dentary flares both ventrally and, more prominently, dorsally. The body is slightly constricted. The dentary contacts only its antimeres anteriorly, but the surangular, prearticular and angular posteriorly, and the splenial and supradentary medially. The dentary of *Tyrannosaurus rex* closely resembles those of most other tyrannosaurids and of *Allosaurus fragilis*, but is slightly deeper posteriorly: it is markedly deeper posteriorly than those of *Ceratopsaurus nasicornis*, *Yangchuanosaurus magnus*, *Yangchuanosaurus shangyouensis* and *Alectrosaurus olseni*. Dentaries are well represented by AMNH 5027, LACM 23844, MOR 008, SDSM 12047 and UCMP 131583. It was described and illustrated by OSBORN (1906, 1912), who also drew attention to the loose condition at the symphysis. MOR 008 clearly shows the symphyseal surface of the right dentary, which surfaces are poorly preserved in LACM 23844 and not available for inspection in the other specimens. The symphyseal surface is flat, with at least five low, slightly curved, longitudinal ridges, mostly directed anteroventrally. Laterally the body of the dentary is gently convex, but medially it is flat with a raised longitudinal bar. Prominent foramina form a line parallel to and just below the dorsal margin on the external surface. They are more closely spaced anteriorly than posteriorly, and extend the length of the element. The interdental plates were overlapped, and hence obscured from view, by the supradentary which was apparently fused to the dentary in most specimens (but not SDSM 12047: BJØRK, personal communication, 1985).

Along the posterior margin of the dentary are three short bladeliike processes (Pl. 13), one extending posteriorly from the posterodorsal "corner" of the dentary and two similarly from the posteroventral "corner": the one situated just dorsal to the other. These processes are flat and bluntly rounded posteriorly. The posteroventral process articulates with the lateral surface of the surangular and the ventralmost process fits against a shallow concavity on the lateral surface of the angular.

This posteroventral angle of the dentary is completely preserved and exposed only in AMNH 5027 (on the left

side — Pl. 13), and incompletely preserved in LACM 23844. Between the two ventral blade-like processes the dentary extends posteriorly as a small, short projection. Conditions similar to this are found in *Albertosaurus libratus*, *Daspletosaurus torosus* (RUSSELL 1970, Fig. 6) and *Tarbosaurus bataar* (as shown on the cast, AMNH 6794). *Nanotyrannus lancensis* (CMNH 7541) apparently has only a single posteroventral process.

The anterior portion of the dentary forms the stout tooth-bearing body of the mandible. As already mentioned, the dentary deepens and thins posteriorly, to form a thin vertical plate. This plate is reinforced along its margins both dorsally and ventrally by bars of bone. The upper marginal bar forms the dorsal margin, bears the posteriormost teeth, and terminates in the posterodorsal process. The ventral marginal bar extends posteriorly from the body to terminate posteriorly in the ventralmost of the posteroventral processes. These bars articulate closely with the dorsal and ventral edges of the splenial, although the ventral edge of the splenial separates from the dentary posteriorly.

Splenial (Pl. 14): The splenial is a flat, thin, roughly triangular element figured but not described by OSBORN (1912, Fig. 18). It is much like that of *Allosaurus fragilis*, but with a larger and more centrally placed foramen. It lays against the dentary laterally, and contacts the prearticular, angular and perhaps the coronoid posteriorly (the coronoid is preserved only in AMNH 5027 and there in articulation, so that its anterior contacts are obscured). Only the medial face of this element is exposed in both AMNH 5027 and MOR 008, and it is incomplete in LACM 23844. Thus a complete description cannot be given.

The posteroventral process of the splenial makes contact with two elements on its lateral surface — the angular ventrally and the prearticular dorsally. The articular surfaces for these two elements are separated by a curved ridge (concave dorsally).

MOR 008 shows that the splenial-dentary contact was particularly close, the dorsal part of the contact being almost indiscernible.

Coronoid: The coronoid is preserved only on AMNH 5027 and was figured by OSBORN (1912, Fig. 18). It is in articulation, thus a complete description is not possible. It is a small triangular plate laying at the anterodorsal angle of the Meckelian fossa. The apex of the triangle is directed anteriorly and the opposing base posteriorly. It is bounded by the surangular dorsally, the Meckelian fossa posteriorly and the prearticular anteroventrally.

Angular (Pl. 15): The angular, in articulation, is figured by OSBORN (1912, Pl. 1, Fig. 18): it is much like that of *Allosaurus fragilis*. Neither of the angulars of AMNH 5027 is completely exposed, but both of LACM 23844 are complete and the right of MOR 008 is almost complete. The angular consists of an elongate posterior plate and a curved anterior stem. The posterior plate is thin, slightly convex laterally, and bears a strong ventral flange anteriorly. The posterior margin is quite irregular — possibly pathological — in MOR 008, unlike that of any other specimen. The plate articulates but loosely with the posteroventral portion of the surangular. The anterior stem is less deep and more robust than the plate and on its medial surface bears a low, curved ridge. This ridge marks the ventral limit of the articulation with the prearticular, that portion ventral to it contacting the splenial. The lateral face of the stem has an extensive, but shallow, depression for articulation with the dentary.

Prearticular (Pl. 14): The medial aspect of the prearticular has been figured and described by OSBORN (1912, Fig. 18) from AMNH 5027, but as neither prearticular was removed from articulation a complete description was not possible. Complete in both LACM 23844 and MOR 008, it is a shallowly crescentic element, concave dorsally, that ventrally bounds the Meckelian fossa. The anterodorsal ramus of the prearticular is a thin, flat plate, but the ventral portion and posterodorsal limb are heavier and almost circular in cross-section. The posteriormost part of the element becomes again quite thin and forms a medial sheath of bone overlying the articular.

Along the ventral surface of the central segment is a flat, elliptical facet, probably for insertion of the *M. branchiomandibularis*. The facet closely resembles, both in form and position, that for the *M. branchiomandibularis* of crocodylians. It shows no variation between AMNH 5027, LACM 23844 and MOR 008.

As mentioned previously, the prearticular closely sheaths the articular along its medial surface and extends around onto the ventral surface. Medially the prearticular comes into contact along its central segment with both splenial and angular. The medial articular surface of the prearticular is divided longitudinally by a sharp ridge separating the splenial-articular face above from the angular-articular face below. In MOR 008 the right prearticular is fused to both surangular and articular.

Surangular (Pl. 15): The surangular, a large thin curved vertical plate with a thick medial flange along its dorsal margin, was described and figured by OSBORN (1906; 1912, Pl. 1). It is deeper than that of *Allosaurus fragilis* but otherwise similar. The vertical plate is marginally overlapped by the angular ventrolaterally and by the prearticular

ventromedially. Posteroventrally there is a broad plane surface on the lateral face, not bounded ventrally, against which the posterior plate of the angular lays. Posterodorsally, just anteroventral to the articular glenoid, the surangular is penetrated by an aperture. A flange extends medially from the posterior portion of the surangular just behind this surangular fenestra, and this flange partially sheaths the anterior face of the articular (the remainder being covered by the prearticular). Well preserved surangulars are found in AMNH 5027, LACM 23844 and MOR 008.

Anterodorsally the surangular sends forward a thin tongue of bone, shaped in cross-section like a I-beam (Pl. 13). This process together with a smaller medial process embrace the posterodorsal process of the dentary.

A foramen lays just in front and lateral to the glenoid surface of the articular. From it a channel enters the element in a posteromedial direction, in the horizontal plane, but the existence of a suspected internal chamber has yet to be confirmed.

On the dorsal margin of surangular there is an anteroposteriorly elongate facet (Pl. 10). This is anterolaterally bounded by a low, but distinct, ridge and comprises two almost plane surfaces slightly inclined to one another. The medial of these planes is nearly horizontal in transverse section and slightly convex upwards in parasagittal section. The lateral faces dorsolaterally and is similar to the medial in form. The angulation separating them becomes indistinct posteriorly and fades out, so that the two planes merge. From comparison with the situation in living crocodylians this feature is taken to represent the area of insertion for the *M. adductor mandibulae externus superficialis et medialis*.

In LACM 23844 the surangular has a shallow roughened concavity, facing dorsolaterally, situated at almost the anterior termination of the dorsal facet. This concavity is rougher and more distinct on the right than on the left surangular. The lateral ridge just above the surangular fenestra is dorsoventrally deeper in the right surangular of LACM 23844 than in the left or in either of those of AMNH 5027. It is penetrated by an anteroposteriorly elongate opening that occupies the middle of the ridge. The ridge is thickened and roughened below this opening. Because of its unusual appearance and unique occurrence this opening is concluded to be pathological, perhaps the result of a puncture by a tooth. The right surangular of this specimen also has a perforation near the anterior margin, not present on the left. This perforation is located on the floor of a small bowl-like excavation, that gives the impression of a partially healed abscess. A similar perforation is to be found 9 cm in front of the surangular fenestra in MOR 008. These features are presumably pathological.

Articular (Pl. 15): The articular of *T. rex* is a roughly tetrahedral element with an anteriorly directed apex and a posterior base, figured in articulation in both medial and dorsal view by OSBORN (1912, Figs. 18 and 19). These figures do not clearly show the large foramen immediately posterior to the medial edge of the glenoid, taken by OSBORN to be a groove for the "hyoid bone". This foramen communicates with a large central sinus (Fig. 8), which occupies most of the central portion of this element but does not extend into the anterior process. It approaches very closely to the posterior surface of the articular, and the bone there is quite thin. Indeed, in both articulators of both AMNH 5027 and LACM 23844 the bone has been crushed forward into the sinus. In the single mandible of MOR 008, on other hand, the anterior process appears to have been displaced posterodorsally slightly into the sinus.

The articular glenoid is trapezoidal, when viewed from above, with an oblique central ridge. It conforms in shape to the quadrate condyle, which fits quite closely.

Unlike those of most lizards, crocodylians and theropods, the articular of *T. rex* does not have a retroarticular process — or, at most, one of only a few mm length, so that practically it may be considered absent. This absence is characteristic of the tyrannosaurids. There is instead a shallow concavity occupying the whole of the roughly semicircular posterior surface of the articular (Pl. 13). This concavity is presumably the insertion scar of the *M. depressor mandibulae*.

Arthrology

Introduction: The form of the joints of a theropod skull has never before been described explicitly. In fact, for dinosaurs this has been done only for ornithopods (WEISHAMPEL 1984) and that format will be followed here. To determine the presence and extent of possible kinesis the form of the joints must be examined. Two specimens of *Tyrannosaurus rex*, LACM 23844 and MOR 008, are of preeminent suitability for this, and this description relies heavily on them.

WEISHAMPEL (1984, Fig. 1) has presented a terminology of contact types that will be used here. Some of his terms correspond to other terms already in use by anatomists: for example his serrate joint corresponds to the suture, and his ellipsoid joint corresponds to the condyloid joint. His terms will be used as the anatomical terms are essentially

descriptive, but WEISHAMPEL's carry the denotation of allowing the possibility of certain movements, while prohibiting absolutely others.

Conclusions drawn as to the motions possible refer to those motions allowed by the form of the bony contact surfaces. These potential motions are the maximum theoretically permitted, and in the living animal may have been limited or prohibited by ligaments or muscles. Because WEISHAMPEL provides the only systematic account of cranial joints in any fossil archosaur, perforce some observations comparing the situation in *Tyrannosaurus* to that of ornithopods will be drawn. Where possible comparisons with other theropods, especially *Allosaurus*, will also be included. Where not otherwise acknowledged the description is based on LACM 23844.

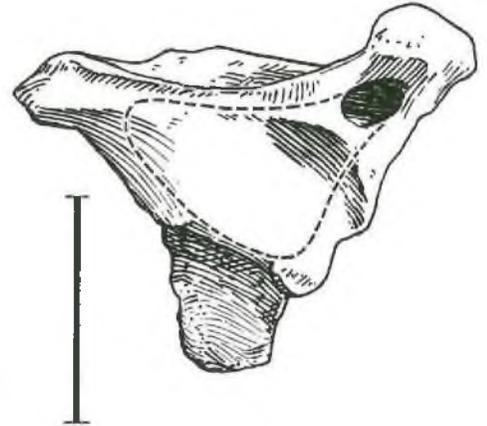


Fig. 8. *Tyrannosaurus rex* OSBORN, diagram of left articular in dorsal view. — Based on LACM 23844. The extent of the sinus chamber is indicated by the dotted line. 0.3x.

Cranial Joints

The joints of the braincase are sutures or are fused in all known specimens and hence provide no suggestion of mobility: most of these will not be treated explicitly.

Premaxilla-Premaxilla Joint: The medial face of the premaxilla is exposed only on LACM 23844 (Fig. 1). This surface is flat with very slight longitudinal ridges, and it extends back 2.5 to 4 cm from the anterior margin of the premaxilla. Posterior to this the medial surface is also flat for 6 to 7.5 cm, but, except for the region just below the narial opening, it is set slightly lateral to the midline and hence presumably not in direct contact with the corresponding face of the opposing premaxilla. This joint is a plane joint.

This medial contact allows slight sliding of one premaxilla upon the other. WEISHAMPEL takes the striate medial face of the premaxilla of ornithopods to suggest the presence of a ligament binding them together. In *T. rex* the ridges are limited to the anterior one-third of the face, presumably so limiting the ligament. Probably however, the narrow gap between the more posterior parts of the medial faces of the premaxillae was also occupied by connective tissue. The amount of motion permitted in the living animal, of course, would depend upon the stiffness of this ligament and connective tissue.

Nasal-Premaxilla Joint: The premaxilla contacts the nasal at two points, both above and below the nares. On no specimen is the ventral of these contacts both preserved and exposed for examination, so only the upper can be discussed here. The appropriate contact surfaces are preserved and exposed only on LACM 23844 and there only on the premaxilla. This joint is a scarf joint, with a plane surface for the nasal on the nasal process of the premaxilla. Slight anteroposterior sliding might be expected at this contact.

Maxilla-Premaxilla Joint: The maxillary contact of the premaxilla is smooth and non-sutural: a passage lays on this contact. Ventral to the opening of this passage (i. e., the foramen), the posterior face of the premaxilla bears a series of low, transverse ridges. Above the passage this surface is largely smooth, with only marginal ridges, orientated perpendicular to the lateral edge. Although the maxilla and premaxilla were articulated when collected, the corresponding face of the maxilla is too poorly preserved for the passage to be traced, much less the form of the contact surface to be examined. The form of the maxilla-premaxilla contact, as revealed by the premaxilla, is a scarf joint, curved such that sliding of the premaxilla on the maxilla is not precluded.

In the holotype of *Nanotyrannus lancensis* (CMNH 7541), on the left side only, and in that of "*Gorgosaurus*" *novojilovi* (PIN 552-2), on the right side (MALEEVA 1974), the ventral margin of the premaxilla is offset dorsad from that of the maxilla. These apparent displacements may reflect a slight mobility of the premaxillae on the maxillae in these taxa. Perhaps a slight movement was possible in *T. rex* as well. As these displacements are found, in at least one instance, on only one side they are not comparable to the angulation of the tooth-bearing margin at the premaxillary-maxillary juncture found in *Coelophysis bauri* and *Dilophosaurus wetherilli*.

Nasal-Nasal Joint: This joint is not exposed on any specimen. It is fused in AMNH 5027, MOR 008 and (probably) SDSM 12047, but not in LACM 23844. Presumably, as in ornithopods, this is a long, slightly curved butt joint.

Nasal-Maxilla Joint: This joint may be examined on both LACM 23844 and MOR 008. The anterior third of the maxillary contact surface consists of shallow pockets with strong intervening ridges. Posterior to this, the surface is a deep, longitudinal groove with a dorsal parallel flange, both of which persist posteriorly to the maxillary-lachrymal contact. In form this is a modified butt joint. The contact surface would seem to have precluded any significant motion.

Lachrymal-Maxilla Joint: The surfaces of this joint are either not exposed or not preserved on any specimen.

Lachrymal-Nasal Joint: Exposed in both LACM 23844 and MOR 008, the surfaces for this joint are more fully preserved in the former so this description relies on that specimen. The lachrymal-nasal joint is a modified butt joint. The articular surface occupies the upper two-thirds of the medial face of the anterior ramus of the lachrymal. On the nasal, the surface for contact consists largely of a deep longitudinal groove that widens and shallows posteriorly. This groove is apparently continuous with that of the posterior half of the maxillary contact surface, but because of the incompleteness of the nasals of LACM 23844 (and MOR 008) this presumed continuation cannot be verified. The posterior part of the groove is bordered above by a low, parallel, longitudinal ridge that occupies a corresponding groove of the lachrymal. A slight amount of anteroposterior sliding of the nasal on the lachrymal is possible at this joint, and trial movements of the nasals on both the maxilla and lachrymal of LACM 23844 verify that slight rocking around a longitudinal axis was permitted at both lachrymal-nasal and nasal-maxillary contacts.

Prefrontal-Lachrymal Joint: The surfaces of this joint are nowhere exposed in material of *T. rex*.

Prefrontal-Frontal Joint: The frontal contact surface for the prefrontal is exposed only in MMS 51-2004, and the corresponding face of the prefrontal is nowhere exposed. In MMS 51-2004 this joint appears to be sutural, that is a serrate joint. The contact face on the frontal is deeply concave and dorsoventrally elongate: in shape it is bipartite, roughly resembling the profile of an hourglass (MOLNAR 1980, Fig. 2). Irregular ridges are strongly developed on the joint surface, and it appears to have been an immobile joint — unlike that in *Albertosaurus megagracilis* (MOLNAR, 1980) and other tyrannosaurids (cf. CURRIE 1987).

Nasal-Frontal Joint: The nasal-frontal joint is exposed to examination only in AMNH 5117, and there only on the frontal. From above this contact has the form of the capital letter "W", with the central apex compressed (CURRIE 1987). The "lower" apices of the "W" are directed anteriorly, each of the "V's" being formed by a process of the frontal. Lateral to each of these processes is a small pocket, presumably occupied by a process of the nasal. These are not to be confused with the pocket described by CURRIE (1987) for the prefrontal in other tyrannosaurids. The lateral nasal processes would embrace those of the frontals, which in turn embraced the central process of the nasals. Some slight rotation about a transverse axis laying in the horizontal plane may have been permitted, but if so it would not have been of significant degree.

Maxilla-Palatine Joint: The maxilla contacts the palatine along a lateral edge of that element, which is extended by short anterior and posterior processes. The anterior process of the palatine of SDSM 12047 is broken, in consequence the form of this joint may be easily seen. Its form is not comfortably accommodated in WEISHAMPEL'S classification: the contact surface of the maxilla is roughly cylindrical and fits into a corresponding trough on the palatine. The maxillary contact face is bounded both above and below by a groove that is more easily felt with the finger than seen. The anterior contact, exposed on SDSM 12047, reveals that the surface bore longitudinal ridges which must have inhibited dorsoventral motion at this joint: some anteroposterior motion may have been permitted. A similar surface may be seen at the back (the only part preserved) of the palatal process of the maxilla of LACM 23844.

Vomer-Maxilla Joint: No maxilla is sufficiently well-preserved to observe this joint surface. The rhom-

boid plate of the vomer of LACM 23844 shows no clear indication of the joint. This suggests that the joint, presumably a lap joint, was loose and so could have allowed sliding.

Jugal-Maxilla Joint: The description of this joint is drawn from LACM 23844, where both elements are well-preserved and exposed. Anteriorly the jugal has lap joints with both maxilla and lachrymal. The maxilla is met along a non-sutural contact, where the jugal forks into a medial and lateral process which lay on either side of the maxilla. The lateral process is further divided into a dorsal and a ventral branch by a cleft, narrow in LACM 23844, broader in SDSM 12047. These two branches fit matching concavities on the lateral face of the jugal process of the maxilla: a ridge on the maxilla occupies the cleft between them. The flat, thin medial process of the jugal fits a concavity on the medial face of the jugal process of the maxilla. The existence of both lateral and medial processes closely appressed to the maxilla eliminates any possibility of motion in a transverse direction. The double process and matching double concavity likewise prevent any significant motion in the plane of the lateral facet (the parasagittal plane). At the apex of the subtriangular maxillary process are the concentric ridges described in the section on the lachrymal-jugal joint (Pl. 5). Slight anteroposterior sliding of the jugal on the maxilla is not prohibited.

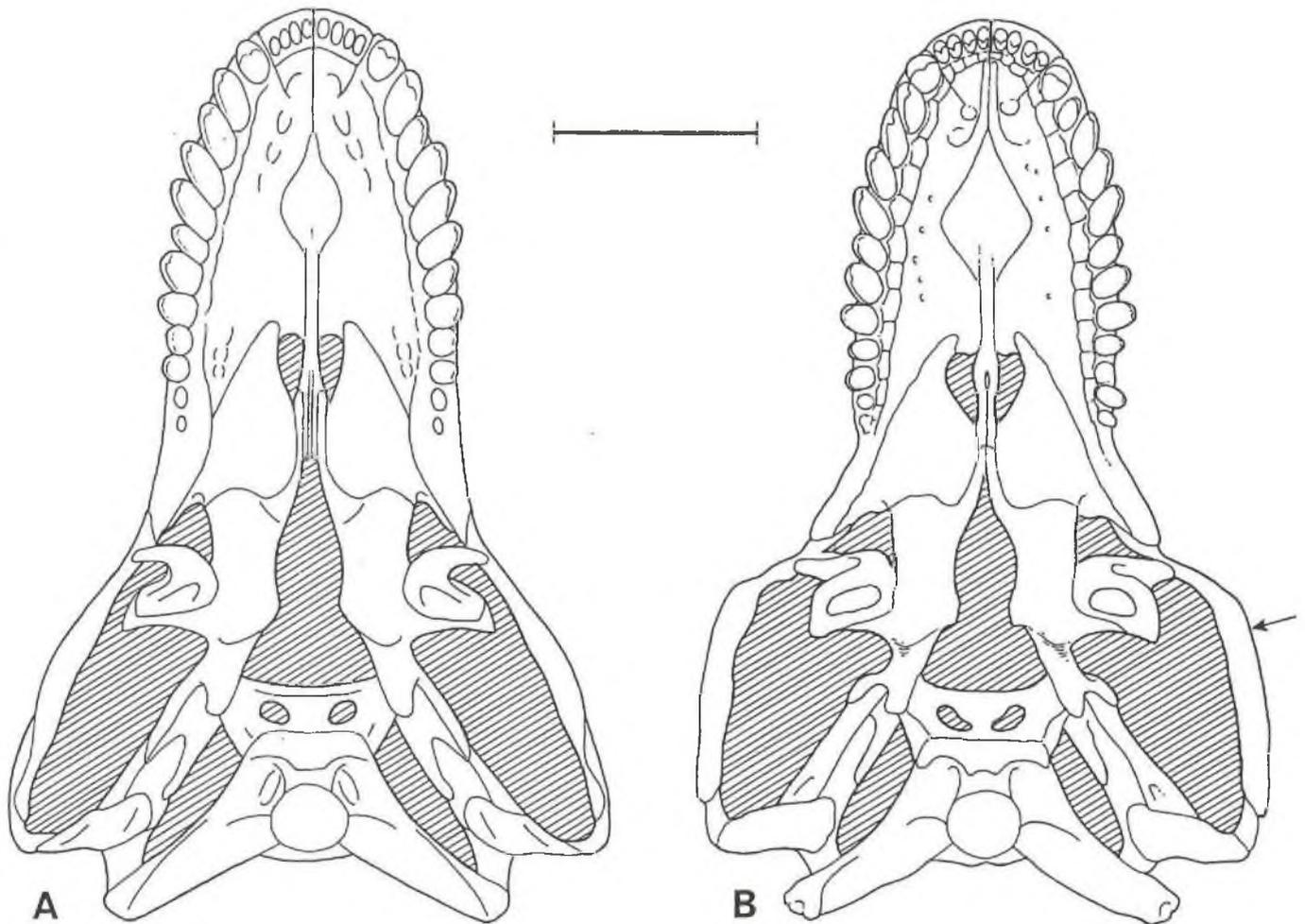


Fig. 9. *Tyrannosaurus rex* OSBORN, reconstruction of the skull in ventral view. A. Ventral aspect as given by OSBORN (1912). Positions of the jugal flexure in SDSM 12047 indicated by arrow. B. Reconstruction proposed here. Scale bar 30 cm.

Lachrymal-Frontal Joint: The frontal articular surface occupies the posterior face of the anterior ramus of the lachrymal of LACM 23844. This face is roughly circular in posterior aspect and is shallowly convex, nearly spherical, in form. It is covered by a large number of low, rounded projections. The surface itself is composed of these low tubercles with a few distinct ridges at the dorsal margin, these however appear to be part of the surface ornament rather than part of the articular face itself. The tubercles lay so close together that, although gaps remain, no bone

from the frontal penetrates into these gaps so that the surface is in effect smooth, providing an elliptical joint. That motion between these elements was possible has been confirmed by manipulating these elements of LACM 23844, but its extent is unclear.

Postorbital-Frontal Joint: Anteriorly, just above the orbital margin and medial to the rugosity, the postorbital sutures with the anterolateral margin of the frontal. The frontal surface is shown by AMNH 5117, LACM 23844 and MMS 51-2004, and that of the postorbital by LACM 23844, MOR 008 and TMP P81.12.1. This contact is a deeply interdigitate serrate joint that would permit no motion.

Jugal-Lachrymal Joint: The ventral margin of the lachrymal broadly overlaps the dorsomedial surface of the maxillary process of the jugal. This joint is a modified scarf joint. The lachrymal is quite thin at this contact. A broad process extends around to the lateral face of the maxillary process of the jugal without, however, extending directly behind the jugal. On the medial face of the maxillary process of the jugal there is an abrupt change in surface level against which the lachrymal closely fits. This face of the jugal is flat, with a series of distinct, but low, ridges extending anterodorsally at various angles.

At the posterodorsal angle of the lateral face of the maxillary process of the jugal on LACM 23844, are two marked ridges arranged in parallel arcs, concave anterodorsally (Pl. 5). The lateral lappet of the lachrymal, that fits over these ridges, bears a corresponding set of ridges which fit between those of the jugal. Trial movements of the jugal on the lachrymal confirm the possibility of rotation about the centre of curvature of these ridges.

Postorbital-Jugal Joint: The ventral contact of the postorbital with the jugal is a smooth and gently curved scarf joint, with the postorbital slightly overlapping the jugal laterally. The appearance, in lateral aspect, of a horizontal suture along the ventral margin of the postorbital is misleading. The anterior margin of the postorbital articular surface for the jugal is marked by an abrupt change of surface level, with a slight overhang. This forms a posteriorly directed rim nearly perpendicular to the internal surface of the postorbital. This almost straight rim lays anterior to the ventral part of the anterior margin of the jugal's ascending process for almost one-third of its height. The rim lays 4 cm from the posterior margin at the top narrowing to less than 0.5 cm at the bottom. The junction is loose — with a single exception — and may well have allowed sliding of the postorbital on the jugal. In MOR 008 on the left side, however, this junction is fused internally, although the joint is still discernible externally. This is the only example of such fusion I have seen among theropods.

Lachrymal-Ethmoid Joint: In LACM 23844, at the top of the posterior margin of the medial ridge of the descending ramus of the lachrymal there is an articular surface, presumably for the ethmoid. Most of this surface is a deep concavity, but there are vertical ridges and grooves dorsally, so that this seems to be a combination of elliptical and serrate joint. The ethmoid of AMNH 5117 seems to have no counterpart surface, either because it was not ossified, or because the lachrymal did not in fact contact the ethmoid — although, if so, what element it did contact remains a mystery. Potential movement at this contact cannot be assessed in the absence of the counterpart surface, but vertical sliding would seem allowed.

Vomer-Palatine Joint: The articulations of the vomer for the palatine are situated on the lateral faces of the two posterior branches of the stem (Fig. 5). These are preserved in both LACM 23844 and MOR 008: on neither specimen however is the palatine sufficiently complete to exhibit the counterpart surface. This precludes determining whether there was a vomer-ptyergoid joint as in *Daspletosaurus torosus* (RUSSELL 1970, Fig. 9). A distinct, overlapping, weakly sigmoid rim marks the anterior limit of the articular surface — which itself is flat with low posteroventrally orientated ridges. This anterior rim would have acted as a stop to anteriorly directed motion of the palatine relative to the vomer, but there seem no other bony limitations to movement at this contact. The palatine-vomer joint is basically a planar joint.

Palatine-Pterygoid Joint: In the only specimen with a disarticulated palatine, MOR 008, the medial margin bears a distinct flange that probably overlapped the palatal plate of the pterygoid. In both LACM 23844 and MOR 008 the dorsal surface of the palatal plate of the pterygoid flexes down at 45° to meet the ventral surface in a sharp edge. This dorsal surface bears short, low, parallel, longitudinal ridges. As the medial flange of the palatine is broader than this beveled edge of the pterygoid, the palatine presumably lapped over the palatal plate to give a plane joint. Anteroposterior sliding may have been permitted.

Jugal-Ectopterygoid Joint: The anterior portion of the ventral margin of each of the jugals of LACM 23844 bears a set of low, nearly parallel ridges. These lay on the margin directly beneath the lachrymal contact of the jugal. The two larger ridges converge slightly posteriorly. There are also at least six smaller ridges. Between the

two major ridges the surface of the jugal is depressed to form a trough (Pl. 5). This structure lays at the region of contact of the ectopterygoid in both AMNH 5027 and SDSM 12047 and hence is identified as the jugal contact surface for the ectopterygoid. The corresponding surface of the ectopterygoid is not present in either LACM 23844 or MOR 008. The joint is a modified butt joint, and may have permitted slight sliding along the long axis of the jugal.

Pterygoid-Ectopterygoid Joint: The ectopterygoid process (or pterygoid 'wing') of the pterygoid is not preserved in LACM 23844. In *Tarbosaurus bataar* it is a short, acutely triangular process (MALEEY 1974, Fig. 9). The pterygoid ramus of the ectopterygoid apparently lay against and just above the pterygoid. Before disarticulation MOR 008 exhibited a flattened element with a smooth ventral face in contact with the dorsal surface of the palatal plate of the pterygoid. Posteriorly the rear portion of the ectopterygoid was exposed just above and lateral to the palatal plate. Thus it seems likely that the fragment laying just above the pterygoid was part of the ectopterygoid.

The dorsal face of the palatal plate of the pterygoid is smooth medially, but bears low, parallel, longitudinal ridges laterally. This lateral area is slightly convex dorsally in transverse section and presumably marks a part of the ectopterygoid articulation. If correctly interpreted this joint would have been a plane joint, and may have allowed slight anteroposterior sliding of the ectopterygoid upon the pterygoid.

Laterosphenoid-Epipterygoid Joint: The dorsal termination of the epipterygoid is not exposed in any known specimen of *T. rex*, however the laterosphenoid of AMNH 5117 is well-preserved. Anteroventral to the postorbital process and anterodorsal to the fenestra ovalis is a dorsoventrally elongate concavity in the lateral wall (Pl. 11). Bounded anteriorly and posteriorly by sharp ridges converging dorsally, it is 3.4 cm long. It is smoothly surfaced and lays in the same relative position as the presumed epipterygoid contact of the braincase of UVP 6000, *Allosaurus fragilis* (MADSEN, personal communication, 1972). So this concavity probably represents the epipterygoid contact of the laterosphenoid in *T. rex*. In the absence of the counterpart face of an epipterygoid the motion possible at this contact cannot be determined: it appears to be an ellipsoid joint.

Pterygoid-Epipterygoid Joint: The epipterygoid is exposed in both AMNH 5027 and MOR 008. In the latter specimen, before preparation, the epipterygoid was in contact with the quadrate wing of the pterygoid. The circular lower plate of the epipterygoid in AMNH 5027 bears a set of low, but strong, roughly parallel ridges on its exposed (presumably lateral) face. These extend up from the ventral margin for one-half the diameter of the plate. The plate of MOR 008, insofar as it was examinable, is roughened: unfortunately the lower portion, exposed in AMNH 5027, was not exposed in this specimen. No comparable indication was found on the quadrate process of the pterygoid. This joint is a plane joint, and could have permitted sliding of the epipterygoid on the pterygoid.

Postorbital-Squamosal Joint: The postorbital sends posteriorly a process that articulates with the dorsal ramus of the squamosal: this contact is preserved in SDSM 12047 but not in AMNH 5027. The posterior process bears medially, along both dorsal and ventral margins, shallow sulci for the squamosal. The lateral face of the squamosal, that contacted the postorbital, is mildly convex with low ridges. The squamosal splits here into upper and lower branches that embrace the posterior process of the postorbital, with almost its entire lateral surface against the medial face of that process. The joint may have allowed some anteroposterior sliding.

Squamosal-Quadratojugal Joint: Although the squamosal is adjacent to the quadratojugal a joint between these elements appears not to have existed in *T. rex*. The quadratojugal ramus of the squamosal seems not to articulate with the quadratojugal but only to slightly overlap it. Prior to disarticulation this could be seen on MOR 008. No dorsally-directed joint surface exists on the sharply-edged squamosal process of the quadratojugal. No indication of joint capsule, ligaments, etc. was observed on the relevant part of either squamosal or quadratojugal in any specimen.

Jugal-Quadratojugal Joint: Posteriorly, the posterior ramus of the jugal contacts the quadratojugal. This posterior ramus of the jugal is bifurcate: the dorsal branch is short and thin, and passes above the ventral process of the quadratojugal, but the ventral process of the jugal is deep and internally overlaps the ventral process of the quadratojugal. This joint matches none of the categories of WEISHAMPEL (1984). The fit is quite loose, and the joint has become slightly disarticulated on the right side in SDSM 12047. Considerable motion may have been allowed between these two elements.

Quadrate-Quadratojugal Joint: Although the lateral face of the body of the quadrate is not well-preserved in LACM 23844, the corresponding face of the quadratojugal affords certainty with regard to the form of this joint. The quadratojugal contacts the quadrate via two medial flanges, separated by the quadrate foramen. The dorsal of these wraps behind the quadrate as, less extensively, does the ventral. The surfaces of these bear ridges and

irregular projections and depressions (Pl. 1). These clearly show that the joint was basically a serrate joint, although perhaps not strictly speaking a suture, and permitted no mobility. In MOR 008, on the right side, this joint is fused.

Squamosal-Exoccipital Joint: The contact surface of the squamosal for the exoccipital-opisthotic is slightly convex in MOR 008, and is bounded both dorsally and ventrally by ridges. The face itself bears low anteroposteriorly directed ridges, and would seem to have permitted slight anteroposterior sliding. The joint is a butt joint.

Frontal-Frontal Joint: The joint faces of the frontal symphysis are exposed only in LACM 23844. Deep interdigitations may be seen along the anterior portion of this joint not only in LACM 23844, but also in AMNH 5117 and MMS 51-2004. This joint is a serrate joint, and allowed no motion. The form of the joint surface differs considerably between *T. rex*, LACM 23844, and *Albertosaurus megagracilis*, LACM 23845 (MOLNAR 1980), although from only a single example of each the taxonomic significance of this cannot be established.

Frontal-Parietal Joint: The articular faces of this joint cannot be inspected on any known material of *Tyrannosaurus*: on all specimens these elements are in articulation. However AMNH 5117 reveals that although this joint was relatively straight distally, medially it was deeply interdigitate.

Parietal-Parietal Joint: This joint is fused on all known specimens, leaving no observable trace.

Laterosphenoid-Postorbital Joint: The postorbital articulation surface for the laterosphenoid lays just behind and adjacent to that for the frontal. In the postorbital of TMP P81.12.1 it is a shallow, broadly oval depression, but in LACM 23844 it has the form of a narrow elongate oval, strongly concave, with the long axis inclined to the vertical at 20°. In general form it is much like that of *Allosaurus fragilis* (GILMORE 1920). In AMNH 5117 the postorbital contact of the laterosphenoid is a dorsoventrally elongate, roughened, oval convexity, implying an ellipsoid joint. (This surface may be clearly seen in OSBORN (1912, Fig. 7) but had become removed sometime prior to my examination of the specimen in 1971.) This joint gives the appearance of having been mobile, but it is adjacent to the immobile postorbital-frontal joint. The fact that its form varies from specimen to specimen (from broadly to narrowly oval) may perhaps be explained by its proximity to joints permitting no motion. These were so arranged that no motion could have occurred at the laterosphenoid-postorbital joint. If so, its form would seemingly not have been exposed to selection.

Basipterygoid Joint: The basipterygoid joint is that between the basipterygoid process of the basisphenoid and the corresponding process of the pterygoid. The basipterygoid processes of *T. rex* descend ventrally and are slightly inclined anteriorly, as is characteristic of theropods. Distally each bears an elongate, convex, elliptical articular face, exposed on the left side in SDSM 12047. A small blunt process of the pterygoid, arising from the posterior edge of the palatal plate just behind the root of the quadrate process, contacts this face. There is no discernible indication of this contact on the smooth dorsal surface of this process of the pterygoid itself, although only two examples, those of LACM 23844, were available for examination. The form of the basipterygoid articular surface does not closely conform to that of the pterygoid, and the joint is best described as a modified (loose) ellipsoid joint. This contact may well have allowed some motion as in *Allosaurus fragilis* (MADSEN 1976).

Quadrate-Pterygoid Joint: The quadrate process of the pterygoid is a thin flat plate orientated in a vertical plane inclined at about 30° to the sagittal plane. This joint is not a suture as was stated by OSBORN (1912). Instead the pterygoid is overlapped laterally by the pterygoid process of the quadrate. This external face is gently convex, with the convexity interrupted over the posterior two-thirds of the plate by a distinct ridge that forms a shallow lateral shelf along the ventral margin of this process. The pterygoid process of the quadrate also bears such a ventral bar. That process is somewhat thicker and more robust than that of the pterygoid, but even so it is not completely preserved in any disarticulated specimen. The contact is a simple overlap, that is a scarf joint, albeit an extensive one. In MOR 008 this contact is close (before preparation there was only c. 0.1 cm of matrix between the facing surfaces) but is not fused.

Squamosal-Quadrate Joint: The quadrate is surmounted by a roughly saddle-shaped (mathematically speaking, a pseudospherical) surface for the squamosal (Fig. 10). Described by MOLNAR (1985) this joint is not a suture, as stated by OSBORN (1912). This surface is relatively smooth in LACM 23844, and delimited by a distinct rim. In dorsal aspect the long axis of this surface is inclined at 45° to the longitudinal axis of the skull. The sides of the saddle dip furthest ventrally anteromedially and posterolaterally, and the highest contour of the saddle is not horizontal, but inclined downward anteriorly. In MOR 008, the only other specimen to exhibit this articular face, its form is similar, but not exactly the same: most of the face is a shallowly rugose hemisphere situated just behind the base of

the pterygoid process. This hemispherical surface is bounded posteromedially by a raised rim, in a circular arc. As in LACM 23844 the surface is highest posteromedially, at the rim, and slopes in the other directions, most strongly posterolaterally and anteromedially, and less strongly anterolaterally.

The quadrate articular surface of the squamosal is preserved only in MOR 008, and conforms much more closely to that of the quadrate of LACM 23844, than to that of its own quadrate: the surface is saddle-shaped. This smooth, ventrally-facing surface is located posteriorly on the squamosal, below the junction of its dorsal and quadratojugal processes. Functionally this is a saddle joint and, although permitting no spins, it would permit swings in several directions. The orientation of the highest contour of the "saddle" is such that these swings would probably occur in, or close to, the plane of the pterygoid process of the quadrate.

Cranio-mandibular Joint

Quadrate-Articular Joint: Both surfaces of the quadrate-articular joint are closely conformable. As in most other theropods (MOLNAR 1974) the quadrate condyle is helical in form, with an internal and external convexity separated by a helical sulcus (Pl. 10). The articular surface of the quadrate condyle extends almost 180° around the ventral end of the quadrate, and along its central segment is bounded posteriorly by a low, but sharp ridge. The articular glenoid is a smooth depression crossed by a diagonal ridge (Pl. 15) corresponding to the groove of the quadrate condyle. The glenoid extends anteromedially into a sharp, strong ridge, and is bounded posteriorly by a more extensive, low but sharp, ridge formed by the dorsal edge of the facet for the *M. depressor mandibulae*.

A modified hinge joint, it apparently reached the close-pack position when the jaws were closed. The helical form of the joint surfaces constrained the articular to slide laterally as the jaws were depressed, and medially as they were closed.

Mandibular Joints

Mandibular joints that appear to have been completely immobile, such as the dentary-splenic, the surangular-articular and the prearticular-articular joints are not treated here. Some comments on these joints have been presented along with the descriptive comments on the respective elements. Joints involving elements preserved only in articulation, specifically the coronoid, also are not treated (in any case these joints appear to have been immobile).

Dentary-Dentary Joint: OSBORN first drew attention to the loose condition of the dentary symphysis of *T. rex*. MOR 008 clearly shows the symphyseal surface on the right dentary, a surface which is poorly preserved in both LACM 23844 and SDSM 12047. This surface is flat with low, slightly curved longitudinal ridges, mostly directed anteroventrally. The contact is a butt joint, and presumably allowed some mobility as in *Allosaurus fragilis* (MADSEN 1976).

Dentary-Surangular Joint: The anterior process of the surangular, arising from the anterodorsal angle of that element, resembles an I-beam in cross-section. In LACM 23844, just above the centre of the medial face, there is a thin longitudinal ridge with an overhanging edge (Pl. 13). This ridge is also present, but less prominent, in MOR 008 (where only its base is preserved). Externally this tongue of bone is smooth, with a surface slightly inset to the general surface level of the surangular. Posterior to this tongue there is a shallow depression which accommodates the process arising from the posterodorsal angle of the dentary. The right surangulars of both AMNH 5027 and LACM 23844 have small processes just ventrolateral to this depression that extend forward lateral to the posterodorsal process of the dentary. Thus this process of the dentary fits between two processes of the surangular. The small surangular process is broken on the left sides of AMNH 5027 and LACM 23844.

Splenic-Prearticular Joint: The dorsal facet of the medial surface of the prearticular contacts the splenic. This facet is placed centrally on the prearticular, dorsal to a sharp ridge that separates it from the facet for the angular. On the splenic, the prearticular contact surface is separated by a curved ridge from the surface for the angular that is ventral to it. This smooth, slightly concave, surface bears a set of longitudinal ridges: dorsoventral motion at this joint would have been prohibited, but motion along the arc of the angular and prearticular may have been permitted.

Splenic-Angular Joint: The ventral portion of the medial face of the stem of the angular contacted the splenic. The articular surface is a smooth trough, open anteriorly, but closed posteriorly by the junction of the rounded medial ridge with the ventral marginal rim. The angular contact on the splenic is also a smooth trough

presumably accommodating, at least in part, the medial ridge of the angular: the contact appears not to have been close. As with the splenial-prearticular joint, motion along the arc of the prearticular may have been permitted.

Dentary-Angular Joint: The lateral face of the angular bears an extensive but shallow depression, delimited posteriorly by a low rim, for contact with the posteroventral process of the dentary. There is no indication of this joint on the dentaries of LACM 23844. Thus there was no close conformity of the surfaces at this modified plane joint.

Angular-Prearticular Joint: The anterior stem of the angular is a thin vertical plate, with a low central ridge on the medial face. This low ridge separates the articulation for the prearticular (dorsally), from that for the splenial (ventrally). The prearticular contact surface on the angular is a distinct, but shallow sulcus, that is slightly curved, concave dorsally. It has only about half the depth, dorsoventrally, of that for the splenial. The medial face of the prearticular has a facet for the angular centrally, below the dividing ridge. This contact is an elongate scarf joint.

Angular-Surangular Joint: The curved, plate-like body of the angular laterally extensively overlaps the equally plate-like body of the surangular. There is no distinct indication of this contact on either element in most specimens of *T. rex*, although it is fused on the right side in MOR 008 — like the postorbital-jugal fusion, this has not been seen on any other theropod. However at least one specimen of *Albertosaurus libratus* (TMP P85.62.1) shows a low posterior bounding rim for the angular on the surangular.

Prearticular-Surangular Joint: Anteriorly the prearticular makes contact with both the coronoid and the surangular, but no sign of a surface for this articulation could be found on either element in LACM 23844. This joint is fused in MOR 008, presenting another instance of fusion seen, so far, only in that specimen.

Discussion

In view of the new description presented here, it is desirable to review the differences of the skull of *Tyrannosaurus rex* from those of related theropods. To provide the appropriate perspective this involves also reviewing the differences of other tyrannosaurids from other theropods. In addition some attention is devoted to certain specific implications of the cranial anatomy, such as the possibility of stereoscopic vision, and to features related to the trophic apparatus and the cranial sinuses. The significance of the reported variation and characters possibly related to age and sex are also discussed.

The skull of the tyrannosaurids, although generally similar in form to those of *Allosaurus* and other large theropods, differs in several points. These are often only vaguely defined in the literature: ROMER (1956), for instance, characterized tyrannosaurids as having a high, massive skull with a vertical quadrate and the frontals and parietals firmly united. These last two features, however, are found widely among less derived theropods. VON HUENE (1956) and STEEL (1970) gave more complete diagnoses, noting that the ventral ramus of the squamosal and the dorsal ramus of the quadratojugal together form a triangular sheet intruding into the lateral temporal fenestra so far that the fenestra is almost bisected. In addition, the postorbital bar is anteroposteriorly widened and the orbit reduced in length compared to less derived theropods. Only very recently have more explicit definitions been proposed (BAKKER, WILLIAMS & CURRIE 1987, MADER & BRADLEY 1989, MOLNAR, KURZANOV & DONG 1990). The literature, with the sole exception of WALKER (1964), gives no attempt to interpret the functional significance of these features.

Hence it is of interest to indicate the differences of the skull and jaws of *Tyrannosaurus rex* from other theropods, and from those of other tyrannosaurids. These are not presented as diagnoses, for diagnoses should make use of as much of the skeletal morphology as possible and I do not wish to distract from the importance of postcranial morphology in the diagnosis. In tyrannosaurids the skull differs from those of all other large theropods in the following features: 1 — quadratojugal with prominent anteriorly directed squamosal and jugal processes, and with a constricted “waist” between them; the squamosal process contributing to a triangular squamosal-quadratojugal sheet intruding deeply into the lateral temporal fenestra; 2 — prominent lateral jugal foramen; 3 — frontals (both together) wider transversely than long anteroposteriorly in mature animals; 4 — supratemporal recesses confluent over parietals; 5 — quadrate hollow with pneumatic foramen; 6 — broad rhomboid plate on vomer; 7 — greater depth of surangular; 8 — large surangular aperture; 9 — large splenial aperture — also found in *Spinosaurus aegyptiacus* (STROMER 1915), where it is probably convergent; and 10 — almost complete absence of a retroarticular process of the articular, with instead a shallow concavity in the posterior face.

Before discussing these features, a few comments on those given by earlier authors are in order. The quadrate of the tyrannosaurids and *Allosaurus* differs from those of certain other theropods not so much in being vertical, as in being relatively short. In tyrannosaurids (and *Allosaurus*) it is about one-half the total height of the skull (including the supraoccipital crest). In other forms, such as *Abelisaurus comahuensis*, *Carnotaurus sastrei*, *Ceratosaurus nasicornis*, *Dilophosaurus wetherilli* and *Yangchuanosaurus shangyouensis*, this element occupies well over one-half of the total height of the skull (not including the various crests and horn-cores). A high quadrate seems to be plesiomorphic (MOLNAR, KURZANOV & DONG 1990).

WALKER (1964) suggested that the function of the quadratojugal-squamosal sheet was to increase the area of origin of the M. adductor mandibulae externus superficialis et medialis, and this is also the conclusion reached in my dissertation. An approach to this condition is found among other saurischians only in *Dilophosaurus wetherilli* (WELLES 1984) where it is less developed. A similar structure is seen in ornithosuchids, particularly *Ornithosuchus*, *Riojasuchus* and *Venaticosuchus*. WALKER (1964) interprets the occurrence of this structure (as well as of the surangular fenestra) as evidence for direct relationship of ornithosuchids to tyrannosaurids, an interpretation recently echoed by CHATTERJEE (1985) in discussing the relationships of poposaurids to tyrannosaurids. However, the evidence is less than compelling, and in view of the marked differences in structure between ornithosuchids (and poposaurids) and tyrannosaurids the possibility that these structures may have arisen in parallel seems more likely. The case for direct descent is further weakened as poposaurids are not closely related to ornithosuchids (BENTON & CLARK 1988). It seems most parsimonious to interpret this quadratojugal-squamosal sheet as an autapomorphy of the Tyrannosauridae, but one that has arisen independently in thecodonts.

The jugal foramen is intimately related to the internal chambers of the jugal. Thus it may reflect greater development of these cavities in the Tyrannosauridae than in less derived theropods.

The form of the frontals and parietals in *T. rex* was related by OSBORN (1912) to the telescoping or abbreviation of the skull relative to *Allosaurus fragilis*. By implication his remarks would apply to the other tyrannosaurids as well.

The extension of the supratemporal fossae will be discussed below with regard to *T. rex*, where they are the most extensively developed.

Among theropods a hollow quadrate has been reported only for *T. rex* and *Labocania anomala* (MOLNAR 1985) but also occurs in *Albertosaurus* and *Troodon* (CURRIE, pers. comm., 1990). There is no question as to the familial relationships of *T. rex*, but *L. anomala* is a poorly known form that has yet to be subjected to phylogenetic analysis. But there is evidence — the triangular obturator process of the ischium and the form and position of the scar for the flexor tibialis internus — that it is a tyrannosaurid. In light of this, it was tentatively suggested that a hollow quadrate is an autapomorphy of the Tyrannosauridae. However it also occurs in birds. Hence it either may indicate a relationship between tyrannosaurids and birds, or, more likely, it may prove to be more widespread among derived theropods than hitherto realized.

T. rex and *A. fragilis* are the only large theropods for which the complete vomer has been illustrated so little can be said about its difference between these two taxa. But RUSSELL's (1970) figure of the palate of *Daspletosaurus torosus* suggests that in that species, too, the vomer was anteriorly broad. So this is tentatively considered an autapomorphy of tyrannosaurids, rather than of *Tyrannosaurus*.

Tyrannosaurids differ from many other theropods in that tyrannosaurids possess two openings in the posterior part of the mandible. One of these, the surangular aperture, is near the posterior margin of the surangular just anteroventral to the cranio-mandibular joint. This aperture is peculiar to acrocanthosaurids, dromaeosaurids, tyrannosaurids and certain advanced thecodonts (e. g. *Ornithosuchus longidens* and *Postosuchus kirkepatricki*). The mandibular fenestra is located at the junction of the surangular, angular and dentary (as in the other archosaurs). This fenestra is quite irregular in shape among tyrannosaurids (and in *Allosaurus fragilis*) — this irregular form possibly being associated with an intramandibular joint — and not smoothly rounded as in *Ceratosaurus*, *Yangchuanosaurus* and many other archosaurs. In crocodylians the greater portion of the jaw adductors inserts on the medial surface of the mandible at the region of the mandibular fenestra, and in *T. rex* that portion of the mandible showing a comparable relationship to the adductor chamber is the medial surface of the surangular in the region of the surangular fenestra. So these openings are analogous in that respect.

In *Allosaurus fragilis*, *Ceratosaurus nasicornis* and *Yangchuanosaurus shangyouensis* the surangular is relatively shallow, at most only slightly more than one-half the total depth of the post-dentary portion of the jaw. In almost all tyrannosaurids it occupies well over one-half of the depth, in effect increasing the depth of the post-dentary moiety

relative to the dentary ramus. Presumably this allows a greater mass of mandibular adductors. The single tyrannosaurid with a relatively low surangular is *Alioramus remotus* (KURZANOV 1976) where, however, it is still more extensive than in *Allosaurus fragilis*.

This increased surangular depth may have a correlate in the form of the skull. In tyrannosaurids the ventral, tooth-bearing margin of the maxilla is convex so that, when the mouth is closed, the level of the maxillary teeth is well below the quadrate-mandibular joint. This is most marked in *T. rex*. It is apparently related to the increased depth of the post-dentary portion of the jaw, that has elevated the dorsal margin of the surangular well above that of the dentary. Thus *T. rex* seems to have combined the two kinds of bite described by COLBERT (1951): the scissors and nut-cracker bites. This may permit the exertion of increased pressure during the bite.

The splenial foramen presumably transmitted a branch of the inferior alveolar nerve and related blood vessels. Why it should be enlarged in tyrannosaurids is unclear. It is also large in *Spinosaurus aegyptiacus* (Stromer 1915), but that species shares few derived characters with tyrannosaurids, so this occurrence is considered to be convergent.

The absence of a retroarticular process presents no problems of interpretation, although it is present in other theropods. The tyrannosaurid mandible could be depressed by simply relaxing the adductors and allowing gravity to act. The condition in *T. rex* (and the other tyrannosaurids) is similar to that in certain gorgonopsian synapsids analyzed by GANS (1966). These forms were more extreme in the shortening of the retroarticular process, which is depressed below the level of the jaw joint and flexed to lay anterior to that joint. GANS accepts PARRINGTON'S (1955) conclusion that this configuration is related to the development of enlarged canines, and provides an increased gape. As will be discussed below, *T. rex* likewise had enlarged teeth in the anterior maxillary region, so it is interesting to see also a retracted retroarticular process (to the point of being practically non-existent). Because this form of the retroarticular process is characteristic of tyrannosaurids in general, it may be suggested that the increased gape may have permitted the development of larger teeth in *T. rex*.

The skull of *Tyrannosaurus rex* differs from those of other tyrannosaurids in several features: 1 — possession of an anterior process of the postorbital extending anteroventrally into the orbit; 2 — a narrow orbit of "keyhole" shape, rather than oval or elliptical; 3 — a deeper antorbital fossa into which the antorbital and maxillary fenestrae open; 4 — the absence of a fenestra at the pterygoid-palatine junction, the consequence of a broader palatine; 5 — a deep (rather than a tapered) anterior process of the lachrymal, lacking any well-developed lachrymal horn core and with a reduced foramen; 6 — constriction of the nasals between the upper rami of the lachrymals; 7 — a well-developed postorbital rugosity (in at least some mature skulls); 8 — foramen for the fourth cranial nerve posterolateral to that for the third; 9 — absence of the basicranial fontanelle, related to anteroposterior compression of basisphenoid region. Comparison of the skulls of *Albertosaurus libratus*, *Daspletosaurus torosus*, *Tarbosaurus bataar* and *Tyrannosaurus rex* reproduced to the same length from tip of premaxilla to quadrate condyle indicates that there are also proportional differences in *T. rex*; 10 — the orbit is relatively further forward; 11 — the maxillary toothrow is relatively shorter; 12 — the anterior maxillary teeth are relatively longer (but the posterior ones are not); 13 — the supratemporal recess is relatively longer anteroposteriorly; 14 — the parietals are relatively longer anteroposteriorly but the frontals are relatively shorter, and; 15 — the quadrate condyles are relatively larger. These features may result from allometric growth, but because *T. rex* is the largest North American tyrannosaurid they may serve as distinguishing features. In addition, the form of the frontal-prefrontal contact differs distinctly between *T. rex* and *A. megagracilis* (MOLNAR 1980). The significance of such difference is unclear as such surfaces remain generally undescribed, even when exposed to inspection.

The postorbital of *T. rex* sends a small anteroventrally directed process into the orbit. Such a process is represented in dashed line in MALEEV'S (1955 b) figure of the holotype skull of *Tarbosaurus efremovi* (now *Tarbosaurus bataar*) and is present in the skull of the unrelated *Carnotaurus sastrei* (BONAPARTE 1985), but nowhere else. No features that could be interpreted as associated with scars of muscles (of the eye) are discernible on this process and, to judge from the position of the lachrymal canal, it lays well ventral to the region of the eyeball. The process presumably marks the ventral limit of the region of the eyeball, the more ventral portion of the bony orbit perhaps being associated with the *M. pterygoideus anterior*, that passes just medial to it.

The gentle curvature of the anterior margin of the body of the postorbital in *T. rex* contrasts with postorbital form in most other tyrannosaurids, where the margins of the body are straight or nearly so. The consequence of this curvature is a constriction of the lower part of the orbit, giving what GAUTHIER (1986) termed a "keyhole" shape. The orbits of most other large theropods (including other tyrannosaurids) are elliptical or oval, although those of

large individuals of *Tarbosaurus bataar* do approach in form that of *Tyrannosaurus rex* (MALEEV 1974). The orbit of *Allosaurus fragilis* is also ventrally constricted. However in *A. fragilis* (and *Yangchuanosaurus shangyouensis*) this shape is due not to the invasion of the postorbital into the orbit, but to the intrusion of the ventral part of the lachrymal. Thus the orbital form is convergent rather than derivative.

The distinct antorbital fossa of *T. rex* is not found in such genera as *Albertosaurus*, where the fossa is so shallow as to be almost non-existent — except, perhaps, in *Tarbosaurus bataar*. The maxillary fenestra is set away from the margin of the antorbital fossa in *Albertosaurus libratus* and *Daspletosaurus torosus* (RUSSELL 1970) and *Alectrosaurus olseni* (PERLE 1977), but it is adjacent to that margin in *Tyrannosaurus rex* and *Tarbosaurus bataar* (MALEEV 1974).

Most of the individual cranial elements of *T. rex* closely resemble their counterparts in other tyrannosaurid genera, the most obvious exception being the palatine. The palatines of tyrannosaurids are figured for only two species, *T. rex* (OSBORN 1912) and *Daspletosaurus torosus* (RUSSELL 1970). That of *D. torosus* (RUSSELL 1970, Fig. 9) has separate pterygoid and vomerine processes (although the latter seems to contact the vomerine process of the pterygoid as well as the vomer itself). *T. rex* lacks these processes but rather has an expanded body, and the intervening palatal fenestra is not found. The palatine of *Albertosaurus libratus* (AMNH 5336) also shows separate pterygoid and vomerine processes. In *T. rex* the palate was a less open, and presumably a firmer, structure than in these taxa.

The lachrymals of both *Albertosaurus libratus* and *Daspletosaurus torosus*, like those of *Allosaurus fragilis*, show distinct, elevated, rugose structures usually interpreted as supports for horns or crests. The upper ramus of the lachrymal, in lateral aspect, tapers forward. That of *T. rex* shows little taper, presumably because of the development of extensive internal chambers, and no comparable rugosity. *Tarbosaurus bataar* is intermediate in showing little or no taper, but having a low rugosity (MALEEV 1974). The lachrymal foramen is larger in that species. It seems likely that the development of the internal chambers and concomitant enlargement of the anterior ramus also accounts for the constriction of the posterior part of the nasals. These features are not found in other tyrannosaurid species and suggest a more extensive development of the chambers in *T. rex*.

The post-orbital rugosity of *T. rex*, which will be discussed in some detail below, is more emphatically developed, at least in some individuals, than in any other tyrannosaurid. It also appears to be different in form: the other taxa have crescentic rugosities that open anteriorly, but that of *T. rex* opens posteriorly.

In *T. rex* the foramen for the fourth cranial nerve opens posterolaterally of that for the third, so that a line segment connecting them would be (roughly) horizontal. In both *Albertosaurus libratus* and *Daspletosaurus torosus* (RUSSELL 1970, Fig. 5) the foramen for the third cranial nerve is ventral to that of the fourth, so that a line segment joining them would be (roughly) vertical. In the only other large theropod for which these foramina have been described, *Piveteausaurus divesensis*, that for the fourth cranial nerve is anterodorsal to that of the third (TAQUET & WELLES 1977), more like the condition of *Albertosaurus libratus* and *Daspletosaurus torosus* than of *T. rex*.

The braincases of almost all theropods exhibit a deep excavation that opens ventrally between the basioccipital and the basisphenoid. This is the basicranial fontanelle, also termed the sinus sphenoidien by TAQUET & WELLES (1977). Anterior to this is a second, smaller excavation, the subsellar fossa. This latter fossa is well-developed in *Allosaurus fragilis*, *Dilophosaurus wetherilli*, *Eustreptospondylus oxoniensis* and *Piveteausaurus divesensis*. The basicranial fontanelle is well-developed in these forms as well as in *Itemirus medullaris* (KURZANOV 1976) and *Albertosaurus libratus* (RUSSELL 1970, Fig. 4). To accommodate this fontanelle the basisphenoid-basioccipital complex is somewhat elongate anteroposteriorly. In *T. rex* this complex is anteroposteriorly compressed, and entirely lacks both subsellar fossa and basicranial fontanelle. The possible functional significance of this is discussed by BAKKER, WILLIAMS & CURRIE (1987).

The differences in proportion of the skull of *T. rex* from other tyrannosaurids are mostly related to the trophic apparatus. The postorbital region of the skull of *T. rex* is relatively wider than those of the earlier tyrannosaurids and other theropods (with the exceptions of *Nanotyrannus lancensis* and *Carnotaurus sastrei*). The widening of the posterior region of the skull allows relatively larger adductor chambers and hence a larger minimum cross-section of the jaw adductors. It has also shifted the orbit slightly forward with respect to its position in other tyrannosaurids. The relatively longer supratemporal fossae, meeting over the parietals, also suggest a relatively greater adductor mass; or at least it provides a relatively greater volume to accommodate the adductors. This may also be related to the relative elongation of the parietals and to the deepening of the surangular, as noted above. It is this change in proportion of the frontals and parietals, especially the extent to which the frontals are invaded by the supratemporal recess, that allows MMS 51-2004 to be identified as *Tyrannosaurus*.

T. rex also seems to have relatively larger anterior maxillary teeth than other theropods, with the possible excep-

tion of *Ceratosaurus nasicornis*. This may be seen on AMNH 5027, CM 9380, LACM 23844 and UCMP 118742, but not on SDSM 12047. This may be due to post-mortem slippage of the teeth out of their sockets, but if so it seems unusual that this would occur in four of five skulls of *T. rex* but in no other tyrannosaurid skulls. It may be related to the relatively shorter tooth row of *T. rex*. Whatever the explanation, it seems likely the *T. rex* had a more powerful deeper bite than other theropods, because both the adductor chamber and the size of the anterior maxillary teeth were increased.

The postorbital broadening also has the effect of directing the orbits anterolaterally rather than laterally as in earlier tyrannosaurids, allosaurids and ceratosaurids. It has led to the suggestion of stereoscopic vision in *T. rex* by WALKER (1964): this construction eliminates any posteriorly directed lines of sight (unless, of course, the head was turned). Measurements from the cast of the reconstructed skull of LACM 23844, from the cast of the skull (which is slightly distorted) of AMNH 5027 and from figures of the reconstructed skull of *T. rex* all indicate a maximum overlap of the visual fields of about 30°. The deep snout of *T. rex* severely limits the amount of possible visual overlap, so this figure represents the maximum possible overlap of the fields assuming that the visual axis was directed perpendicular to the plane of the orbit and that each eye had a field of about 170° as is usual for tetrapods (WALLS 1942). The angle of overlap was determined by measuring the angle between the reconstructed lines of sight in a horizontal plane. Each line of sight was taken to have extended from the centre of the upper third of the orbit, tangentially passing the dorsolateral wall of the snout to intersect the corresponding line from the opposite side. That the eye occupied the dorsal portion of the orbit is indicated by the opening of the lachrymal canal at the top of the orbit.

Most if not all mammalian predators, and many predatory birds and reptiles, have a greater degree of overlap of visual fields than the herbivores of their respective groups. For example, most lizards have 10° to 20° of overlap but varanids have about 30°. *Testudo* has 18° but *Chelydra* has 38° (WALLS 1942): in mammals this overlap is greater for both herbivores and carnivores, but the difference persists. As predators tend to have a greater degree of overlap than herbivores they have often been presumed to have stereoscopic vision. However anteriorly directed orbits and marked overlap of the visual fields do not necessarily imply stereoscopic vision, as has been shown by studies on the oilbird, *Steatornis caripensis* (PETTIGREW & KONISHI 1984). Stereoscopic vision is indeed present in some birds (e.g. PETTIGREW 1979 a), but the orientation of the orbits is no guarantee of stereoscopy. There are no sighting grooves (such as in *Dryophis*) or analogous structures on the skull of *Tyrannosaurus* that might indicate anterior direction of the visual axes. Possible concomitants of stereoscopic vision in the soft structures are not preserved, hence the evidence for stereoscopic vision in *Tyrannosaurus* rests entirely on the orientation of the orbits and the inferred predatory habits of the creature. This suggests, but is unfortunately insufficient to demonstrate, stereoscopic vision.

The advantage of stereoscopic vision to predators seems to be the resulting high image quality in the central visual field of the retina (ALLMAN 1977). Other possible advantages are the accurate determination of prey distance resulting from stereoscopy (WALLS 1942) and the perception of camouflaged prey (JULESZ 1971). It is interesting that the other large theropods, with the exception of *Nanotyrannus lancensis* and *Carnotaurus sastrei*, all show much lesser amounts of overlap of the visual fields (estimated at 15° in *Allosaurus fragilis*). It cannot be shown that stereoscopic vision was absent in these forms, and even if it was absent accurate distance determinations could have been made by movements of the entire head.

Laterally directed orbits imply the possibility of wide visual fields, reducing the effective blind area from which predators or other enemies may attack. Although it may be difficult to credit most large theropods with contemporaneous predators larger and more powerful than themselves (although there were contemporaneous giant crocodylians such as *Deinosuchus*) intraspecific aggression may have been as intense as among modern crocodylians (COTT 1961), and this could have resulted in selection for wide visual fields and laterally directed orbits in these earlier theropods. Another possible explanation arises from the observation that frontally directed orbits relate to nocturnality, in that they provide better retinal image quality at low light intensities (PETTIGREW 1979 b). In related species of birds the nocturnal forms have orbits directed more anteriorly than in their diurnal relatives (PETTIGREW 1979 b). This suggests that *Tyrannosaurus*, *Carnotaurus*, and *Nanotyrannus* may have been nocturnal or crepuscular in their hunting.

The premaxillary channel is a feature apparently lacking in some earlier theropods, although present in *Allosaurus fragilis*, *Yangchuanosaurus shangyouensis* (DONG, ZHOU & ZHANG 1983, Pls. 23 & 27), *Albertosaurus libratus*, *Daspletosaurus torosus* and *Tarbosaurus bataar*. A foramen (the foramen intermaxillare of JANENSCH 1935 and the subnarial foramen of MADSEN 1976) is found in this position in several archosaurs, including *Brachiosaurus brancai*,

Diplodocus sp., *Tienshanosaurus zdanskyi*, *Saurolophus osborni*, *Parasaurolophus walkeri*, and *Uruguaysuchus aznarezi*. This foramen is not apparent in primitive archosaurs. In some forms related to those with a foramen intermaxillare, such as *Kritosaurus* (LULL & WRIGHT 1942), *Saurolophus angustirostris* and *Nemegtosaurus mongoliensis* (NOWINSKI 1971, p. 5), a large foramen may be seen entirely within the maxilla, but quite near the premaxilla-maxilla contact. The existence of foramina at the maxilla-premaxilla junction in some taxa, with close relatives having a similar foramen entirely within the maxilla, suggest that the premaxillary-maxillary channel carried the same structure as the foramen in the maxilla. Among reptiles the terminal branches of the profundus branch of the trigeminal nerve pass out of the chondrocranium via the foramen epiphanae and the foramen apicale (GOODRICH 1930). The positions of these two foramina in the chondrocranium of *Lacerta* (GOODRICH 1930, Fig. 263) and of *Crocodylus* (DE BEER 1937, Pl. 93) are such that the branch passing through either of these foramina could lay between the premaxilla and the maxilla. This suggests that premaxillary-maxillary channel (and the foramen intermaxillare) carried a terminal branch of the profundus nerve (V_1).

The everted anterior margin of the quadratojugal has been related above to increased area of origin of the M. adductor mandibulae externus superficialis et medialis. This feature is also found in *Albertosaurus libratus* (AMNH 5434 and USNM 12814), in *Daspletosaurus torosus* (NMC 8506; STERNBERG 1946, Pl. 6) and in (the cast of) *Tarbosaurus efremovi* (AMNH 6794), but on none of these is this feature as prominent as on *T. rex*. This suggests increased size of this muscle in *T. rex* relative to the other tyrannosaurids.

Examination of the joint forms reveals no evidence for cranial kinesis, a conclusion in accord with previous workers. The only significant motion appears to have been permitted at the quadrate-squamosal and quadratojugal-jugal junctions. The quadrate-squamosal joint would seem to have allowed swings in a vertical plane. The quadrate was rigidly attached to the quadratojugal, but the junction of that element with the jugal may have permitted both up-and-down and fore-aft movement. The quadrate also extensively overlaps the pterygoid, but considerable sliding could have been permitted. The form of the quadrate-squamosal would have directed the swings in the plane of the quadrate-ptyerygoid overlap — insofar as can be determined from the disarticulated and incomplete specimens. This is the only instance in which permitted motion at several skull joints is correlated, so limited streptostyly may have been possible. However, verification on better material is desirable.

Prominent aspects of the structure of the skull and jaws of *T. rex* are the internal chambers. They are presumably homologues of the paranasal sinuses found in mammals (cf. MOODIE 1915). Such chambers are found not only among the tyrannosaurids but also in *Allosaurus fragilis* (MADSEN 1976), *Ceratopsaurus nasicornis* and *Labocania anomala* (MOLNAR 1985) at least. Perhaps associated with these are the ectopterygoid vacuities characteristic of many post-Triassic theropods. In the absence of soft structures it is impossible to demonstrate that these chambers were connected with the respiratory system and hence air-filled. It is likewise not possible to discuss their significance when the functional significance of the paranasal sinuses of living forms (among them humans) is unknown. Suggested functions of cranial sinus chambers include: lightening of the skull bones; resonating chambers; and a mechanism to allow increase in size of the element during ontogenetic growth without concomitant weight increase (FRANCIS 1964). In all cases observed in *T. rex* the sinus chambers open through a foramen to the surface of the bone, so there is no a priori case against their being air-filled. In the case of the basisphenoid sinus this air, if there were free circulation, could act as a coolant for the blood supply of the brain. If the basisphenoid sinus chambers communicated with the respiratory system (which can be supposed but not demonstrated in the absence of the soft tissues) as does the sphenoid sinus of mammals, and if there was a relatively rapid turnover of air in the chamber, then the blood of the carotids might have been cooled by its passage along the chamber. As pointed out by BAKKER, WILLIAMS & CURRIE (1988), the relatively large size of the entrances suggests that air circulation was facilitated. This system may have acted as does the carotid rete of mammals (SCHMIDT-NIELSEN 1972) and the carotids of the lizard *Sauromalus obesus*, where the carotids are “so close to the surface that they are visible in the pharynx...” (CRAWFORD 1972, p. 431). In both cases the effect of this arrangement is to cool blood passing to the brain.

Although the ectopterygoid vacuities have been several times described (e.g. COLBERT & RUSSELL 1969, OSTROM 1969) no suggestion as to their significance has been put forth. They may be no more than the ectopterygoid equivalents of the sinus chambers of the other cranial elements.

The anatomy of the cranial sinuses has recently assumed much potential importance in view of the assertions that such structures are common only to the crocodylians and the birds among the archosaurs (e.g. WHETSTONE &

MARTIN 1979, WHETSTONE & MARTIN 1981, WITMER 1984). As demonstrated here and reported elsewhere (MOLNAR 1985) this is not correct.

Recently PAUL (1988) commented that two species of large tyrannosaurid might be subsumed under *T. rex*, a suspicion that has been voiced, but not published, ever since OSBORN synonymized *Dynamosaurus imperiosus* with *T. rex*. There are some striking differences in the material assigned to *T. rex* (MOLNAR 1990), such as the form of the post-orbital rugosity discussed below. The variation may be assigned to several categories: differences of form and position; differences in degree of development; fusions of joints; and differences due to pathology or post-mortem deformation. This final category is obviously not relevant to the present discussion, and it is intended to discuss the palaeopathology elsewhere. There is also evidence, mentioned above, that maxillary tooth number may have varied by one.

The first category includes the different heights of the palatal process of the maxilla above the ventral margin, and the different forms of the maxillary fenestra, laterosphenoid-postorbital contact and premaxillary process of the nasals. The position of the palatal process would determine the volume of the oral cavity, but the potential significance of the other differences is obscure. In view of the more or less continuous variation in the form of the maxillary fenestra and the apparent absence of motion at the laterosphenoid-postorbital contact, it may be suggested that these features would not be obviously subject to selection and hence represent individual variation.

Differences in the degree of development include the development of the external sculpture, the sinus chambers, and the extent of the rhomboid plate of the vomer. Development of the sculpture is generally held to reflect the age of the individual, and this interpretation is adopted here. This suggests that the presently unstudied skull, TMP P81.6.1, with very subdued sculpture, represents an immature individual. Variation in form and development of sinus chambers is well known in humans (GARDNER, GRAY & O'RAHILLY 1975, Fig. 62-7 on p. 739) and so the variation recorded above is not unexpected. The significance of the size of the rhomboid plate of the vomer in LACM 23844 is unclear. There may also be a difference in the development of the quadrate process of the pterygoid, but the specimen showing this (CM 1400) is fragmentary and the contemporaneous *Albertosaurus megagracilis* has a massive quadrate process (MOLNAR 1980). Thus there is a possibility of misidentification or intrusion of an *A. megagracilis* pterygoid into the specimen.

MOR 008 shows the greatest number of joint fusions. The postorbital-jugal, quadrate-quadratojugal, squamosal-quadratojugal, angular-surangular and prearticular-surangular joints are all fused, usually only on one side. Some of these fusions, jugal with postorbital and angular with surangular, have not been seen in any other theropod. The tendency for joints to fuse with age suggests that MOR 008 was an elderly, or gerontic, individual. The occurrence of the most prominently developed nasal rugosity of any *T. rex* in this specimen, and of rugosities along the everted margin of the quadratojugal not found in other specimens, corroborate this interpretation.

The postorbital rugosity is one of the most strongly varying features of the *T. rex* skull, and it is the most obvious. As described above it ranges from being almost non-existent in LACM 23844 and TMP P81.12.1 to being very prominent in AMNH 5027 and MOR 008. Furthermore in AMNH 5027 it is roughly hemispherical, quite unlike the eave-like form in MOR 008 — that of SDSM 12047 is intermediate in form. The sequence of increasing prominence may be understood by noting that the rugosity is most strongly developed in the same specimen, MOR 008, that exhibits the greatest number of fusions of its cranial elements. This specimen is believed to derive from an elderly individual, and so suggests that the sequence of increasing prominence of the postorbital rugosity may reflect, in part, increasing age of the individual animals.

However, this cannot be the entire explanation, for all of the specimens are of approximately the same size — at least within 10%. LACM 23844 may be a more immature specimen than the others, because its nasals are unfused, which correlates with the very subdued postorbital rugosity. However its skull was no smaller than that of AMNH 5027. Perhaps this specimen is immature, but it may also be that it derives from a different sex than those of SDSM 12047, AMNH 5017 and MOR 008. This raises the possibility that the postorbital rugosity in *T. rex* was a species-specific mate recognition structure, presumably of the male. It is not clear how this interpretation may be distinguished from that of immaturity, and it is supported over that interpretation only by the single observation that the skulls are all more or less of a size.

PAUL (1988) concluded that it is unlikely that two species have been conflated as *T. rex*, but the question is still open. No consistent pattern of variation was seen in this study, but the small number of specimens available, the nature of some of the differences and the absence of information on related species suggests that further discoveries will be needed to finally resolve this issue.

Finally, this study has shown little reason to alter the form of the skull of *T. rex* as depicted by OSBORN (1912). However the form in ventral aspect may be incorrect, in that post-mortem deformation of the skull probably caused the sharp flexures of the jugals. These flexures are different in different specimens, both in degree and position. They are not seen in the jugals of LACM 23844, where the cranial elements were disarticulated, and hence less subject to deformation. Both AMNH 5027 and SDSM 12047 have been crushed. In AMNH 5027 the jugal flexures are both of about 60°, but the right is about 10 cm further from the quadrate condyle, than the left. In SDSM 12047 the left is flexed at about 60° and the right at 45–50°, and the flexures again are at different positions. It seems more likely that an initially straight element can be flexed by crushing than that an initially flexed one can be straightened, because there are more ways of being flexed than of being straight. Thus a new interpretation of the palatal aspect of the *T. rex* skull is presented in Fig. 9, in which the jugals are considered to have been initially unflexed or only slightly flexed. The width of the occipital region is left unaltered in this interpretation.

Summary

Tyrannosaurus rex differs from other tyrannosaurids in fifteen features. Six of these relate to the trophic apparatus, apparently resulting from an enlargement of the adductor chambers in the postorbital region of the skull. This enlargement is shown most obviously by the transverse expansion of the postorbital region. But it is also indicated by the increased overlap of the frontals by the supratemporal fossae. This enlargement continues a trend seen in other tyrannosaurids, where the confluence of the supratemporal fossae over the parietals and the deeper surangular suggest increased adductor size relative to earlier large theropods. The everted anterior margin of the quadratojugal and the quadratojugal-squamosal sheet that intrudes into the lateral temporal fenestra are other tyrannosaurid features that suggest increased muscle size. The enlarged adductor chambers and the enlarged anterior maxillary teeth suggest that *T. rex* was capable of a very powerful bite.

Other differences of the trophic apparatus of *T. rex* include the relatively shorter maxillary tooth row and the relatively longer anterior maxillary teeth. The increased tooth length may correlate with the extreme diminution of the retroarticular process, most obvious in *T. rex*, which may provide an increased gape (GANS 1966). The different form of the palatine gives a more closed palate in *T. rex*.

The postorbital expansion involved re-orientation of the orbits, so that they were directed anterolaterally, rather than laterally. This may well have provided the anatomical basis for stereoscopic vision. However, the keyhole-like form of the orbit in *T. rex* is more likely convergent to that of *Allosaurus fragilis*, rather than providing evidence for descent.

Two proposed characteristic features of tyrannosaurids, the jugal foramen and the hollow quadrate, are related to the system of sinus chambers. As with the increased adductor mass, there is evidence that this trend was carried further in *T. rex*. The enlarged anterior rami of the lachrymals house (presumably) enlarged internal chambers, and constrict the posterior part of the nasals. The function of these chambers is unclear, but it seems possible that the sphenoid chamber could have acted to cool blood flowing to the brain. The basicranial fontanelle, however, is lost: BAKKER, WILLIAMS & CURRIE (1988) related this to cervical muscular function.

The form of the joints between the skull elements suggests that streptostyly may have been present, but provides no good evidence for cranial kinesis, at least in mature individuals. The apparently loose character of several mandibular articulations suggests that an intramandibular joint was present, as proposed by several workers. Such a joint may have existed at the junction of the dentary (and splenial) with the post-dentary elements, and been activated by the lateral displacement of the articular concomitant on opening the mouth.

MOR 008 is believed to be an old specimen because of the prominence of the nasal rugosity and the presence of fusions not found in others. The postorbital rugosity is well-developed in three specimens, but subdued in two others. This may indicate sexual differentiation, and this structure might represent a species-specific recognition structure. However, although variation is present in the form and development of certain structures, the absence of any consistent pattern provides no support for speculation regarding the existence of two species of North American *Tyrannosaurus* at this time.

The enlarged adductor mass, enlarged anterior maxillary teeth, and possible intermandibular joint indicate that

T. rex was capable of being an active predator. The potential for stereoscopic vision suggests a possible difference in hunting strategy from those of most other large theropods. This may have related to increased depth perception, or crepuscular or nocturnal hunting.

Acknowledgements

I am very grateful to the following persons for their assistance with various aspects of this study: E. C. OLSON (University of California, Los Angeles), P.P. VAUGHN (UCLA), G.A. BARTHOLOMEW (UCLA), D.S BERMAN (CM), P. BJORK (SDSM), M. BRETT-SURMAN (USNM), E. BUFFETAUT (Université Paris VI), K. CAMPBELL (LACM), W. CLEMENS (University of California, Berkeley), P.J. CURRIE & J. DANIS (TMP), DONG Z. (IVPP), L. DREW (then at MOR), B. ERICKSON (MMS), T. FORD, E. S. GAFFNEY (AMNH), J. HORNER (MOR), N. HOTTON III (USNM), J.H. HUTCHISON (UCB), J. JENSEN (Brigham Young University), N. G. LANE (then at UCLA), W. LANGSTON, Jr. (University of Texas, Austin), R. LONG (UCB), J. A. MADSEN, Jr. (then at UUVF), A. MILNER (BM(NH)), B. J. K. MOLNAR, W. J. MORRIS (then at Occidental College), M. J. ODANO (LACM), G. OLSHEVSKY, J. H. OSTROM (YPM), J. D. PETTIGREW (University of Queensland), S. PICKERING, H. P. POWELL (Museum, Oxford), D. A. RUSSELL (NMC), S. P. WELLES (UCB), D. WHISTLER (LACM), F. N. WHITE (UCLA), and R. WILD (Staatliches Museum für Naturkunde, Stuttgart). Mr. LAURIE BIERNE produced the line drawings. K. CARPENTER, P. CURRIE, J. O. FARLOW and R. WILD deserve special thanks for their comments and assistance.

References

- ALLMANN, J. (1977): Evolution of the visual system in the early primates. — *Progress Psychol. Physiol. Psychol.* 7: 1–53.
- BAKKER, R. T., WILLIAMS, M. & CURRIE, P. J. (1988): *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana. — *Hunteria* 1, 5: 1–26.
- BARSBOLD, R. (1983): Khishchnie dinovavri Mela Mongolii. — *Sovmest. Sov-Mong. Paleont. Yeksped., Trudi*, 19: 1–131.
- BENTON, M. J. & CLARK, J. M. (1988): Archosaur phylogeny and the relationships of the Crocodylia. — In: M. J. BENTON (Ed.): *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds.* — p. 297–338.
- BEER, G. R. DE (1937): *The development of the Vertebrate Skull.* — Oxford (Oxford University Press), 552 pp.
- BELLAIRS, A. D'A. (1957): *Reptiles: Life History, Evolution and Structure.* — London (Hutchinson), p. 192.
- BJORK, P. R. (1982): On the occurrence of *Tyrannosaurus rex* from northwestern South Dakota. — *Proc. S. Dakota Acad. Sci.*, 61: 161–162. (Abstract only)
- BONAPARTE, J. F. (1985): A horned Cretaceous carnosaur from Patagonia. — *Nation. Geograph. Res.*, 1: 149–151.
- CHATTERJEE, S. (1985): *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. — *Phil. Trans. Roy. Soc. London, (B)*, 309: 395–460.
- COLBERT, E. H. (1951): *The Dinosaur Book.* (Second edition) — New York (McGraw-Hill) 156 p.
- COLBERT, E. H. & RUSSELL, D. A. (1969): The small Cretaceous dinosaur *Dromaeosaurus*. — *Amer. Mus. Natur. Hist. Novitates*, 2380: 1–49.
- COPE, E. D. (1892): Fourth note on the Dinosauria of the Laramie. — *Amer. Natur.*, 26: 756–758.
- COTT, H. B. (1961): Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. — *Trans. Zool. Soc. London*, 29: 211–357.
- CRAWFORD, E. C., Jr. (1972): Brain and body temperatures in a panting lizard. — *Science*, 177: 431–433.
- CURRIE, P. J. (1987): Theropods of the Judith River Formation of Dinosaur Provincial Park, Alberta, Canada. — In: P. J. CURRIE & E. H. KOSTER (Eds.): *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers.* — p. 52–60.
- DONG Z. (1979): Fossil dinosaurs of the Cretaceous Period in southern China. — In: *Red beds of the Mesozoic-Cenozoic Periods in southern China.* — p. 342–350.
- DONG Z., ZHOU S. & ZHANG Y. (1983): The dinosaurian remains from Sichuan Basin, China. — *Paleont. Sinica, (C)*, 23: 1–145.
- FRANCIS, C. C. (1964): *Introduction to Human Anatomy*, fourth ed. — St. Louis (C. V. Mosby), 478 pp.
- GANS, C. (1966): The functional basis of the retroarticular process in some fossil reptiles. — *J. Zool.*, 150: 273–277.
- GARDNER, E., GRAY, D. J. & O'RAHILLY, R. (1975): *Anatomy.* (Fourth edition.) — Philadelphia (W. B. Saunders), p. 821.
- GAUTHIER, J. (1986): Saurischian monophyly and the origin of birds. — In: K. PADIAN, (Ed.): *The Origin of Birds and the Evolution of Flight.* — p. 1–55.
- GILLETTE, D. D., WOLBERG, D. L. & HUNT, A. P. (1986): *Tyrannosaurus rex* from the McRae Formation (Lancian, Upper Cretaceous), Elephant Butte Reservoir, Sierra County, New Mexico. — In: *New Mexico Geological Society Guidebook, 37th Field Conference, Truth or Consequences.* — p. 235–238.
- GILMORE, C. W. (1920): Osteology of the carnivorous Dinosauria in the United States National Museum with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. — *U.S. Nation. Mus., Bull.*, 110: 1–154.
- (1946): A new carnivorous dinosaur from the Lance Formation of Montana. — *Smiths. Misc. Coll.* 106: 1–19.
- GOODRICH, E. S. (1930): *Studies on the Structure and Development of Vertebrates.* — London (Macmillan), 837 pp.
- HAY, O. P. (1908): On certain genera and species of carnivorous dinosaurs, with special reference to *Ceratosaurus nasicornis* MARSH. — *Proc. U. S. Nation. Mus.*, 35: 351–366.

- HU, C.-C. (1973): (Title in Chinese). — *Acta Geol. Sinica*, 2: 179–206.
- HU, S.-Y. (1964): Carnosaurian remains from Alashan, Inner Mongolia. — *Vert. PalAs.*, 8: 42–63.
- HUENE, F. VON (1956): Paläontologie und Phylogenie der niederen Tetrapoden. — Jena (Gustav Fischer Verlag), 716 pp.
- HUENE, F. VON & MATLEY, C. A. (1933): The Cretaceous Saurischia and Ornithischia of the Central Provinces of India. — *Mem. Geol. Surv. India, Palaeont. Indica*, (ns), 21: 1–74.
- JULESZ, B. (1971): Foundations of Cyclopean Perception. — Chicago (University of Chicago Press), p. 406.
- KUHN, O. (1937): Saurischia. — *Fossilium Catalogus, I: Animalia*, 87: 1–124.
- KURZANOV, S. M. (1976): Novie pozdneemelovoi karnozavr iz Nogon-Tsava, Mongolii. — *Paleont. Biostrat. Mongol., Trudi*, 3: 93–104.
- LAMBE, (1904): On *Dryptosaurus incrassatus* (COPE) from the Edmonton series of the North-west Territory. — *Contrib. Canad. Paleont.*, 3, 3: 1–27.
- LAWSON, D. (1976): *Tyrannosaurus* and *Torosaurus*, Maestrichtian dinosaurs from Trans-Pecos Texas. — *Jour. Paleont.*, 50: 158–164.
- LOZINSKI, R. P., HUNT, A. P., WOLBERG, D. L. & LUCAS, S. G. (1984): Late Cretaceous (Lancian) dinosaurs from the McRae Formation, Sierra County, New Mexico. — *N. Mexico Geol.*, 6: 72–77.
- LULL, R. S. & WRIGHT, N. E. (1942): Hadrosaurian dinosaurs of North America. — *Geol. Soc. Amer., Spec. Paper*, 40: 1–242.
- MADER, B. J. & BRADLEY, R. L. (1989): A redescription and revised diagnosis of the syntypes of the Mongolian tyrannosaur *Alectrosaurus olseni*. — *J. Vert. Paleont.*, 9: 41–55.
- MADSEN, J. A. (1976): *Allosaurus fragilis*: a revised osteology. — *Utah Geol. Mineral Survey, Bull.*, 109: 1–163.
- MALEEY, E. A. (1955 a): Gigantskie khishchnie dinozavri Mongolii. — *Dokl. Akad. Nauk SSSR*, 104: 634–637.
- (1955 b): Novi khishchnie dinozavri iz verknego Mela Mongolii. — *Dokl. Akad. Nauk SSSR*, 104: 779–782.
- (1974): Gigantskie karnozavri semeistva Tyrannosauridae. — *Sovmest. Sov-Mong. Paleont. Yeksped., Trudi*, 1: 132–191.
- MARSH, O. C. (1892): Notes on Mesozoic vertebrate fossils. — *Amer. Jour. Sci.*, 44: 171–176.
- MOLNAR, R. E. (1974): A distinctive theropod dinosaur from the Upper Cretaceous of Baja California (Mexico). — *Jour. Paleont.*, 48: 1009–1017.
- (1980): An albertosaur from the Hell Creek Formation of Montana. — *Jour. Paleont.*, 54: 102–108.
- (1985): Alternatives to *Archaeopteryx*: a survey of proposed early or ancestral birds. — In: M. K. HECHT, J. H. OSTROM, G. VIOHL & P. WELLNHOFER (Eds.): *The Beginnings of Birds*. — p. 209–217.
- (1990): Variation in theory and in theropods. — In: P. J. CURRIE & K. CARPENTER (Eds.): *Dinosaur Systematics*. — Cambridge (Cambridge University Press), p. 71–79.
- MOLNAR, R. E. & CARPENTER, K. (1989): The Jordan theropod referred to the genus *Aublysodon*. — *Geobios.*, 22: 445–454.
- MOLNAR, R. E., KURZANOV, S. M. & DONG Z. (1990): Carnosauria. — In: D. B. WEISHAMPEL, P. DODSON & H. OSMOLSKA (Eds.): *The Dinosauria*. — Berkeley (University of California Press), p. 733.
- MOODIE, R. L. (1915): A sphenoidal sinus in the dinosaurs. — *Science*, 41: 228–289.
- NEWMAN, B. H. (1970): Stance and gait in the flesh-eating dinosaur *Tyrannosaurus*. — *Biol. Jour. Linn. Soc.*, 2: 119–123.
- NOWINSKI, A. (1971): *Nemegtosaurus mongoliensis* n. gen. n. sp. (Sauropoda) from the uppermost Cretaceous of Mongolia. — *Palaeont. Polonica*, 25: 57–81.
- OSBORN, H. F. (1905): *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. — *Bull. Amer. Mus. Natur. Hist.*, 21: 259–265.
- (1906): *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur. (Second communication). — *Bull. Amer. Mus. Natur. Hist.*, 22: 281–296.
- (1912): Crania of *Tyrannosaurus* and *Allosaurus*. — *Mem. Amer. Mus. Natur. Hist.*, (ns), 1: 1–30.
- (1916): Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. — *Bull. Amer. Mus. Natur. Hist.*, 33: 733–771.
- OSTROM, J. H. (1969): Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. — *Peabody Mus. Natur. Hist., Bull.*, 30.
- (1978): The osteology of *Compsognathus longipes* WAGNER. — *Zitteliana*, 4: 73–118.
- PARRINGTON, F. R. (1955): On the cranial anatomy of some gorgonopsians and the synapsid middle ear. — *Proc. Zool. Soc. London* 125: 1–40.
- PAUL, G. S. (1988): *Predatory Dinosaurs of the World*. — New York (Simon and Schuster) 464 p.
- PERLE, A. (1977): O pervoi nakhodke alektrosavra (Tyrannosauridae, Theropoda) iz pozdnego Mela Mongolii. — *Probl. Geol. Mong.*, 3: 104–113.
- PETTIGREW, J. D. (1979 a): Binocular visual processing in the owl's telencephalon. — *Proc. Roy. Soc. London, (B)*, 204: 435–454.
- (1979 b): Comparison of the retinotopic organization of the visual Wulst in nocturnal and diurnal raptors, with a note on the evolution of frontal vision. — In: S. J. COOL & E. L. SMITH (Eds.): *Frontiers of Visual Science*. — p. 439–449.
- PETTIGREW, J. D. & KONISHI, M. (1984): Some observations on the visual system of the oilbird (*Steatornis caripensis*). — *Nation. Geogr. Soc. Research Repts.*, 1975: 439–449.
- PHILLIPS, J. (1871): *Geology of Oxford and the Valley of the Thames*. — Oxford (Clarendon Press), p. 523.
- ROMER, A. S. (1956): *Osteology of the Reptiles*. — Chicago (University of Chicago Press), 772 pp.
- ROZHDESTVENSKY, A. K. (1965): Vozrastania izmenchivost i nekotoryi voprosi sistematiiki dinozavrov Azii. — *Paleont. Zhurn.*, 1965: 95–109.
- RUSSELL, D. A. (1970): Tyrannosaurs from the Late Cretaceous of western Canada. — *Nation. Mus. Natur. Sci., Public Palaeont.*, 1: 1–34.
- SCHMIDT-NIELSEN, K. (1972): *How Animals Work*. — Cambridge (Cambridge University Press), 114 pp.
- STEEL, R. (1970): Saurischia. — In: O. KUHN (Ed.): *Handbuch der Paläoherpetologie*. T. 14. — 87 pp.
- STERNBERG, C. M. (1946): Canadian dinosaurs. — *Nation. Mus. Canada, Bull.*, 103: 1–20.
- STROMER, E. (1915): Ergebnisse der Forschungsreisen Prof. E. STROMER's in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* n. gen., n. sp. — *Abh. Bayer. Akad. Wiss.*, 13: 1–32.
- SUES, H.-D. (1978): A new small theropod dinosaur from the Judith River Formation (Campanian) of Alberta Canada. — *Zool. Jour. Linn. Soc. London*, 62: 381–400.
- TAQUET, P. & WELLES, S. P. (1977): Redescription du crane de dinosaure theropode de Dives (Normandie). — *Ann. Paleo. (Vert.)*, 63: 191–206.

- TONG Y. & WANG J. (1980): Subdivision of the Upper Cretaceous and Lower Tertiary of the Tantou Basin, the Lushi Basin and the Lingbao Basin of W. Henan. — *Vert. PalAs.*, 18: 21–27.
- WALDMAN, M. (1974): Megalosaurids from the Bajocian (Middle Jurassic) of Dorset. — *Palaeontology*, 17: 325–339.
- WALKER, A.D. (1964): Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. — *Phil. Trans. Roy. Soc. London (B)*, 248: 53–134.
- (1972): New light on the origin of birds and crocodiles. — *Nature*, 237: 257–263.
- WALLS, G. L. (1942): The vertebrate eye and its adaptive radiation. — *Cranbrook Inst. Sci. Bull.*, 91: 1–785.
- WEISHAMPEL, D. B. (1984): Evolution of jaw mechanisms in ornithomimid dinosaurs. — *Advances Anat. Embryol. Cell Biol.*, 87, 1–110.
- WELLES, S. P. (1985): *Dilophosaurus wetherilli* (Dinosauria, Theropoda) osteology and comparisons. — *Palaeontogr.*, (A), 185: 85–180.
- WHESTONE, K. N. & MARTIN, L. D. (1979): New look at the origin of birds and crocodiles. — *Nature*, 237: 257–263.
- (1981): Common ancestry for birds and crocodiles? (reply). — *Nature*, 289: 98.
- WHITE, T. E. (1973): Catalogue of the genera of dinosaurs. — *Ann. Carnegie Mus.*, 44: 117–155.
- WITMER, L.M. (1984): Bird origins and the siphuncular system of birds and crocodiles. — *Abst. Amer. Ornithol. Union 102nd Mtg.* (Abstract only)
- YEH (1975): The Mesozoic Red Beds of Yunnan. — Beijing (), p. 201.
- YOUNG, C.-C. (1958): The dinosaurian remains of Laiyang, Shantung. — *Paleont. Sinica (C)*, 16: 1–138.
- ZHAI R., ZHENG J. & TONG Y. (1978): Stratigraphy of the mammal-bearing Tertiary of the Turfan Basin, Sinkiang. — *Mem. Inst. Vert. Paleont. Paleanthrop.*, Acad. Sinica, 13: 68–81. [Chinese]

Explanation of Plates

Plate 1

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana), LACM 23844.

Fig. 1. Right lachrymal in lateral view.

Fig. 2. Right lachrymal in medial view. The medial wall of the posterior part of the horizontal ramus is missing, revealing the internal chambers.

Fig. 3. Right premaxilla in lateral view. The lateral tooth (arrow) has apparently been broken, after which the broken surface was planed off.

Fig. 4. Left quadratojugal in medial view. The articular surfaces for the quadrate are seen at the left.

Fig. 5. Left quadratojugal in lateral view.

Scale bars 10 cm.

Plate 2

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) (LACM 23844) and Custer (Montana) (MOR 008).

Fig. 1. Right maxilla of LACM 23844 in medial view. Anterodorsal and posterodorsal to the maxillary fenestra the medial walls of the internal chambers are missing, so that they are exposed to view. Only the posterior part of the palatal process is preserved.

Fig. 2. Right squamosal of MOR 008 in dorsal view. Anterior is to the left.

Fig. 3. Right squamosal of MOR 008 in ventral view. Anterior is to the right.

Scale bars 10 cm.

Plate 3

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) (LACM 23844) and Custer (Montana) (MOR 008).

Fig. 1. Anterior part of left nasal of MOR 008 in lateral view, showing the prominent nasal rugosities.

Fig. 2. Left jugal of LACM 23844 in lateral view.

Fig. 3. Left jugal of LACM 23844 in medial view. Part of the medial wall of the vertical internal canal is missing, revealing the vertical canal.

Scale bars 10 cm.

Plate 4

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) (LACM 23844) and Custer (Montana) (MOR 008)

Fig. 1. Right postorbital of LACM 23844 in lateral view.

Fig. 2. Right postorbital of LACM 23844 in medial view.

Fig. 3. Left postorbital of MOR 008 in lateral view. The prominent eave-like projection over the orbit of MOR 008 may be seen, as well as the low roughening in that area in LACM 23844.

Scale bars 10 cm.

Plate 5

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana), AMNH 5027 and LACM 23844.

Fig. 1. Right jugal of LACM 23844 in ventral view, showing the presumed articular surface for the ectopterygoid (arrows).

Fig. 2. Right jugal of LACM 23844 in lateral view, showing the articular surface for the lachrymal adjacent to scale bar.

Fig. 3. Dorsal portion of left lateral temporal fenestra of AMNH 5027 in lateral view, showing the smooth surface (just in front of the "Sq.") interpreted as an attachment area for the external mandibular adductors.

Scale bars 10 cm.

Plate 6

Tyrannosaurus rex OSBORN, Hell Creek Fm., Custer (Montana), MOR 008.

Fig. 1. Right palatine in lateral view.

Fig. 2. Right palatine in ventral view.

Fig. 3. Right palatine in dorsal view. The anterolateral portion of this element has been broken away.

Scale bars 10 cm.

Plate 7

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) (CM 9379) and Custer (Montana) (MOR 008), and Lance Fm., Converse Co., (Wyoming) (AMNH 5117).

Fig. 1. Occipital face of AMNH 5117. Part of the posterior wall of the paroccipital process has collapsed forward into the internal chamber of that process, thus revealing its presence.

Fig. 2. Right half of the occipital face of CM 9379.

Fig. 3. Left ectopterygoid of MOR 008 in ventral view.

Fig. 4. Right ectopterygoid of MOR 008 in dorsal view.

Scale bars 10 cm.

Plate 8

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) (LACM 23844), and Lance Fm., Converse Co., (Wyoming) (AMNH 5117).

Fig. 1. Right pterygoid of LACM 23844 in posterior view.

Fig. 2. Right pterygoid of LACM 23844 in lateral view.

Fig. 3. Right pterygoid of LACM 23844 in dorsal view.

Fig. 4. Articulated frontals and parietals of AMNH 5117 in dorsal view.

Scale bars 10 cm.

Plate 9

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) AMNH 5027.

Fig. 1. Right epipterygoid in anterolateral view. 0.6x.

Fig. 2. Right epipterygoid in lateral view. The epipterygoid has been displaced forward in this specimen to lay at the back of the left antorbital fenestra. Abbreviations on specimen: Ec.pt., ectopterygoid; Ep.pt., epipterygoid; 'La', lachrymal. 0.6x.

Plate 10

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) LACM 23844.

Fig. 1. Stereo view of the dorsal articular surface of the quadrate (for the squamosal).

Fig. 2. Left quadrate in anteromedial view. The aperture connecting with the internal chambers is visible at lower right, just above the medial articular condyle.

Fig. 3. Stereo view of the right surangular in dorsal view, showing facet interpreted as the attachment area for the *M. adductor mandibulae externis superficialis et medialis*.

Scale bar 10 cm.

Plate 11

Tyrannosaurus rex OSBORN, Lance Fm., Converse Co. (Wyoming) AMNH 5117.

Fig. 1. Braincase in anteroventral view.

Fig. 2. Laterosphenoid region of the braincase in oblique lateroventral aspect.

Scale bars 10 cm.

Plate 12

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) LACM 23844.

Fig. 1. Left dentary in medial view.

Fig. 2. Left dentary in lateral view.

Scale bar 10 cm.

Plate 13

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) (AMNH 5027 and LACM 23844) and Custer (Montana) (MOR 008).

Fig. 1. Stereo view of the right articular of MOR 008 in posterior view, showing the concave posterior face.

Fig. 2. Part of the articular surface on the surangular, for the dentary of LACM 23844 in lateral view.

Fig. 3. Detail of the dentary-angular contact of AMNH 5027 in lateral view. A metal supporting bracket for the skull passes over this contact.

Scale bars 10 cm.

Plate 14

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) LACM 23844.

Fig. 1. Left splenial, in two pieces not sharing a contact, in lateral view.

Fig. 2. Left splenial, in two pieces not sharing a contact, in medial view.

Fig. 3. Left prearticular in medial view.

Fig. 4. Left prearticular in lateral view.

Scale bars 10 cm.

Plate 15

Tyrannosaurus rex OSBORN, Hell Creek Fm., Jordan (Montana) LACM 23844.

Fig. 1. Right surangular in lateral view. The pit (white arrow) visible in the lateral buttress, just above the surangular fenestra, is apparently the result of an injury sustained during life.

Fig. 2. Right surangular in medial view.

Fig. 3. Left angular in medial view.

Fig. 4. Left angular in lateral view.

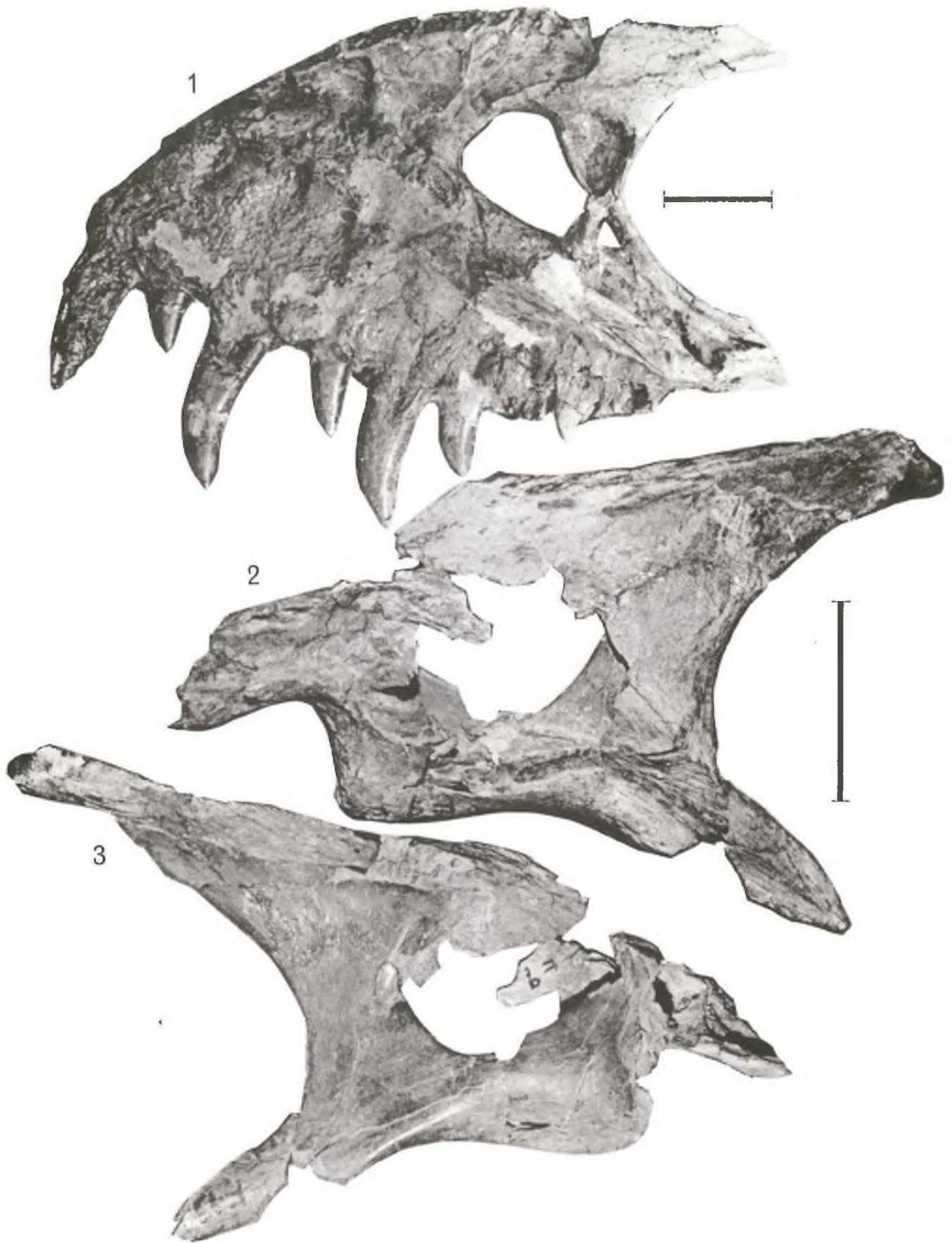
Fig. 5. Left articular in medial view.

Fig. 6. Left articular in dorsal view.

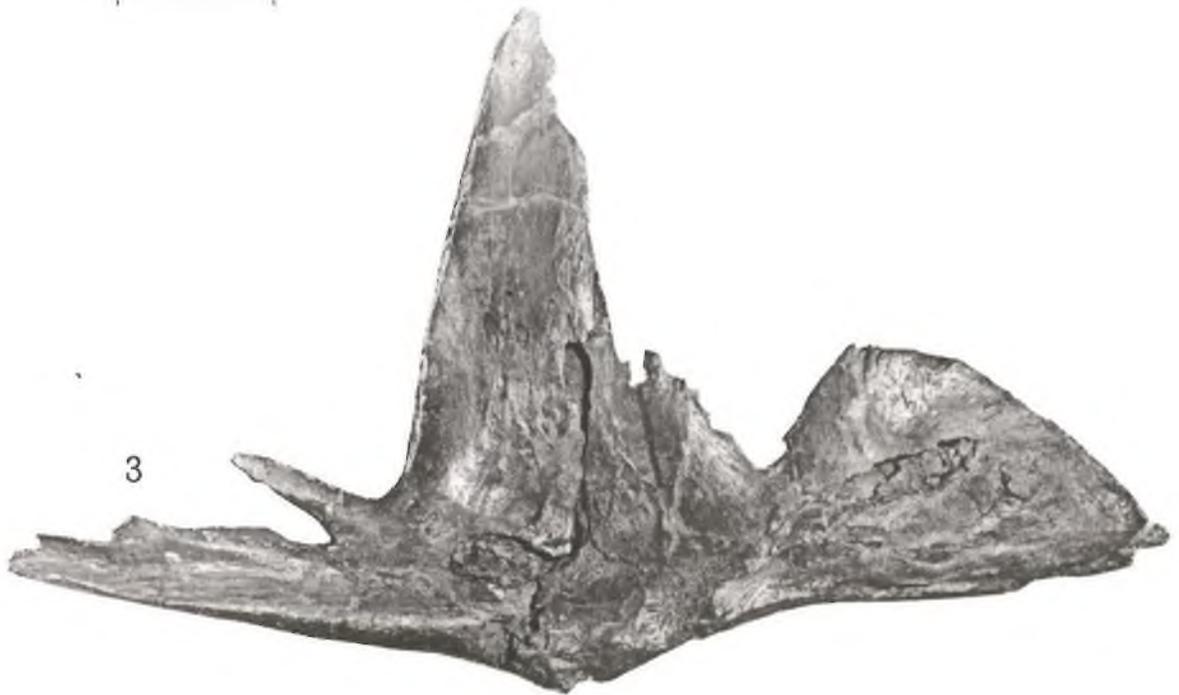
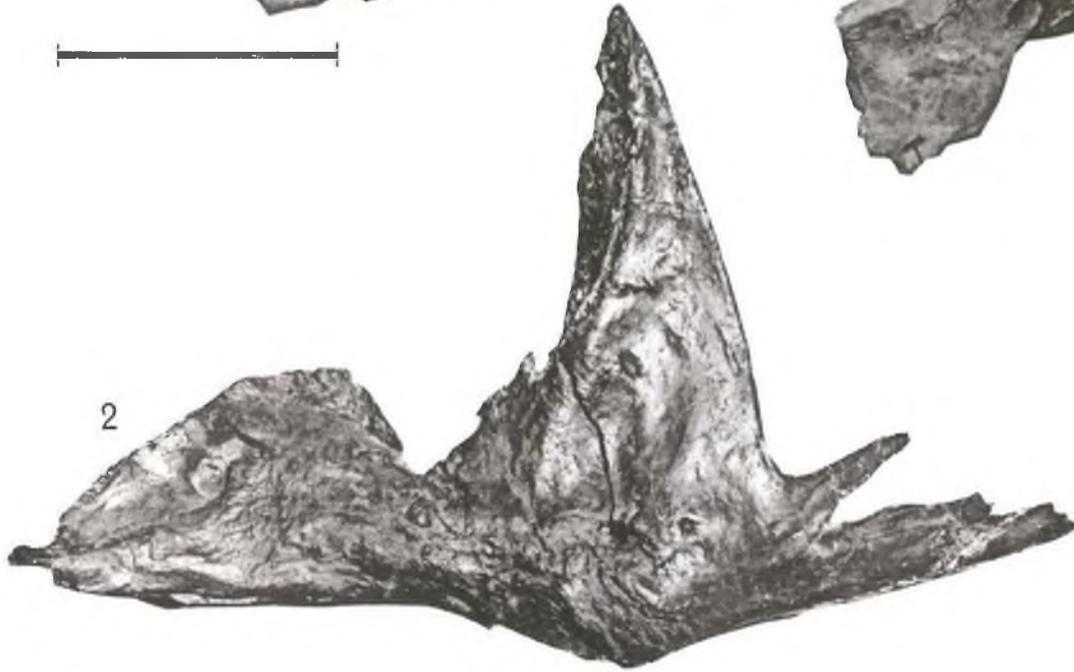
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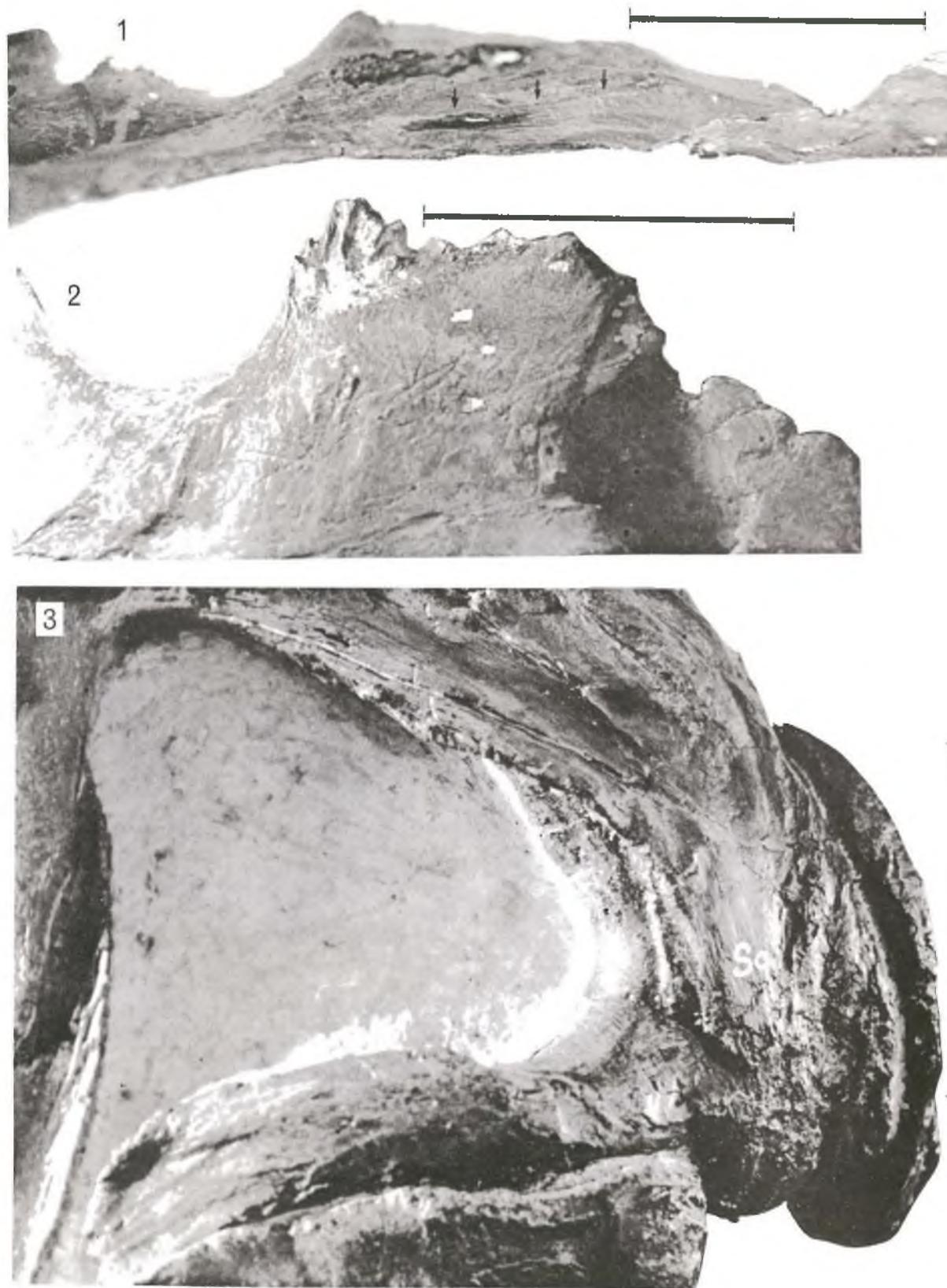
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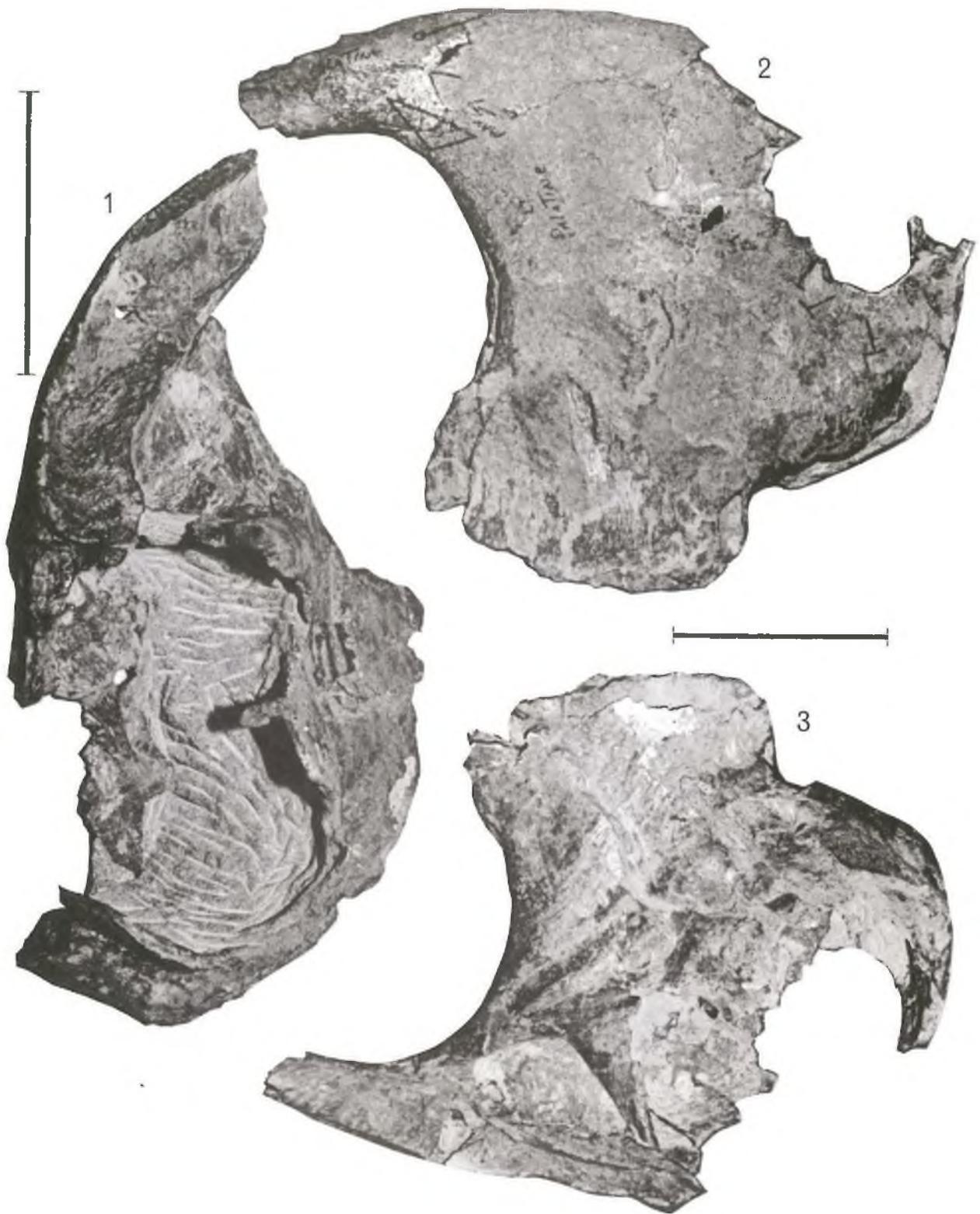
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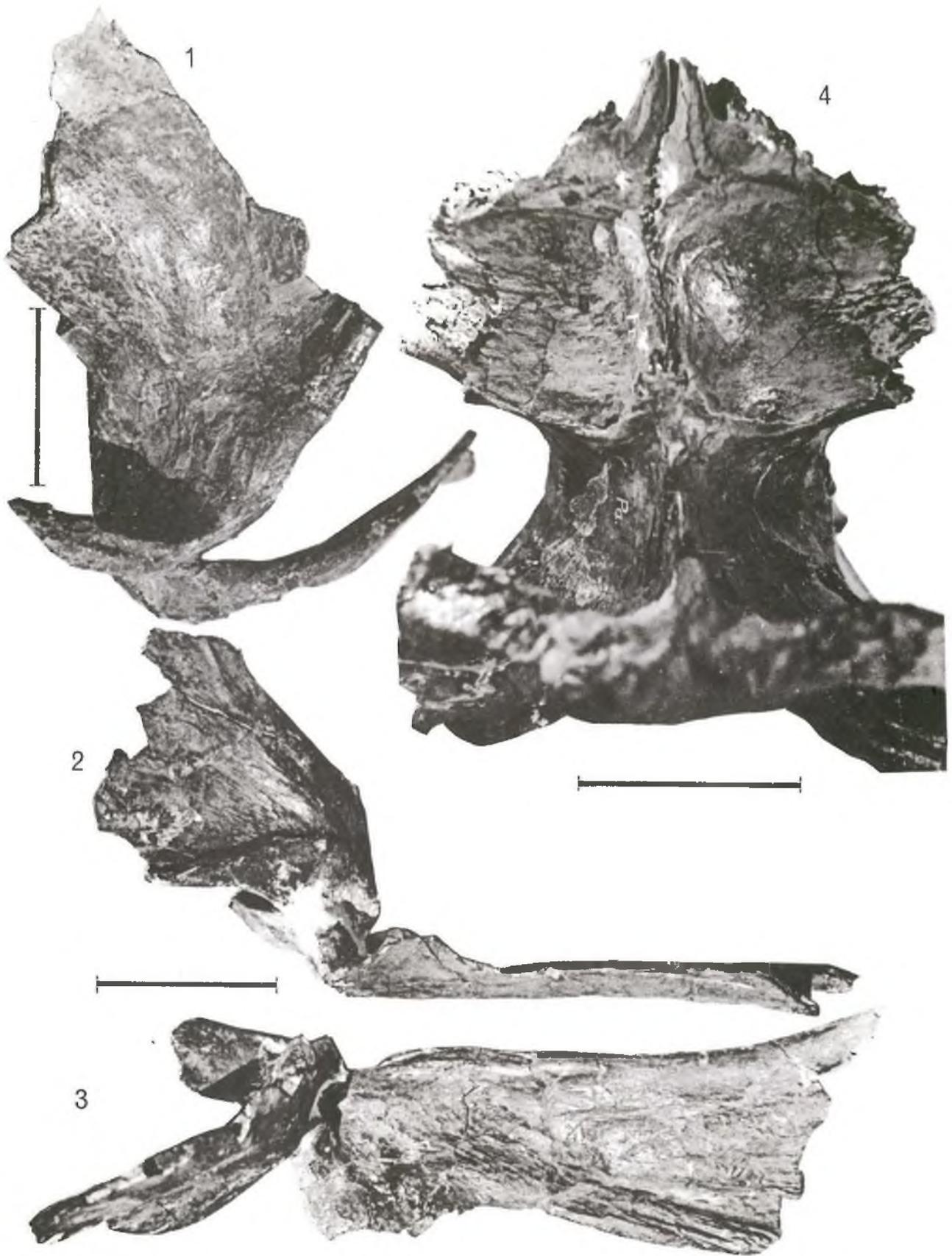
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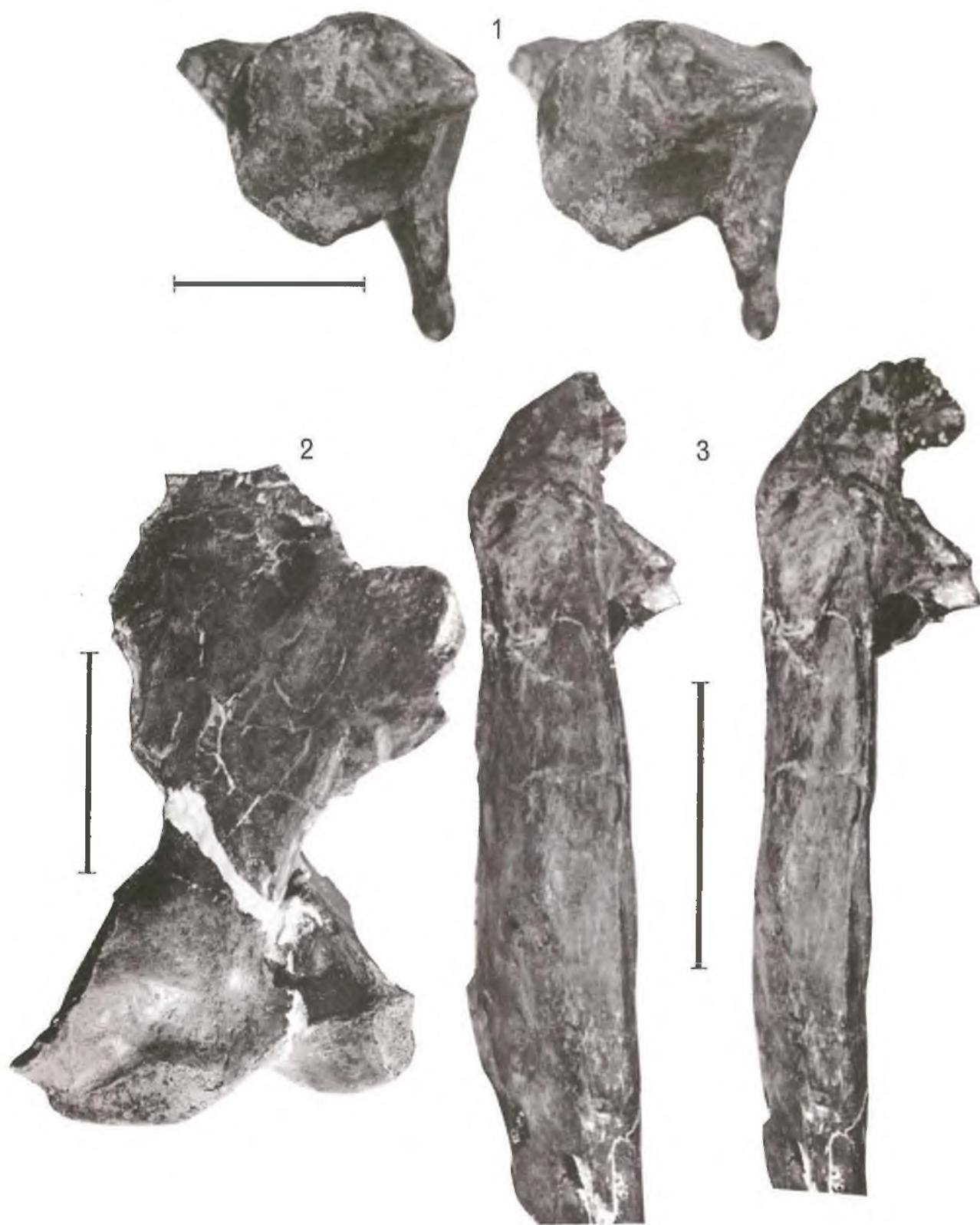
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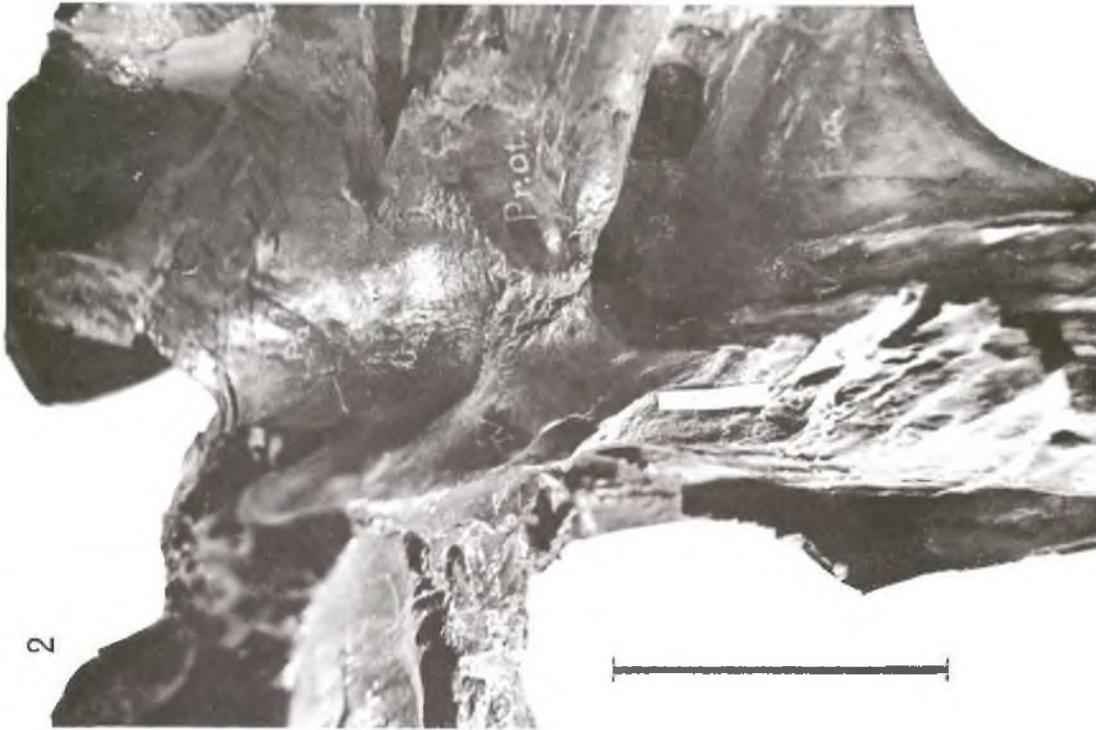
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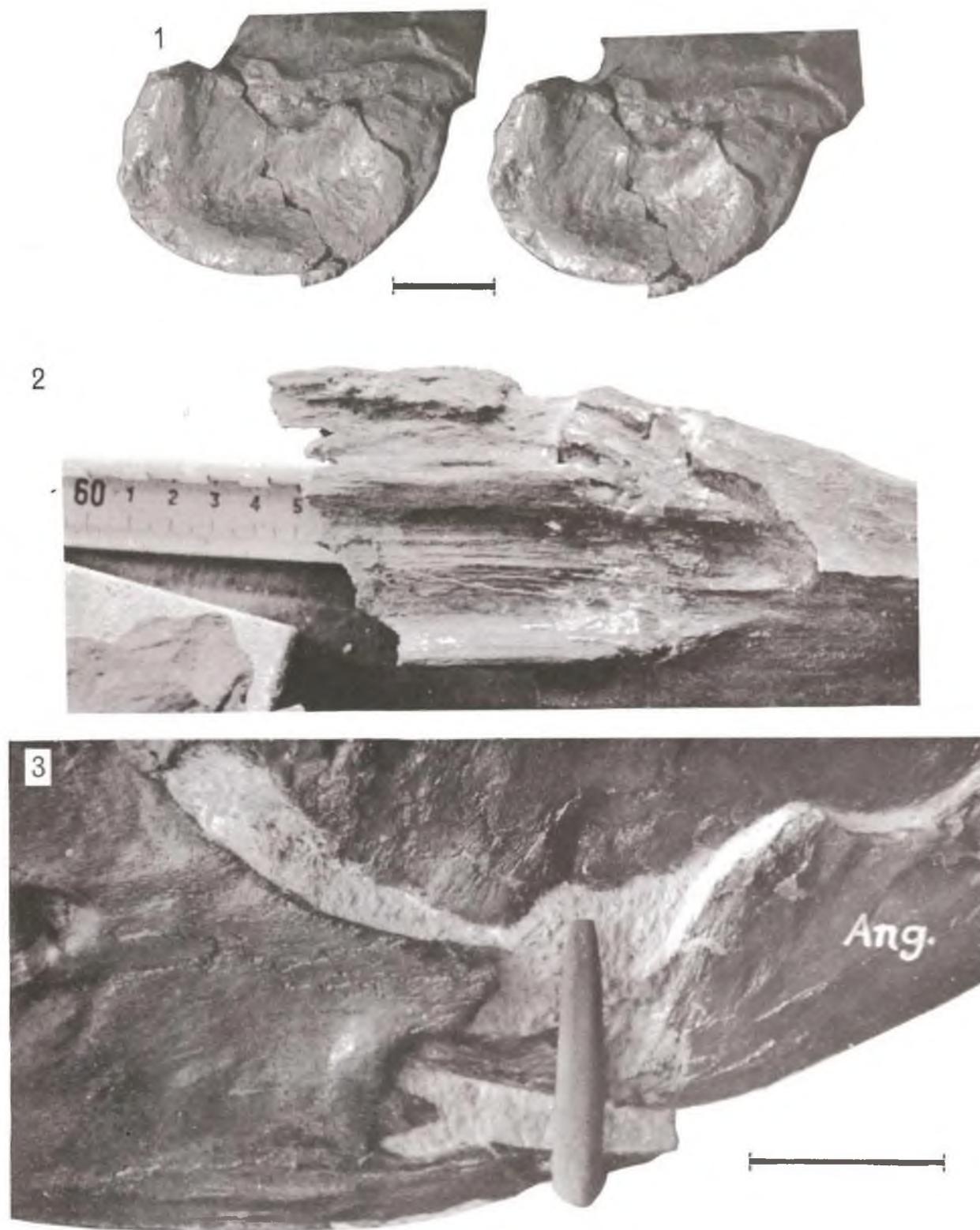
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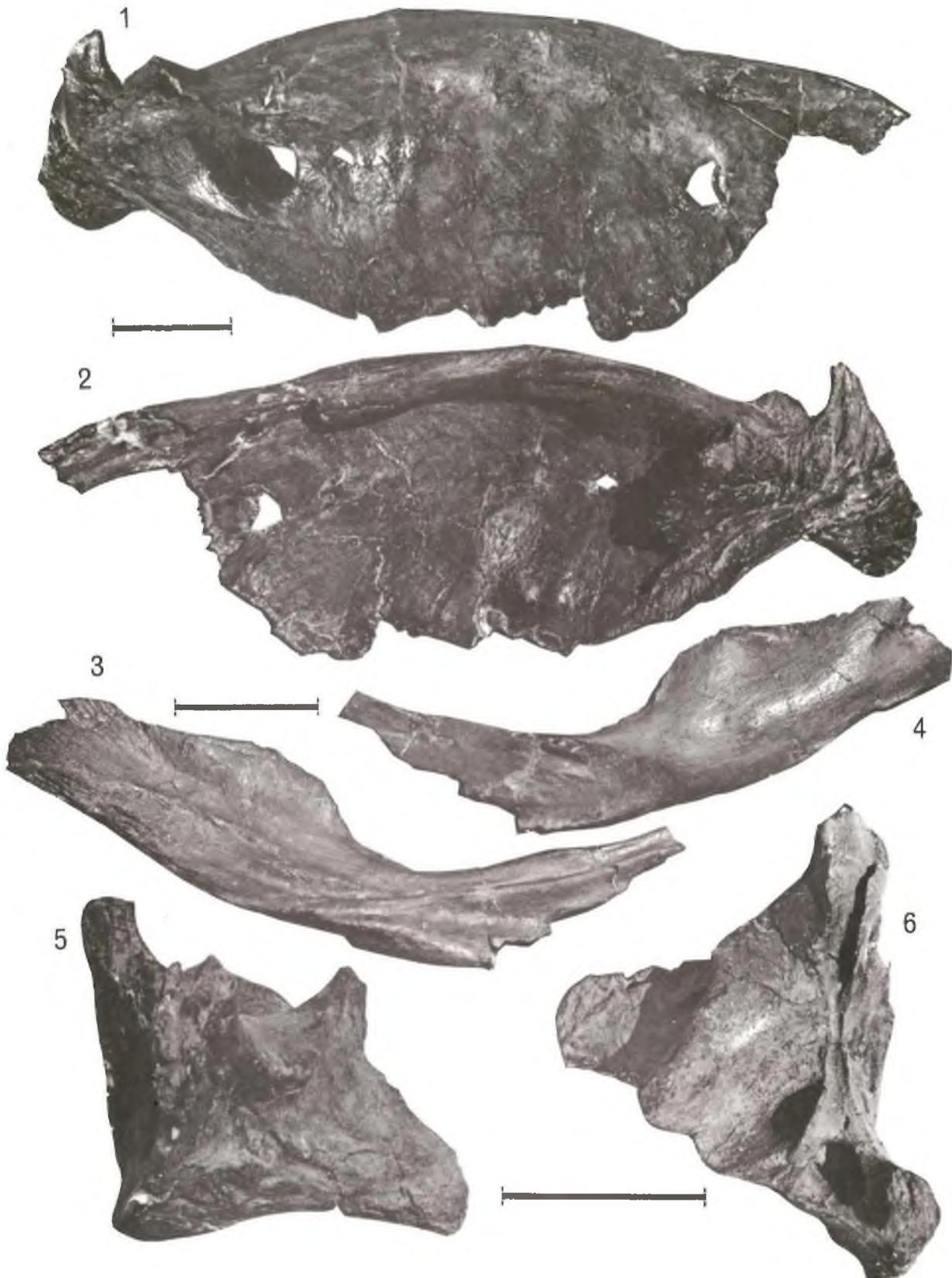
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