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CONTENTS

Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with Emphasis on the Osteology of *Torvosaurus tanneri*

BROOKS B. BRITT

Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0, and Department of Geology and Geophysics, University of Calgary, Calgary, Alberta T2N 1N4

Thesis Chair: WADE E. MILLER

ABSTRACT

The Dry Mesa Quarry assemblage includes five positively identified genera of theropod dinosaurs: *Torvosaurus, Ceratosaurus, Allosaurus, Marshosaurus, Stokesosaurus,* and several indeterminate elements, possibly of *Coelurus* and/or *Ornitholestes,* and elements of a deinonychosaur or bird. This is the first reported occurrence of *Stokesosaurus* and *Marshosaurus* outside their type locality, the Cleveland-Lloyd Quarry, Utah. Six sauropod genera (*Diplodocus, Barosaurus, Supersaurus, Apatosaurus, Brachiosaurus* [=?*Ultrasaurus*], and *Camarasaurus*) and four ornithischian genera (*Dryosaurus,* ? *Othnelia, Camptosaurus,* and *Stegosaurus*) have been identified, making this the most prolific of all Morrison Formation quarries in terms of the number of identified dinosaurian taxa. Newly discovered cranial and postcranial elements of *Torvosaurus* demonstrate that this genus shares diagnostic characters with the type of *Megalosaurus,* indicating the former is assignable to the Megalosauridae *sensu stricto.* In addition to previously reported characters, *Torvosaurus* is further diagnosed by the following characters: skull height ~40% of length, all but the posteriormost two presacrals opisthocoeleous, all postaxial presacral centra pleurocoeleous, and nearly all postaxial presacral centra strongly keeled ventrally. Previously known only from the Dry Mesa Quarry, *Torvosaurus* also occurs in the Dinosaur National Monument Quarry, Utah, and the Freezeout Hills Quarry N and Como Bluff Quarry 9, Wyoming. A comparison of *Allosaurus* elements from Dry Mesa with those referred to *Allosaurus fragilis* from the Cleveland-Lloyd Quarry, Utah, indicates the specimens differ at the specific level.

INTRODUCTION

The extraordinary Dry Mesa Quarry contains the most diverse Upper Jurassic or Lower Cretaceous dinosaur assemblage known in North America. Located near the southwest corner of Dry Mesa in west central Colorado (fig. 1), the quarry has yielded approximately 80% of the previously reported Morrison Formation dinosaur genera (see Morrison faunal list, table 1) and several new ones. Seventeen dinosaur genera (without counting *Dystylosaurus* and *Ultrasaurus* [Jensen 1985a]) have been recovered including 4 ornithischians, 6 sauropods, and approximately 7 theropods (see Dry Mesa assemblage list, table 2). Prior to this report the maximum numbers of genera reported from any single Morrison quarry was 10 for Dinosaur National Monument (Dodson and others

1980) and 10 to 13 for the Cleveland-Lloyd Quarry (Madsen 1976b, Stokes 1985).

Previous studies containing discussions of Dry Mesa theropod materials are those of Galton and Jensen (1979), in which they initially described the genus and species *Torvosaurus tanneri,* and Jensen (1985b), which included a description of some of the same *Torvosaurus* material considered in the present study. Jensen and Padian (1989) reported the occurrence of a dromaeosaurid or bird based on a small femur previously identified by Jensen as avian (1981). The nondinosaurian assemblage includes a diverse but generally fragmentary "microvertebrate" assemblage. Pterosaurs were first reported from this quarry by Jensen and Ostrom (1977), and *Mesadactylus ornithosphyos,* a pterodactyloid pterosaur, was recently de-

1

Table 1. Systematic paleontology of the Morrison Formation dinosaur fauna following Dodson and others (1980) but modified to include Galton's (1982) reported occurrence of Elaphrosaurus *and* Supersaurus *(Jensen 1985a).*

Class REPTILIA

Subclass ARCHOSAURIA
  Order SAURISCHIA
    Suborder THEROPODA

      Family COELURIDAE
        Ornitholestes Osborn 1903
        Coelurus Marsh 1879

      Family ORNITHOMIMIDAE
        Elaphrosaurus Janensch 1920

      Family MEGALOSAURIDAE
        Torvosaurus tanneri Galton & Jensen 1979

      Family CERATOSAURIDAE
        Ceratosaurus Marsh 1884

      Family ?TYRANNOSAURIDAE
        Stokesosaurus Madsen 1974

      Family ALLOSAURIDAE
        Allosaurus Marsh 1878

      Family ?DROMAEOSAURIDAE
        Marshosaurus Madsen 1976

    Suborder SAUROPODAMORPHA
      Family Cetiosauridae
        Haplocanthosaurus Hatcher 1903

      Family BRACHIOSAURIDAE
        Brachiosaurus Riggs 1904

      Family CAMARASAURIDAE
        Camarasaurus Cope 1877

      Family DIPLODOCIDAE
        Diplodocus Marsh 1878
        Barosaurus Marsh 1890
        Supersaurus Jensen 1985
        Apatosaurus Marsh 1877

  Order ORNITHISCHIA
    Suborder ORNITHOPODA
      Family FABROSAURIDAE
        Nanosaurus Marsh 1877

      Family HYPSILOPHODONTIDAE
        Dryosaurus Marsh 1894
        Othnelia Galton 1977

      Family IGUANODONTIDAE
        Camptosaurus Marsh 1885

    Suborder STEGOSAURIA
      Family STEGOSAURIDAE
        Stegosaurus Marsh 1877

Table 2. Systematic paleontology of the Dry Mesa Quarry dinosaur assemblage. The Dry Mesa Quarry assemblage also includes two fishes, a ?paleoniscid (Jensen and Padian 1989), and a lungfish, Ceratodus *(Prothero and Jensen 1983); an amphibian (Jensen and Padian 1989);* Glyptops *(Eugene Gaffney personal communication 1985); a possible lepidosaur (Jensen and Padian 1989), a crocodile;* Mesadactylus ornithosphyos *(ibid.), a pterodactyloid pterosaur; and a prototherian mammal (Prothero and Jensen 1983).*

Class REPTILIA

Subclass ARCHOSAURIA
  Order SAURISCHIA
    Suborder THEROPODA

      Family COELURIDAE
        ?Ornitholestes Osborn 1903
        ?Coelurus Marsh 1879

      Family MEGALOSAURIDAE
        Torvosaurus tanneri Galton & Jensen 1979

      Family CERATOSAURIDAE
        Ceratosaurus Marsh 1884

      Family ?TYRANNOSAURIDAE
        Stokesosaurus Madsen 1974

      Family ALLOSAURIDAE
        Allosaurus Marsh 1878

      Family ?DROMAEOSAURIDAE
        Marshosaurus Madsen 1976
        small ?dromaeosaurid Jensen and Padian 1989
        theropod of indeterminate genus (teeth, may be *Marshosaurus*, this paper)

      Family INCERTAE SEDIS
        theropod (caudal vertebra, this paper)
        theropod (ischia, this paper)

    Suborder SAUROPODAMORPHA
      Family DIPLODOCIDAE
        Diplodocus Marsh 1878
        Barosaurus Marsh 1890
        Supersaurus Jensen 1985
        Apatosaurus Marsh 1877

      Family BRACHIOSAURIDAE
        Brachiosaurus Riggs 1904 (= ? *Ultrasaurus* Jensen 1985a)

      Family CAMARASAURIDAE
        Camarasaurus Cope 1877

  Order ORNITHISCHIA
    Suborder ORNITHOPODA
      Family HYPSILOPHODONTIDAE
        Dryosaurus Marsh 1894
        ?Othnelia Galton 1977

      Family IGUANODONTIDAE
        Camptosaurus Marsh 1885

    Suborder STEGOSAURIA
      Family STEGOSAURIDAE
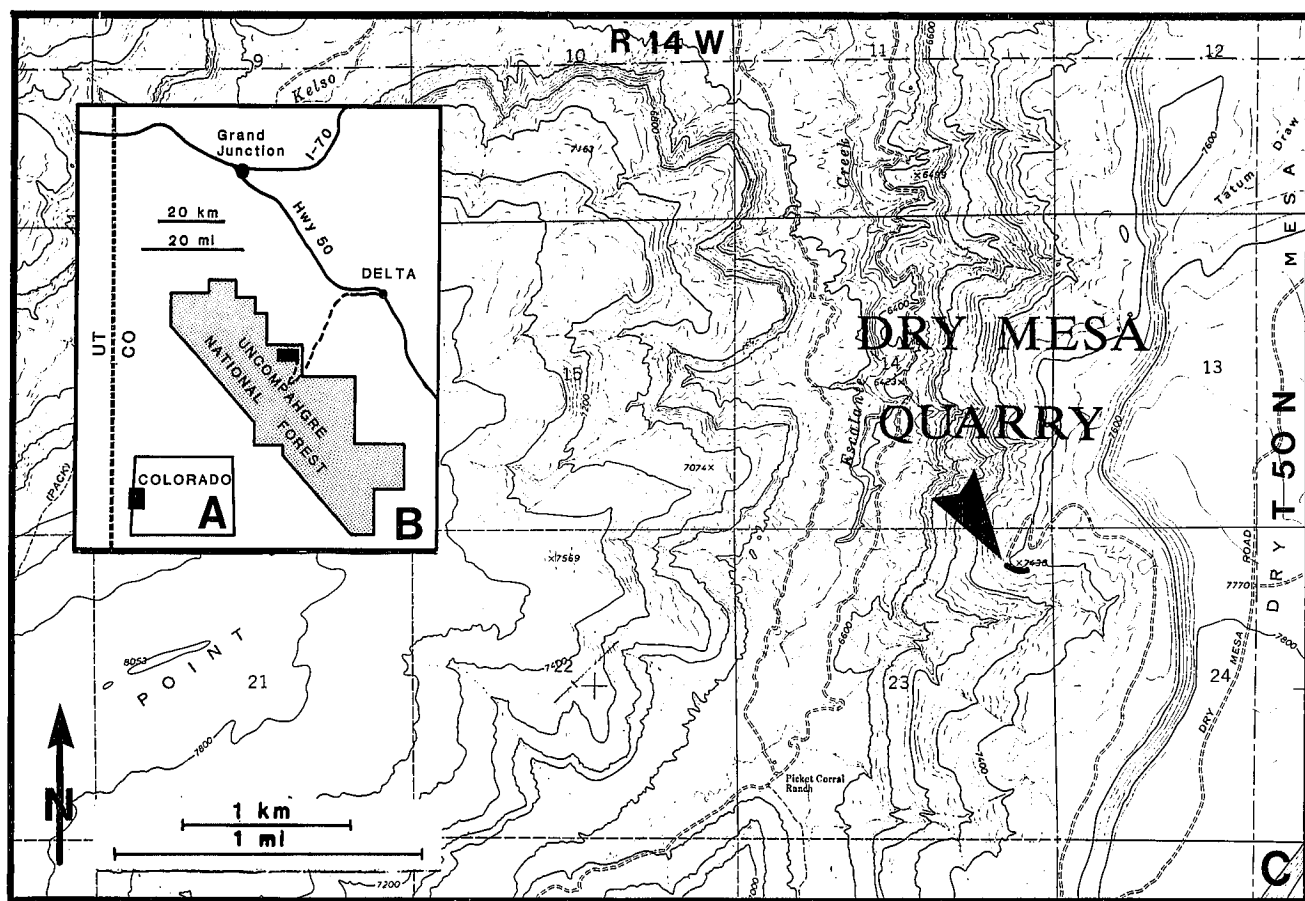   *Stegosaurus* Marsh 1877

FIGURE 1.—*Locality maps. A, the state of Colorado indicating the location of B, the Uncompahgre Plateau region showing the location of C, the southwest end of Dry Mesa and the Dry Mesa Quarry. The Dry Mesa Quarry is located at an elevation of 2242 m (7356 ft) on the southwest flank of Dry Mesa, a part of the Uncompahgre Plateau, 33 km (20.6 mi) west southwest of Delta, Colorado, in section 23, T. 50 N, R. 14 W, Mesa County, Colorado. Base Kelso Point 7½-Minute Quadrangle.*

scribed by Jensen and Padian (1989). *Mesadactylus* is based on specimens previously identified by Jensen (1981) and in Marx (1978) as avian. Jensen and Padian (1989) analyzed other small vertebrate specimens and reported the occurrence of a fish (thought to be a paleoniscid), an amphibian, and possibly a lepidosaur but, unfortunately, the specimens consist of isolated and fragmentary elements. Prothero and Jensen (1983) reported the occurrence of a prototherian mammal based on a humerus, a crocodilian, and *Ceratodus*. *Glyptops* also occurs in the quarry (Eugene Gaffney personal communication 1985). With the exception of gastropods, invertebrate and plant fossils are represented only by fragmentary remains (personal observation).

The quarry site is in the Brushy Basin Member of the Morrison Formation and was discovered during the summer of 1971 by Eddie and Vivian Jones of Delta, Colorado. They recognized the significance of their find and

notified James A. Jensen of Brigham Young University's Earth Sciences Museum. That fall Jensen visited the Joneses and was shown the "discovery bone," an extremely large theropod phalanx now cataloged as *Torvosaurus tanneri*, BYUVP 5026. A brief trip to the locality shortly thereafter convinced Jensen the site would be worth developing. Quarrying began in April 1972 in hopes of discovering additional bones of the large theropod.

During the 19 years since its discovery, the quarry has been worked parts or all of 12 field seasons, producing a collection of several thousand bones. However, nearly all the large theropod elements belonging to the genus *Torvosaurus* were collected during the first field season. The disarticulated bones of two large and one relatively smaller *Torvosaurus* were concentrated in a rather small area at the south end of the quarry. Ironically, the quarry did not become well known for the theropods but for its

extremely large sauropods including *Brachiosaurus* (=?*Ultrasaurus* sensu Jensen, 1985a), *Diplodocus*, *Barosaurus*, and *Supersaurus*.

Excavations were conducted from 1972 to 1981 by James A. Jensen of Brigham Young University. I worked in the quarry during the 1974 field season. Quarry operations have continued to the present under the direction of Wade E. Miller and Kenneth L. Stadtman, also of Brigham Young University.

Included in this study are a few elements of *Allosaurus* and *Camptosaurus* collected from a small accessory quarry, known as Jones' Hole, located approximately 200 m north of the main Dry Mesa Quarry. The Jones' Hole Quarry is approximately at the same stratigraphic level in rocks lithologically similar to the main quarry. The two quarries may represent different segments of a single channel. Fossils collected from these quarries are not differentiated from each other in this paper because all genera present in Jones' Hole are also present in the main quarry.

With the exception of the theropods, most bones collected from the two quarries are still unprepared. Additional theropod remains undoubtedly will be discovered in large blocks containing sauropod bones, but the present collection of prepared materials probably represents the faunal assemblage of the deposit. This paper is based on the analysis of nearly 400 prepared theropod bones.

INSTITUTIONAL ABBREVIATIONS

AMNH = American Museum of Natural History, New York City, New York; BYUVP = Brigham Young University Vertebrate Paleontology, Provo, Utah; CLDQ = Cleveland-Lloyd Dinosaur Quarry, Cleveland, Utah; CM = Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; DNM = Dinosaur National Monument, Jensen, Utah; DMNH = Denver Museum of Natural History, Denver, Colorado; MWC = Museum of Western Colorado, Grand Junction, Colorado; TMP = Tyrrell Museum of Palaeontology, Drumheller, Alberta; UCM = University of Colorado Museum, Boulder, Colorado; USNM = United States National Museum, Washington, District of Columbia; UUVP = University of Utah Vertebrate Paleontology, Salt Lake City, Utah.

ACKNOWLEDGMENTS

GEOLOGY

GEOLOGIC SETTING

The base of the Dry Mesa Quarry is in the Morrison Formation, 133 m (437 ft) stratigraphically above the top of the Entrada Sandstone and approximately 25 m (82 ft) below the overlying Burro Canyon Formation. The Burro Canyon Formation is equivalent to the Cedar Mountain Formation west of the Colorado River and correlative with the Lytle-Purgatoire Formation of Colorado and the Cloverly Formation of Montana (Dodson and others 1980). The main quarry is at an elevation of 2242 m (7356 ft) above sea level. The base of Dry Mesa Quarry is 100 m (329 ft) above the base of the Morrison Formation in a dominantly light yellow gray sandstone of the Brushy Basin Member. Craig and others (1955) considered the Morrison Formation to be "undifferentiated" in this portion of Colorado. I believe there are enough lithologic differences within the Morrison Formation in the Dry Mesa area to identify the two commonly recognized members: the lower Salt Wash Member and the upper Brushy Basin Member. However, more recent lithostratigraphic studies of this rock package have resulted in more refined formational subdivisions and definitions.

The Morrison Formation conformably overlies the uppermost, beach-type, laminar sand unit of the Summerville Formation. The 33 m (107 ft) of Summerville Formation lies above the cliff-forming, large scale, cross-bedded Entrada Sandstone and below the Morrison Formation. The Summerville consists mainly of drab, brown red mudstones interbedded with thin red brown sandstone beds and lenses. The basal sandstones of the Summerville Formation are poorly sorted, very fine grained reddish sandstones and siltstones. The formation contains interbedded pale yellow gray and light brown red sandstones up to 1 m (3 ft) thick. The upper part of the formation has two thick, laminate beds that exhibit numerous oscillation ripple marks. No fossils were observed. All stratigraphic measurements were made with a Jacob's staff and clinometer.

Photogeologic maps that include the Dry Mesa area were made by Hackman (1958) and Williams (1964) in which the Morrison Formation was divided into the Salt Wash and Brushy Basin members. The quarry is in their Brushy Basin. In both cases, however, the bulk of their Brushy Basin Member seems to be Burro Canyon Formation because palynomorphs from this horizon are Aptian/Albian in age (F. X. Miller personal communication, to James L. Baer, 1974).

The Salt Wash Member in the quarry area is 90 m (294 ft) thick. It is composed of coarse sediments and abundant sandstone lenses in a mudstone and siltstone matrix. A medium-bedded limestone bed, approximately 1 m (3 ft) thick, occurs 3.3 m (11 ft) above the base of the Morrison

Formation. This limestone is medium gray on fresh surfaces, weathers to a light blue gray, and is fine grained. Slope-forming mudstones and shales, with occasional thin, laminar sandstones, occur above the limestone. Numerous paleochannel fills are exposed between the limestone and the quarry floor. The channel fills are composed of resistant cross-bedded sandstone lenses with rip-up mudstone clasts at their bases. Channels range from two to several meters wide. The uppermost zone of abundant sandstone lenses is used as the top of the Salt Wash Member. The only body fossils observed in this member are in the limestone unit and consist of fragments of thin-shelled gastropods. Channels and channel bases are commonly bioturbated, containing vertical and horizontal burrows.

The Brushy Basin Member consists of the same lithologic types as the Salt Wash Member, but the resistant sandstone lenses are less abundant. The Brushy Basin Member is 35 m (115 ft) thick in the area immediately adjacent to the quarry and has been the source of most dinosaurs collected from the Morrison Formation (Dodson and others 1980). The dinosaur quarry is approximately 10 m (32 ft) above the base of the Brushy Basin Member. The bone-bearing layer ranges from .6 m (2 ft) to 1.5 m (4.8 ft) thick. Small, thin-shelled gastropods have been found in the quarry sediments as well as an obviously reworked upper Paleozoic fusulinid. Gastroliths in the Morrison Formation and pebbles in the Buckhorn Conglomerate, which overlies this formation to the west in the San Rafael Swell area, frequently contain fusulinids (Stokes 1944, p. 979). The presence of the fusulinid indicates some of the clastics were derived from upper Paleozoic formations.

The total thickness of the Morrison Formation in the area is approximately 125 m (412 ft), but the exact thickness is not known because the formation is difficult to distinguish from the overlying Burro Canyon Formation. The same problem of differentiation is also true for the Morrison Formation and Cloverly Formation (the latter being the northern equivalent of the Burro Canyon/Cedar Mountain Formation) in Montana and Wyoming (Ostrom 1970, p. 11). For the purposes of this paper, the first bench below the Dakota Formation can be considered as the division between the Morrison Formation and the Burro Canyon Formation in the Dry Mesa area because the bench is readily recognizable over much of the region near the quarry. For convenience, the thin sandstone unit defending this bench will be considered the basal unit of the Burro Canyon Formation on the southern end of Dry Mesa.

QUARRY SEDIMENTOLOGY

The following description of the bone-bearing litho-

some is based on a relatively small area exposed in August 1987 by quarrying operations and may not be entirely representative of the quarry as a whole. The lithologies and structures observed, however, appear to be generally similar to those contained in blocks removed in previous years from other areas of the quarry. The orientation of long bones has been shown to be useful in determining paleocurrent directions and water depth by Voorhies (1969), but because only two small areas of the quarry have been mapped (in recent field seasons), it is not possible to determine either at this time.

The quarry extends 117 m along the face of the hill in roughly a north-south direction, but the full extent of the bone-bearing lithosome has yet to be exposed. However, a bulldozer excavation approximately 10 m north of the 1987 excavation revealed unfossiliferous, maroon, silty mudstones with minor light green, silty mudstone layers. This indicates that the bone-bearing lithosome pinches out rapidly in this direction. Jensen (personal communication 1988) indicated that earlier excavations in the southernmost portion of the quarry showed that the lithosome is only one bone thick, and the bones are less concentrated than in other areas of the quarry. Consequently, excavation in this direction was discontinued.

The maximum observed thickness of the bone-bearing lithosome is slightly less than 1.5 m. This unit is composed of trough cross-bedded, conglomeratic (chert pebble), sandstone lenses up to 3 m wide. Each trough consists of a fining-upward sequence with a basal lag of light green, mudstone, rip-up clasts. Pebbles of bone, exhibiting various stages of rounding, are also a common component. The mudstone clasts range up to 10 cm or more in diameter, are composed of hydrophilous "bentonitic" clay, and occasionally exhibit liesegang banding. The conglomeratic sandstone is generally loosely cemented; calcite is the dominant cement, though clay also appears to play a part. The bones lie on the rip-up clast zones.

The base of the trough cross-bedded unit is incised into the underlying, moderately sorted, clayey, very fine sandstone unit; contact between the two units is undulatory on a decimeter scale. Grains in the lower unit are encased in a bentonitic clay matrix that acts as the cement. The top of the unit is light green in color but grades into a pale purple green within about .1 m of depth. Such color changes are thought to be indicative of a secondary reduction of oxidized sediments and/or the removal of ferric ions by waters in the overlying paleostream (McPherson 1980).

A preliminary study of quarry matrix run through a sieve stack indicates clasts less than 500 μ in diameter are dominantly clear quartz, while those with a diameter greater than 500 μ are dominantly chert (red and green in color) with some limestone clasts. More specifically, the fine sand fraction (<250 μ) is mainly subrounded to rounded, clear quartz, with subrounded grains dominant. Chert and biotite make up approximately 10% of this fraction. The medium sand fraction (250–500 μ) contains rounded to well-rounded, frosted, clear quartz grains. Angular to subangular chert and other lithics, including biotite, make up approximately 10% this fraction. In the coarse sand fraction (500 μ to 1 mm), chert and other rock fragments are the most abundant constituents, with clear quartz sand present only in the smaller size range (circa 500 μ). These clear quartz grains are rounded to subrounded, but the larger chert and rock grains are subangular to subrounded. Limestone fragments are a rare component. The very coarse sand fraction (1–2 mm) is dominantly angular to subrounded green and red chert with uncommon limestone fragments. Fine pebbles (>2 mm) are subangular to subrounded and dominantly chert. About 15% of this fraction is made up of limestone clasts. The amounts of red and green chert are approximately equal. Red and green bands can frequently be observed in the same pebble, often with the two colors blending into each other, indicating the red and green chert grains found in the smaller fractions are from the same source.

The presence of (1) rounded to well-rounded, frosted monocrystalline quartz; (2) angular to subrounded chert; (3) limestone clasts; and (4) euhedral biotite books in the same rock implies this conglomeratic sandstone has a complex sedimentological history. The monocrystalline quartz component appears to have been subjected to several sedimentological cycles, perhaps including an eolian one. The relative angularity of the chert component (some large ones contain Paleozoic marine fossils) and the presence of limestone clasts, which could not survive much transportation, apparently underwent relatively less transport and reworking than the monocrystalline component. And, finally, the euhedral biotite books suggest that this component has undergone very little transport. The biotite is likely derived from a local volcanic ash bed or beds, which are common in the Brushy Basin Member of the Morrison Formation (Stokes 1944).

The bone-bearing lithosome is interpreted to represent a channel-floor deposit. This is supported by the presence of an erosional base, lag-type sediments with abundant clay clasts, and trough cross-bedding. Apparently the deposit was laid down in at least two major stages because the bones in the uppermost portions of the rock body are frequently poorly preserved; these bones are often soft, exhibiting varying degrees of "pitting" and dark green and purple colors. The cause of the pitting is unknown, though an organic agent is suspected because some bones exhibit peculiar patterns of pitting. A theropod rib preserved in a subvertical position supports the hypothesis that at least two depositional periods are represented. The rib is enclosed in two superimposed trough crossbeds. It exhibits excellent preservation on its lower por-

tion and poor preservation on its upper portion. The lower part is hard and gray with brown mottling. In contrast, the upper portion is soft, pitted, and purple in color. Apparently the lower part of the rib was entrained in a sandwave during the last stages of a depositional period leaving the uppermost portion either subaqueously and/or subaerially exposed for some period of time, thus allowing its deterioration. During a later depositional period the upper portion was covered. The sedimentology and taphonomy of the quarry has yet to be worked out in detail, and it is hoped that this brief overview will interest others conducting an in-depth sedimentological study of the Dry Mesa Quarry.

AGE

The Morrison Formation was not formally named until 1896 by Eldridge, but numerous informal names were previously applied by various paleontologists and those making territorial surveys. The age of the Morrison Formation has long been a point of debate (Lee 1915, Mook 1915, Osborn 1915), but for many years it has been generally listed as Late Jurassic (Baker and others 1936, Imlay 1952, Peterson 1972, Simpson 1926, Stokes 1944). As recently as 1980, Berman and others wrote, "The Morrison is unquestionably Upper Jurassic, but its exact age is unknown although it is generally considered to be Kimmeridgian" (p. 118). Kowallis and others (1986) used the fission-track method to date a Morrison Formation locality near Capitol Reef National Park, Utah. All but one of the samples have been dated as being 132 or 143 Ma, indicating the Morrison Formation in the park ranges from Late Jurassic to Early Cretaceous in age, using an age of 138 Ma as the Jurassic/Cretaceous boundary (Dietrich and others 1982). Bilbey-Bowman (1986) stated the Morrison Formation ranges from Tithonian (Upper Jurassic) to Neocomian (Lower Cretaceous) age at Dinosaur National Monument, thus supporting to some degree the Kowallis and others (1986) age assignments.

Samples of altered, bentonitic volcanic ash were collected in the Dry Mesa Quarry and dated by Kowallis (personal communication 1986). He selected only the most euhedral crystals in the sample, dated them by the external detector method of fission-track dating, and calculated a normal age probability distribution as described by Hurford (1984). This process results in a more distinct "peak age" than the conventional method of fission-track dating (Kowallis and others 1986). The sample yielded a zircon fission-track age of 127 Ma. This age compares well with the conventionally computed fission-track zircon age of 128 ± 15 Ma. In the conventional method of fission-track dating, a large number of crystals are analyzed without removing the obviously reworked ones. Accord-

ing to Kowallis and others (1986), this may result in erroneously old age assignments, because samples often contain older, reworked crystals. As determined by Kowallis, the apatite peak age for the quarry strata, though poorly defined by a broad peak, is 104 Ma. The apatite age of the Morrison Formation yielded by the conventional fission-track method is 130 ± 30 Ma (Kowallis and others 1986). Therefore, the Dry Mesa Quarry horizon, based on the "Kowallis" method of sampling, is Hauterivian in age (Early Cretaceous).

Jensen noted the Dry Mesa assemblage does not match that of other Morrison Formation quarries (1985a). He attributed at least part of the difference to "substantial evolution at the generic level" (1985b), but no specific evidence is given. However, the analysis of the Dry Mesa theropods indicates that two allosaur morphs are present in the Morrison Formation, a finding that may lend support to Jensen's hypothesis. For example, the short-skulled allosaur typical of the Dry Mesa assemblage is apparently not found associated with the long-skulled form that dominates the Cleveland-Lloyd assemblage, suggesting the latter may have evolved into the former. Currently, however, this hypothesis is almost purely speculative as there are a number of other possibilities. (These allosaur morphs are discussed more fully in the Allosauridae section of this paper.) Thus, while it is probable that significant change did occur within a given lineage during Morrison time, much stratigraphic work must be done before sites can be adequately correlated to substantiate such claims, and more dating of the formation is needed before an accurate estimation of the time involved can be figured into the problem.

PRESERVATION

The vertebrate fossils from the Dry Mesa Quarry consist almost entirely of disarticulated elements displaying a wide scope of stream abrasion, ranging from pristine, unabraded bones to well-rounded bone pebbles. The articulated theropod materials known to date are an *Allosaurus* cranium, four *Torvosaurus* cervical vertebrae, and two partial caudal vertebrae series—one *Torvosaurus* and one *Allosaurus*. Some *Allosaurus* pelvi, an *Allosaurus* pes, and various vertebral elements have also been found in articulation. The quality of the petrified bones varies from excellent to very poor, with the bulk of the bones being fairly well preserved, though generally highly fractured. Some are also compressed to varying degrees. The compression, when it has occurred, apparently resulted from diagenetic compaction, while the fracturing may be attributed to tectonic activity, unloading, and, to a greater degree, slope creep and cyclic contraction/expansion of hydrophilous clays.

METHODS

The fossil bones utilized in this study were collected and prepared utilizing conventional vertebrate paleontological techniques. The matrix was removed with air scribes, small chisels, and with dental tools. Soaking the matrix with water and/or a mixture of water and acetone often facilitated its removal when it contained swelling-type clays, which was frequently the case. The bones were "hardened" with Vinac dissolved in acetone, and pieces were glued together with one or more of the following: carpenter's glue, various epoxy and polyester resins, and Hydrocal.

Measurements of the significant parameters of each bone were taken and entered into a database on a MS-DOS-based personal computer along with notes on preservation, general observations, and comparisons. The database was programmed to calculate indices using selected sets of measurements for each type of element. These indices were used to pick groupings of elements with similar indices. The indices were then compared with published indices, particularly those of Madsen (1976b). Also, indices were calculated based on measurements derived from published illustrations when possible. Final identifications were made by comparing the elements to specimens in the BYUVP collections, particularly those from the Cleveland-Lloyd Quarry, as well as to descriptions and figures in the literature.

COMPARATIVE MATERIALS

To avoid repetitive citations of the fossils used for comparative purposes, the main specimens and references used while engaged in this study are here noted. The bulk of the *Allosaurus* elements used for comparison were collected at the Cleveland-Lloyd Quarry, Emery County, Utah. Most of this collection, which consists of about 6000 separate bones bearing UUVP catalog numbers, is housed at Brigham Young University. Madsen's (1976b) classic monograph on the osteology of *Allosaurus fragilis* was utilized extensively in conjunction with original specimens. Gilmore (1920) was also used, but in his report several specimens of *Allosaurus* from different localities are discussed and figured, some of which may belong to different species. In the present paper the genus *Allosaurus* should be read to mean the specimens referred to *Allosaurus fragilis* from the Cleveland-Lloyd Quarry unless otherwise noted.

Only three reasonably complete North American specimens of *Ceratosaurus* are known. All three were used for comparative purposes in this study. Both original specimens (most with UUVP numbers) and unpublished illustrations of the Cleveland-Lloyd *Ceratosaurus* were used with the kind permission of James H. Madsen, Jr., former

State Paleontologist for Utah, who is currently preparing a paper on the osteology of this genus. Original elements and unpublished illustrations of another specimen (MWC PF-QB) were also used. These illustrations are also part of Madsen's manuscript on the osteology of *Ceratosaurus*. The MWC specimen was collected near Fruita, Colorado, and is part of the Museum of Western Colorado's paleontology collection. Illustrations of the holotype of *Ceratosaurus nasicornis* (USNM 4735), as figured by Marsh (1884) and by Gilmore (1920), have also been extensively utilized along with personal observation of the holotype. Though the three *Ceratosaurus* specimens may represent two different species (Madsen personal communication 1986), they serve well as comparative materials at the generic level.

SYSTEMATIC PALEONTOLOGY

Class Reptilia
Order Saurischia
Suborder Theropoda
Family Megalosauridae

Genus *Torvosaurus* Galton and Jensen 1979

Monotypic genus *Torvosaurus tanneri* Galton and
 Jensen, 1979
1977 "to be described"; Galton 1977, p. 230
1978 "to be described" by Galton and Jensen; Olshevsky,
 p. 21
1980 new large theropod; Dodson and others, p. 212
1983 *Torvosaurus tanneri*; Dodson and others, p. 152
1984 tentatively synonymized with *Megalosaurus*; Paul,
 p. 178
1984 *Torvosaurus tanneri*; Russell, p. 22
1984 *Torvosaurus tanneri*; Dong, p. 217
1985b *Torvosaurus tanneri*; n. family Torvosauridae;
 Jensen, p. 710
1986 *Torvosaurus tanneri*; Torvosauridae; Bonaparte,
 p. 43

The infraordinal classification of the Theropoda is presently unsettled. In the past, theropods were commonly divided into two infraorders, Carnosauria and Coelurosauria (Huene 1926, Romer 1956). However, it became difficult to place all theropod genera into just two infraorders (e.g., *Deinonychus* Ostrom 1969b, p. 145). An expanded classification proposed by Barsbold (1977) lists five infraorders—adding the Deinonychosauria, Ornithomimosauria, and Oviraptosauria. Barsbold's classification is followed by Russell (1984). Gauthier (1986, p. 8) indicated the traditional infraorders, Carnosauria and Coelurosauria, are poorly defined because they have been based on the same synapomorphies. For these reasons neither *Torvosaurus*, nor any of the other theropods

discussed herein, is referred to an infraorder. *Torvosaurus*, however, falls within the taxon Ceratosauria, as defined by Gauthier (1986).

TYPE SPECIMEN

Galton and Jensen (1979) specified the type as BYUVP 2002, the "left and right long bones of forelimb." None of these elements, however, were found in articulation (a point discussed in detail under the *Torvosaurus* forelimb section of this paper). While I have little doubt that all of the long bones are, in fact, from a single species of *Torvosaurus*, it cannot be proven, and it is improbable that all belong to a single individual. It seems prudent, therefore, to restrict the designation of holotype to a single diagnostic element—the left humerus bearing the number BYUVP 2002. This element is chosen because it is the best preserved of the two humeri.

REFERRED SPECIMENS

All elements listed as *Torvosaurus* in the appendix, plus a posterior dorsal vertebra, DMNH 2243; a tooth CM 1254; and an unnumbered tooth figured by Lull (1927, plate 16).

DISTRIBUTION

Known only from the Brushy Basin Member of the Morrison Formation of Colorado, Utah, and Wyoming. The holotype is from the Dry Mesa Quarry, near Delta, Colorado. Galton and Jensen (1979) tentatively referred a large ungual phalanx, BYUVP 2020, to *Torvosaurus*; it was collected at another Uncompahgre Plateau locality, the BYUVP Calico Gulch Quarry, Moffit County, Colorado. A posterior dorsal vertebra, DMNH 2243, collected at the Dinosaur National Monument Quarry is here referred to *Torvosaurus*, as are two large teeth, CM 1254, and a Yale specimen discussed below. CM 1254 is from Gilmore's Quarry N, Freezeout Hills, Carbon County, Wyoming, and is identified as *Torvosaurus* based on its similarity in both size and general morphology to *Torvosaurus* teeth in the BYUVP collection. The tooth is incomplete, lacking both the root and a considerable portion of the distal end of the crown. As preserved, the crown measures 95 mm long and 45 mm wide at the crown base.

Recently John S. McIntosh and Daniel Chure brought to my attention a photograph of a large theropod tooth from Marsh's Quarry 9, Como Bluff, Wyoming. This tooth is figured by Lull (1927, plate 16). Assuming the scale given for the tooth is accurate, the tooth, lacking most of its root, is about 130 mm long, with the crown consituting over 100 mm of its length. The morphology of the tooth is similar to teeth referred to *Torvosaurus*. In addition, its great size may indicate it belongs to *Torvosaurus*, but *Ceratosaurus* also has large teeth. The original specimen, which Lull (1927, text of plate 16) states is housed in the "Yale Museum," may be one of the large theropod teeth referred to by Arthur Lakes in a letter to Marsh dated July 5, 1879, as "carniv good sized teeth [*sic*]" (Ostrom and McIntosh 1966, p. 26). It seems reasonable that *Torvosaurus* may range throughout the Brushy Basin Member of the Morrison, but is a very rare member of the fauna. Theropod elements collected at these and other localities are housed in various institutions, but in many cases they have never been studied in detail or even completely prepared. I suspect that future investigations will demonstrate that *Torvosaurus* is more common than present occurrences indicate.

DIAGNOSIS

Large (~9 m, adult length), robust, megalosaurid; moderately long skull with height ~40% of length; particularly narrow rostrum; 3 (or possibly 4) teeth in premaxilla; minimum of 11 but probably 13 teeth in maxilla; minimum of 10 but probably 13 teeth in dentary. Maxilla dorsoventrally high with large, fused interdental plates making up one-half the medial surface of the maxillary body, no preantorbital fenestra.

Cervical vertebrae strongly opisthocoeleous, with ball-like anterior surfaces surrounded by a posteriorly sloping rim, which occupies about 50% of the anterior surface; posterior face deeply concave; long epipophyses; highly excavated, dual chambered centra and strongly V-shaped venter. All but the posteriormost dorsal vertebrae are also opisthocoeleous with articular ends having the same form as those found on cervical vertebrae; well-developed pleurocoels on anterior portion of series that grade into simple, large lateral excavations on posterior members of dorsal vertebrae series; fenestrae passing from side to side through neural arch anterior to hyposphene; neural spines thin with poorly developed anterior and posterior supportive laminae. Posterior dorsal vertebrae with vertically elongate parapophyses.

Caudal vertebrae mildly amphicoeleous, anterior caudals with small, shallow, elongate fossae; posterior chevron facets much larger than anterior; shallowly grooved venters; transverse processes long and backswept at about 35° to axial plane; neural spines narrow with anterior and posterior margins converging dorsally terminating in rounded, unexpanded apices. Transverse processes and spine intersections are a straight line uninterrupted by pre- or postzygapophyses. Chevrons slender with somewhat rectangular cross section, anterior and posterior surfaces concave except for laterally compressed dis-

tal end that terminates in posteriorly pointing "foot," anterior articular surfaces with a pair of digitlike projections.

Ilia long and low, height to length index = 29, narrow preacetabular notch. Pubes terminate distally in small, slightly expanded "foot," completely enclosed obturator foramen. Ischia terminate distally in small, anteroposteriorly rounded expansion. Pubes and ischia subequal in length and joined mesially by well-developed ventromedian symphysis.

Forelimb short with humerus/radius index = 220. Humerus straight shafted, large deltapectoral crest, circumference to length index = 48.

Femur unknown. Tibial circumference to length index = 47. Fibular circumference to length index = 20. Metatarsals robust with no collateral pits.

GENERAL DESCRIPTION AND COMPARISONS

CRANIAL SKELETON

Skull

When Galton and Jensen (1979) originally described *Torvosaurus*, no skull elements were known. Subsequently, skull elements have been discovered and prepared as part of this study. Enough important elements have been discovered to allow a very general reconstruction of the *Torvosaurus* skull to be made (fig. 2). None of the elements were found in articulation, but there is little doubt they belong to *Torvosaurus* because all the skull elements, with the exception of the lacrimal, seem to be from one or two individuals of the same size, and most are unusually robust. The "fit" of the premaxilla and maxilla
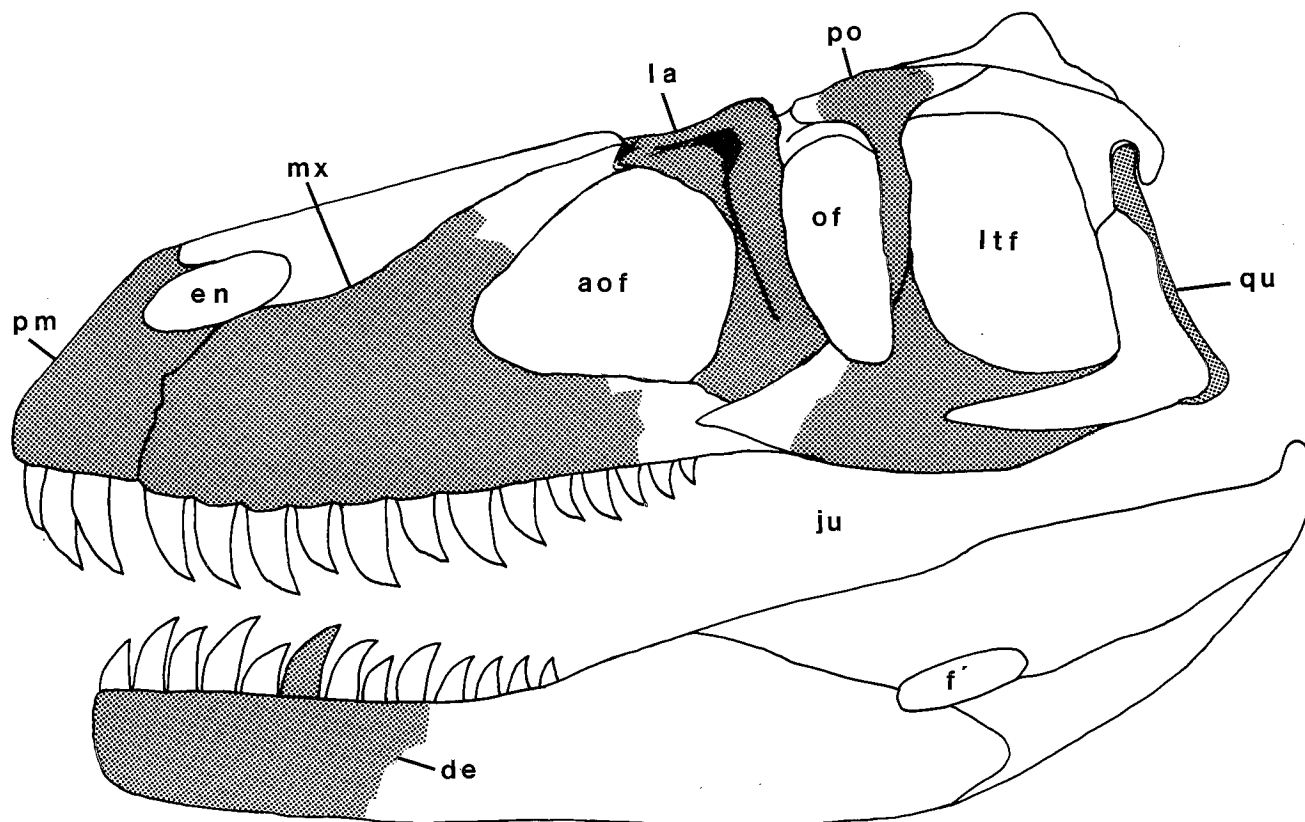
FIGURE 2.—*Tentative reconstruction of the skull and mandible of* Torvosaurus tanneri. *Lateral view. Estimated skull length is 1180 mm. Most unknown elements and contacts are based on the skull of* Ceratosaurus nasicornis *as figured by Gilmore (1920, plate 18). Abbreviations: aof = anteorbital fenestra, de = dentary, en = external nares, f = external mandibular foramen, ju = jugal, la = lacrimal, ltf = lateral temporal fenestra, mx = maxilla, of = orbital fenestra, pm = premaxilla, po = postorbital, qu = quadrate. Known elements are shaded.*
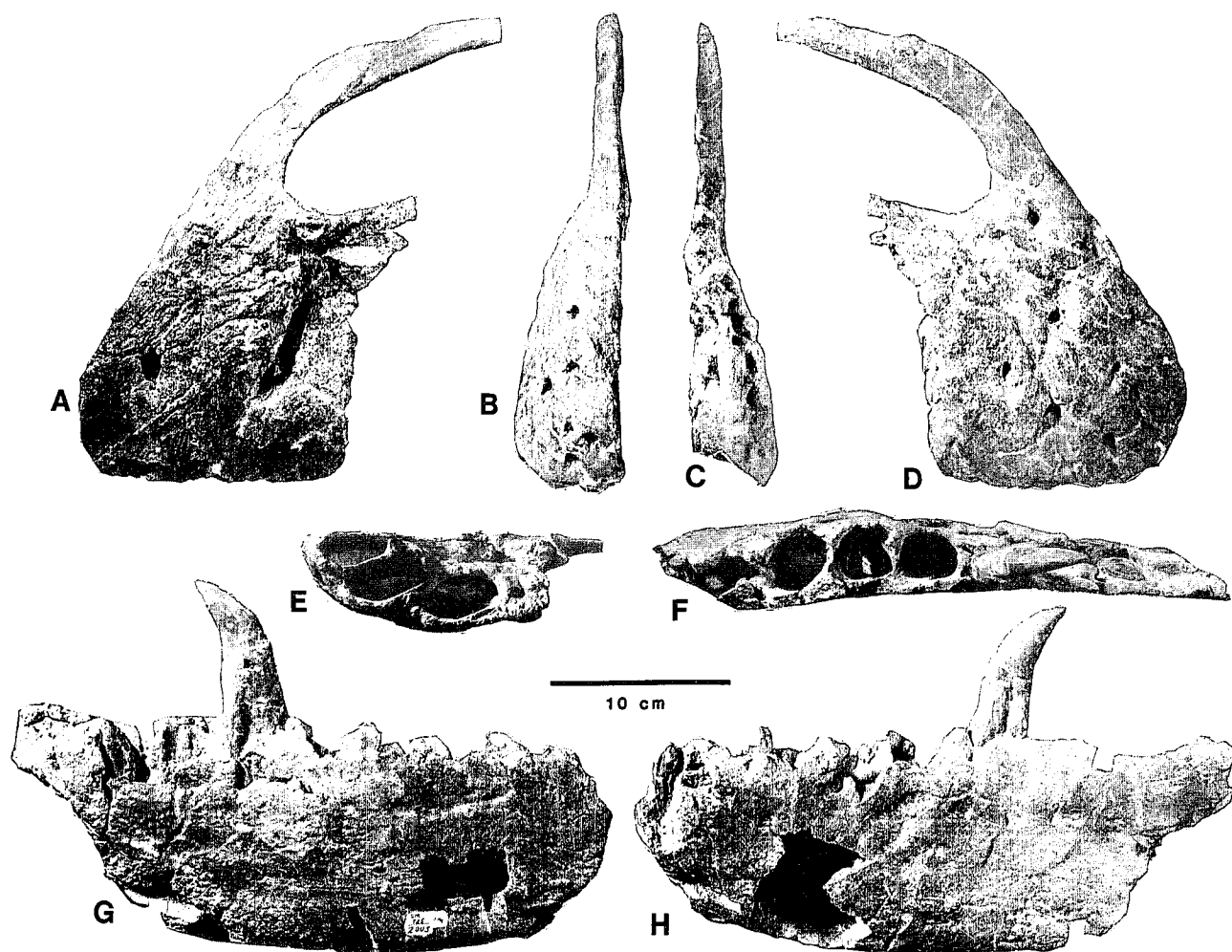
FIGURE 3.—Torvosaurus tanneri *skull and mandibular elements. Right premaxillary, BYUVP 4882 (A–E). Left dentary, BYUVP 2003 (F–H). Lateral (D,H), medial (A,G), anterior (B), posterior (C), ventral (E), and dorsal (F) views.*

indicates they are probably from the same individual, and, finally, the jugals were found as a closely appressed pair, indicating they are of a single individual.

The known skull and mandibular elements are: a right premaxilla, BYUVP 4882 (fig. 3, A–C); a left maxilla, BYUVP 9122 (fig. 4, B and C); most of the tooth-bearing portion of a left dentary, BYUVP 2003 (fig. 3, E–G); a left lacrimal, BYUVP 5286 (fig. 4, A and D), a pair of jugals, BYUVP 4883 (fig. 6, I and J); a right postorbital, BYUVP 9249 (fig. 6, E–H); and most of a right quadrate, BYUVP 5110 (fig. 6, A–D). In addition, several teeth (fig. 5, A–D) assignable to this genus were found in the quarry associated with these elements. Unfortunately, actual quarry associations are not known because the few quarry maps made early on are incomplete. Also, except for the last several years, comparatively few notes were kept concerning the quarry operations, thus exacerbating the problem.

The known skull elements allow a reasonable estimate of the skull's length and height to be made at several critical points. The reconstructed skull is moderately low and massive with the height being equal to about 40% of the length. As is the case with the postcranial elements, the skull elements are more robust than those of any other known Morrison Formation theropod. The robust nature alone is usually sufficient to differentiate *Torvosaurus* elements, except vertebrae (which are readily differentiated on nonsize characters), from other Morrison genera. The adult skull is estimated to have been 1180 mm in length and 450 mm high.

The premaxilla bore 3 teeth. The maxillary tooth count appears to have been about 13. The dentary tooth count is less certain, but is estimated to have been approximately 13. A detailed discussion of the tooth count is included under the descriptions of the respective tooth-bearing elements.

Premaxilla. Since the original description of *Torvosaurus* by Galton and Jensen (1979), a left premaxilla assignable to the genus has been discovered. The premaxilla, BYUVP 4882 (fig. 3, A–E), is well preserved and uncrushed. Only the tip of the nasal and most of the maxillary processes are missing. No erupted teeth are present. The body of the *Torvosaurus* premaxilla is roughly trapezoidal in outline, with the labial margin and the lower margin of the external naris subparallel. The anterior margin slopes rearward, resulting in a low-angled snout. The posterior margin slopes slightly posteriorly. The width of the bone from the medial symphysis to its lateral margin is only about 70 mm, indicating the premaxillary portion of the skull was only about 140 mm wide.

The premaxillary body of *Ceratosaurus* is rectangular in outline, the rectangle distinctly higher than long. In contrast, the premaxillary body of *Allosaurus* is more square in outline, but is slightly longer than high. The length to height index of the premaxillary body in *Torvosaurus* is 97, *Ceratosaurus* 80, as derived from UUVP 674 and MWC PF-QB:24J, and *Allosaurus* 115, based on five UUVP specimens.

In *Torvosaurus* the angle formed between the ventral and anterior margins (or "premaxillary angle") is approximately 55°. Measurements of the same angles on *Ceratosaurus* premaxillae UUVP 674 and MWC PF-QB:24J average about 80°. The average angle for the same aspect of *Allosaurus* is about 72°, based on measurements of five UUVP specimens. While allometric growth may affect this angle, it does not appear to do so in *Allosaurus* elements. Therefore, it is apparently possible to differentiate *Torvosaurus* from *Ceratosaurus* and *Allosaurus* based on the premaxillary angle and/or the length-to-height index.

The medial symphysis of the premaxilla in *Torvosaurus* is broad, covering half the bone's medial surface (fig. 3, A). This symphysis extends halfway up the nasal process to the point where the nasal processes diverge. Thin projections of the nasal bones separated the tips of the maxillary nasal processes in life. The medial symphysis is equally large in *Ceratosaurus*, but in *Allosaurus* it covers only one-third of the medial surface. The elongate maxillary articulation has a slight channel along its length that is filled with ridges and deep pits. This indicates a fairly strong union with the maxilla but not a co-ossified one. Just below the ventral margin of the external naris and anterior to the base of the maxillary process is a small, 11-mm-long by 5-mm-tall foramen (fig. 3, A). Another similarly sized foramen exists immediately behind it in the anterior portion of the maxillary process, but only the anterior half of it is preserved.

Torvosaurus has three teeth in the premaxilla. This tooth count is shared by only one other Late Jurassic theropod, *Ceratosaurus*. (For lists of the number of pre-maxillary teeth in theropods see Chatterjee 1978, p. 578; Madsen 1976a, p. 59.) Although no erupted teeth are present in the specimen at hand, several characters of the teeth can be derived from the shapes and orientations of the alveoli. The teeth were quite large; the alveolus of tooth position 3, once cleared of matrix, indicates the root was about 100 mm long. Crowns of theropod teeth are slightly shorter than their roots, so a 90-mm-long crown is a reasonable estimate. This estimate is well within the size range of some large isolated teeth, with crowns over 100 mm long, found within the section of the quarry where most of the *Torvosaurus* elements were found.

The labial surface of a well-developed, but unerupted, tooth is visible in the second alveolus; it has 11 denticles per cm. A "window" was cut into the medial surface of the bone to reveal the basal lingual surface of the tooth. Though fractured, it is clear that the surface is smooth with no vertical ridges. This characteristic clearly separates *Torvosaurus* and *Ceratosaurus* because the lingual surface of *Ceratosaurus* premaxillary teeth have distinct vertical ridges (Madsen 1976b, p. 17).

In ventral view (fig. 3, E), all alveoli are elliptical, with the leading edge of each ellipse pointing anteriorly and, to a lesser degree, labially. There is no doubt this is the original shape of the alveoli because the bone is not deformed. Anterior premaxillary teeth of some theropods, such as *Allosaurus*, and especially *Albertosaurus* and *Tyrannosaurus*, are more or less D-shaped in cross section, with the curve of the D facing labially; the shape is a result of the anterior carina (serrated ridge) having been rotated lingually. However, this is not the case with *Torvosaurus*. Its premaxillary teeth were likely scimitar-like in lateral view, with an ovoid cross section, and thus do not differ from the nonpremaxillary teeth. The anterior carina points labially, and the posterior carina points lingually. In *Torvosaurus* the first alveolus is very narrow and elongate. The same alveolus in *Ceratosaurus* is also elongate, but not nearly to the same degree. In *Allosaurus* the first, as well as all other premaxillary alveoli, are round in ventral view. Viewed medially, the labial parapet of the alveoli is lower than the ventral portions of the interdental plates (lingual parapet). The interdental plates are large, except for the posteriormost one, but they are difficult to differentiate because they are highly fused to each other and surrounding bone.

The labial side of each premaxillary alveolus is overlapped by the alveolus behind it (fig. 3, E). The alveolus of PM2 overlaps about 75% of PM1 while PM3 overlaps PM2 by only 25%. The same style of overlap occurs in *Ceratosaurus*, but to a lesser degree. *Allosaurus* is quite different in this aspect, for there is seldom any overlap, but if it does occur, the anterior tooth overlaps the lingual side of its adjacent posterior tooth.

Ventrally, a 25-mm-long shelf of bone occurs between

the last alveolus and the posterior edge of the premaxilla (fig. 3, E). This shelf has a central depression, and a small interdental plate occurs just posterior to this depression. This small diastema may represent either a vestigial alveolus or one that is in a formative stage. A similar condition is exhibited by the posteriormost alveolus of a *Tyrannosaurus* dentary described by Osborn (1905).

Numerous well-developed foramina perforate the lateral surface of the premaxilla (fig. 3, D). The openings of most foramina open downward and have channels leading away from them. Such foramina are commonly found on premaxillae and anterior regions of the dentary of theropods, other saurischians, as well as other extinct and extant reptiles. Also, comparable foramina occur in rows along the labial margin of the maxilla and dentary of *Torvosaurus* and other dinosaurs. Foramina rows have been described by several authors (e.g., Camp 1930, p. 135; Ostrom 1969b, p. 17 and 30; Welles 1984, p. 144). Ostrom (1969b) postulated that blood vessels and nerves exited through the foramina. Bakker (1986) ascribed the same function to them and suggested the vessels and nerves serviced lips. Russell (1967) described and illustrated obviously equivalent rows of foramina on mosasaurs. He stated that the terminal portions of the premaxillary, maxillary, and mandibular branches of the trigeminus nerve exit via these openings. No mention of their specific function is given. It seems most plausible that the nerves exiting the foramina served a tactile function.

In addition to the rows of foramina, many other equivalent foramina are located on the anteriormost portions of the snouts of theropods, that is, the premaxillae and terminal portion of the dentaries (e.g., Madsen 1976b, plate 1; Osborn 1912, fig. 3). The occurrence and orientation of the terminal rostral foramina on theropod and avian muzzles is strikingly similar, and in the latter they are located beneath the keratinous covering of the beak. Perhaps specialized scales sheathed these areas of the theropods and sauropods. These scales may have housed Pacinian corpuscles (encapsulated sense organs surrounded by onionlike layers of connective tissue that sense pressure).

Camp (1930) reported homologous foraminae in phytosaurs and concluded that they housed tactile organs similar to those of the modern alligator, a conclusion that I came to independently. In birds these foramina lead to Herbst corpuscles (thought to be unique to birds) located in the skin of the bill. These corpuscles are especially abundant in the soft-beaked birds such as ducks and

waders (Yapp 1970). Such birds use their bills to probe mud in search of food. The exact function of Herbst corpuscles is not known, but they are thought to serve as pressure and motion detectors. Perhaps similar, if not the same, types of tactile corpuscles were imbedded in protective/sensory scales or horny sheaths on theropods and other dinosaurs. During feeding such corpuscles could have provided important sensory feedback on prey movement and the position of bone versus soft tissue. A comparative study of the location and arrangement of these foramina may lead to a better understanding of the feeding behavior of dinosaurs, but will not be conducted herein.

In summary, the external foraminae of the premaxilla, maxilla, and dentary of theropods housed sensory receptors that are homologous to those of extant Aves and Reptilia, and I suggest that Herbst corpuscles were present at the exits of the rostral foraminae described above. This hypothesis can be tested by comparing the histology of the external rostral sensory units of extant archosaurians (crocodilians) with the Herbst corpuscles of birds.

Maxilla. The body of the left maxilla, BYUVP 9122 (fig. 4, B and C), is fairly complete, but laterally compressed. It lacks the upper one-half of the nasal process, the most posterior part of the body, the tip of the vomer process, and the upper anterolateral margin. No erupted teeth are present, but there are unerupted replacement teeth in most alveoli. The body of the maxilla is triangular in outline, with the dorsal and ventral margins each more than twice as long as the short, anterior margin. In lateral view, most of the maxilla's undulating ventral edge is slightly convex with a slight upturn on the anterior one-third. The premaxillary contact reclines gently posteriorly. A ridge along this contact fits into a matching groove on the premaxilla.

Ten maxillary alveoli are preserved. There is evidence of an eleventh, but the alveolus is incomplete. Judging from the intersection of lines drawn along upper margins of interdental plates and lateroventral edges of the alveoli, the maximum possible number of maxillary teeth is 12 or 13. The tooth count for the maxilla of *Allosaurus* is 14–16 (Madsen 1976b), while the tooth count for the same element of *Ceratosaurus* is 11 to 15 (Gilmore 1920, Madsen personal communication 1986).

Alveoli numbers 2 through 6 are large and subequal in size. Their average anteroposterior length is 50 mm. Alveoli 1 and 7 through 10 contain smaller teeth. These

FIGURE 4.—*Torvosaurus* tanneri *skull elements. Left maxilla,* BYUVP 9122 *(B,C) and left lachrimal of new unnamed genus,* BYUVP 5286 *(A,D). Lateral (C,D) and medial (A,B) views.*
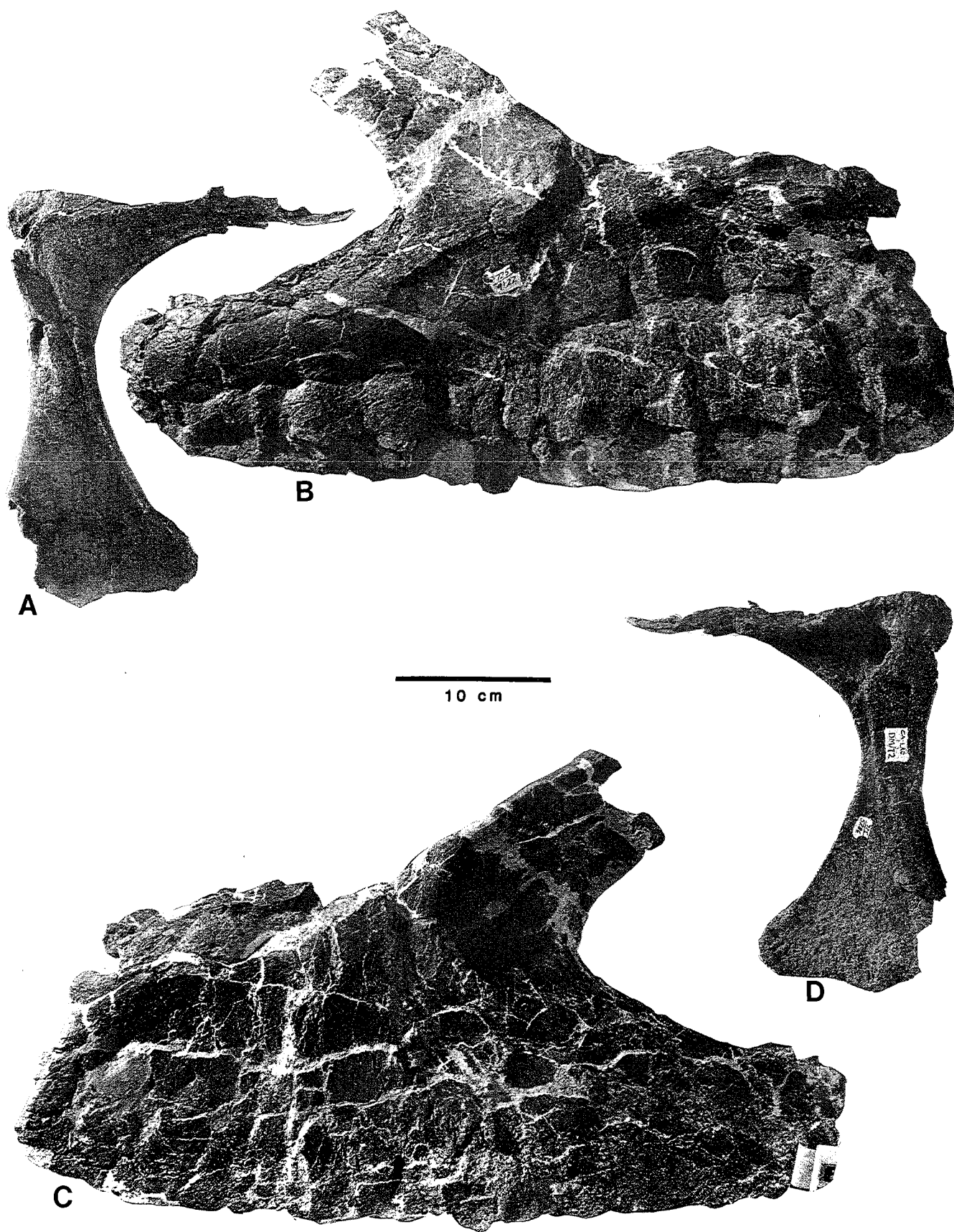
FIGURE 5.—Torvosaurus tanneri *tooth, BYUVP 9246 (A–D), an indeterminate theropod tooth, BYUVP 9597 (E–F), and a dromaeosaurid-type tooth, BYUVP 9603 (G–I). Lateral (D,F,I), medial (A,E,G), anterior (B,H), and posterior (C) views.*
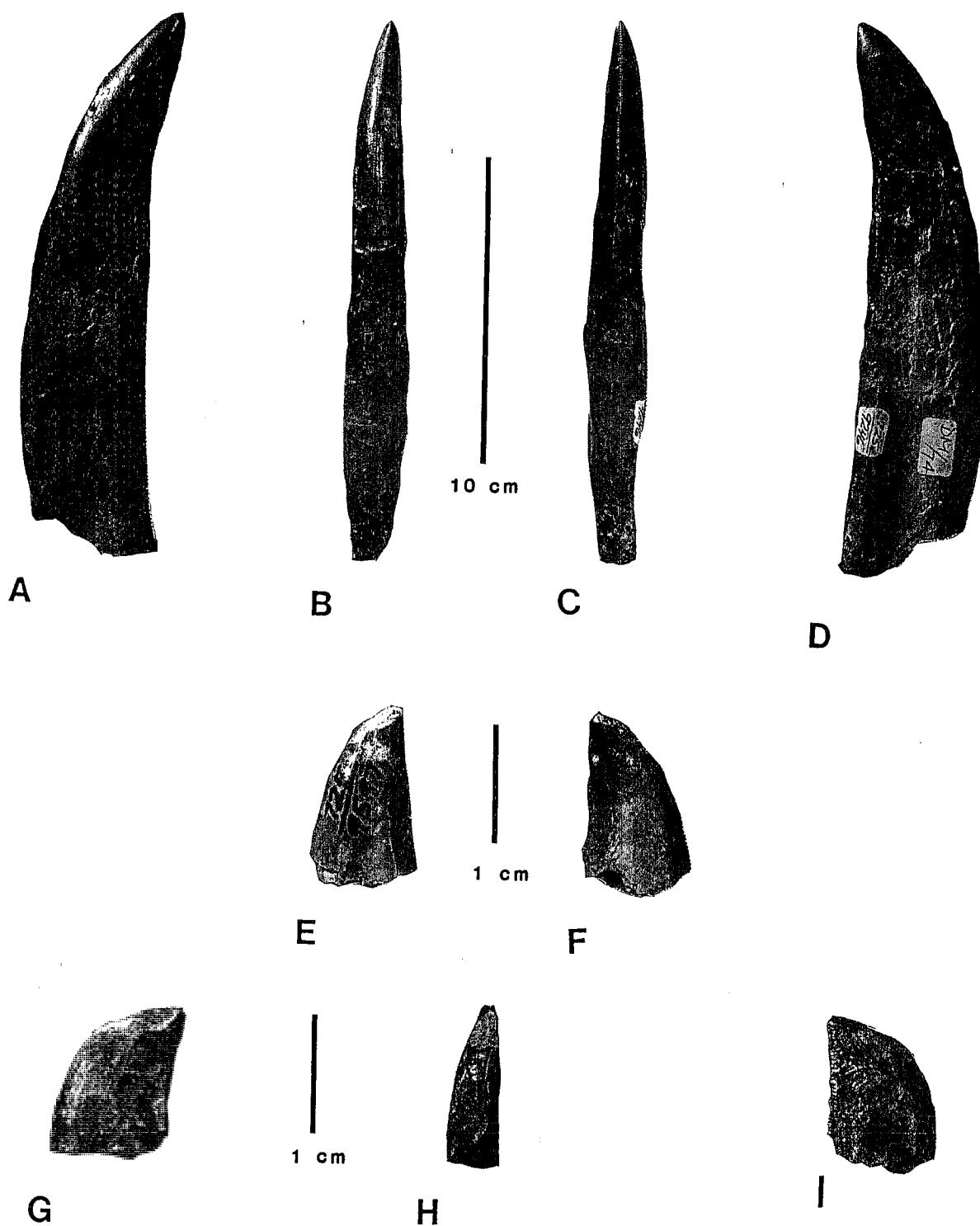
alveoli average 47 mm in anteroposterior length. *Allosaurus* maxillary alveoli have roughly the same design, but the tooth count is greater. Most of the alveoli in BYUVP 9122 are slightly crushed, so an accurate determination of tooth alignment is not possible.

In *Torvosaurus* the undulating lower margin of the interdental plates ends well above the labial parapet of the maxilla (fig. 4, B). If this character is not due to crushing, the high termination readily distinguishes *Torvosaurus* from both *Ceratosaurus* and *Allosaurus,* in which the lingual and labial margins of the alveoli are nearly coincidental.

The nasal process originates in the middle of the maxillary body and rises posteriorly at an angle of 35° from vertical. The same process in *Allosaurus* arises from a similar position but has a well-developed second antorbital fenestra near its base. *Ceratosaurus* has no second antorbital fenestra, only a small foramen, and the nasal process arises from the anterior edge of the maxilla. In *Torvosaurus* four alveoli on the ventral margin occur in front of the broad, flattened, leading edge of the nasal process. There is a deep depression in the base of the nasal process that slightly invades the body of the maxilla forming the anterior margin of the antorbital fossa. The floor of this depression is divided along its length by a ridge 15 mm high. There is no foramen in this depression. This is in contrast to *Ceratosaurus,* which has a small foramen at the deepest portion of the excavation near the base of the nasal process. This may represent a "proto" second antorbital fenestra, though neither *Torvosaurus* or *Ceratosaurus* have preantorbital fenestrae. The lack of this fenestra is probably a plesiomorphic condition not commonly retained in medium to large theropods.

Indosuchus (Chatterjee 1978) and *Carnotaurus* (Bonaparte 1985) are apparently the only large-sized theropods other than *Torvosaurus* and *Ceratosaurus* that retain this primitve condition. The anterolateral edge of the nasal process begins to curve posteriorly, immediately before it reaches the body of the bone, forming the ventral ridge of the antorbital fossa. This ridge becomes less prominent posteriorly and is a particularly diagnostic feature. The same ridge in *Ceratosaurus* and *Allosaurus* does not begin to curve posteriorly until after contacting the maxilla body. In *Ceratosaurus* the lower portion of the ridge bisects the area between the dorsal and ventral margins of the maxilla, but in *Allosaurus* it lies just above the ventral margin in all of the BYUVP and UUVP specimens housed in the BYUVP collections.

The anteromedial process of the maxilla arises just below the anterior dorsal edge. Both the dorsolateral and dorsomedial edges of this process are deeply grooved and interlock with the corresponding ridges on the maxillary process of the premaxilla.

In medial view (fig. 4, B), the most striking aspect of the maxilla is the enormous size of the tongue-shaped interdental plates that constitute nearly half of the medial surface of the maxilla and terminate ventrally in broad, V-shaped points. The plates are fused to each other, except at their constricted bases. Between the bases of all interdental plates is a small window, the suprainterdental plate foramen, through which the unerupted teeth are clearly visible. These foramina allowed blood vessels to enter the alveoli and, ultimately, the teeth themselves (Osborn 1912). *Ceratosaurus* has similar fenestra between interdental plates, but they are located between alveoli or at the posterior end of an alveolus. This is because in *Ceratosaurus* some of the plates are located, to a greater degree, over individual teeth, not between them. *Allosaurus* has very small suprainterdental foramina, located at the midline of the alveoli. But in mature individuals they are usually covered by the medial overhang of the maxilla.

Lacrimal. BYUVP 5286 (fig. 4, A and D) is a nearly complete left lacrimal, lacking only the posterior part of the jugular contact. This element has been referred to *Torvosaurus* by Jensen (1985b). The jugular ramus of the lacrimal is essentially perpendicular to the nasal ramus. Other described genera of Late Jurassic age, except *Ornitholestes* and *Proceratosaurus,* have rami separated by more acute angles. The jugular ramus is wide and flares distally into an unusually broad ventral flange that articulated with the jugal and maxilla. The flange is about 115 mm wide in the anteroposterior dimension, including the missing posterior edge. The nasal ramus of the lacrimal tapers rapidly anteriorly from the apical rugosity to a small irregularly shaped process. The anterior half of this ramus bears several short, anteriorly directed, fingerlike projections that interdigitated with the nasal and maxilla. The dorsoposterior part of the bone bears a small, blunt, rugose boss similar to, but smaller than, those of most theropods. The boss is 65 mm long, 30 mm high on the lateral surface, and 15 mm tall on the medial surface. Similar lacrimal protrusions are interpreted to have supported a supraocular hornlike scale or scales that functioned as a brow or sunshade, as well as for protection in other theropods (Gilmore 1920, p. 17; Madsen 1976b, p. 21; and Osborn 1903, p. 701).

The lateral lacrimal vacuity opens anteriorly and is simple with no septum. Three foramina, similar to those described as occurring on *Allosaurus* by Madsen (1976b, p. 20), are present. The lateral foramen is located 55 mm below the top edge of the lacrimal near the posterior edge of the jugular ramus. An anteriorly located groove curves down into the foramen. A much larger foramen, the posterior lacrimal foramen (approximately 6 mm in diameter), is located one-third of the way down the orbital side of the

10 cm

A

B

C

D

E

F

G

H

10 cm

I

J

10 cm
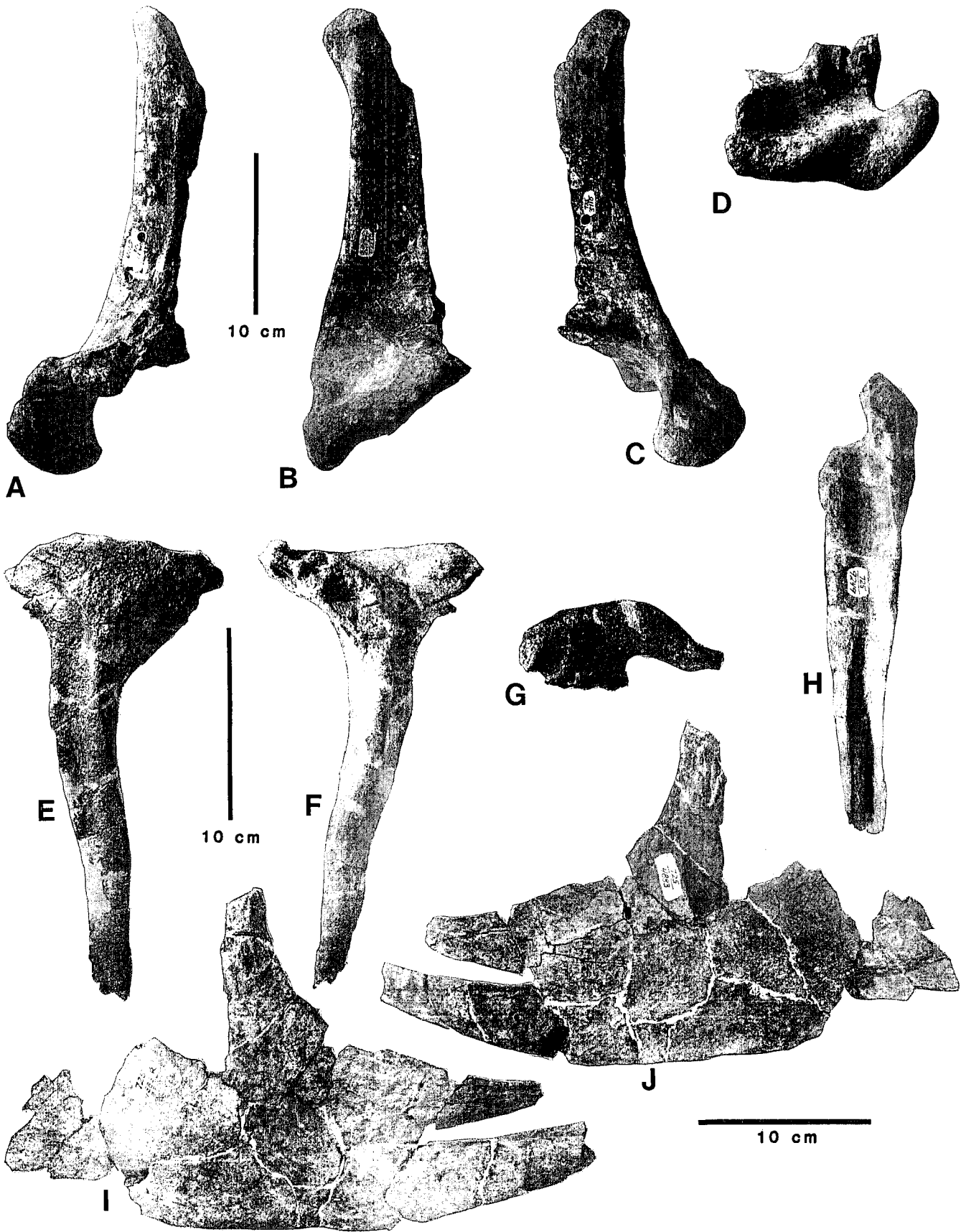
jugular ramus. It opens into a distinct groove that rapidly widens ventrally and soon disappears. The equivalent foramen on *Allosaurus* opens into a groove that descends the length of the jugular ramus (Madsen 1976b, p. 20). The smallest foramen, the anterior lacrimal foramen (6 mm tall and 3 mm wide), is located one-third of the way down the antorbital fenestra border of the jugular ramus. The medial surface of the jugular ramus is simple and smooth except for a pair of ridges. These ridges are separated by a groove between them representing the articulation zone of the postfrontal. The jugular ramus of most theropod lacrimals consists, figuratively, of two blades, one on top of the other. On this specimen the medial blade is anteroposteriorly broader, but on *Allosaurus* the lateral blade is consistently the largest of the two. *Ceratosaurus* also has a dominant lateral blade and, like *Allosaurus*, the anterior edge of the lateral blade overhangs the antorbital fenestra.

The geometry of this lacrimal is roughly similar to, but much larger than, that of *Ornitholestes* (Osborn 1903). This points to the possibility, though very remote, that the lacrimal assigned in this paper to the unnamed theropod may belong to *Ornitholestes*. If this is true it would mean that the described specimens of *Ornitholestes* may be a juvenile, but this cannot be resolved at the present because of a lack of specimens and adequately figured elements.

Postorbital. A nearly complete right postorbital, BYUVP 9249 (fig. 6, E–H), is here referred to *Torvosaurus*. Only the anterior and posterior processes of the dorsal region are missing. The bone is triradiate with a long jugular process. The anterolateral surface of the postorbital body bears a triangular rugose area. The dorsal ridge, or uppermost surface of the bone, is smoothly rounded. The upper two-thirds of the jugular process is L-shaped in cross section—the base of the L being the lateral surface of the bone, which points posteriorly. The lower one-third of the same process is a U shape, with the open part of the U facing posteriorly (fig. 6, H). It wrapped partially around the postorbital contact. The U-shaped groove extends two-thirds of the way up the jugular process, indicating where the postorbital process of the jugal contacted the postorbital.

The postorbital of *Torvosaurus* differs from that of *Allosaurus* in that the latter has a rugose area that extends most of the way down the jugular process. The jugular process is noticeably shorter, being subequal in length to

the anterior and posterior processes, and the postorbital process of the jugal ascends less than one-half the way up the jugular process of the postorbital. Postorbitals of both forms have deep concavities to receive the lateral arm of the laterosphenoid. In addition, *Allosaurus* has a broad web, or flange, spanning the area between the squamosal and jugular processes, which is poorly developed on *Torvosaurus*.

The postorbital of *Ceratosaurus* is closer in appearance to that of *Torvosaurus* than *Allosaurus* because both *Torvosaurus* and *Ceratosaurus* have long jugular processes. In lateral view, the flange that forms the anterodorsal corner of the lateral temporal fenestra is broader in *Ceratosaurus* than *Torvosaurus*, but not nearly as broad as *Allosaurus*. In posterior view, the jugular process of the *Ceratosaurus* postorbital is narrower than the same process of *Torvosaurus*.

Jugal. A right (fig. 6, I and J) and left jugal, BYUVP 4883, were found together, aligned, one on top of the other, in the quarry with their medial surfaces in contact. No other skull elements were found in the block of matrix from which they were removed. Since no adequate quarry maps were made, it cannot be determined whether other *Torvosaurus* skull materials were in direct association with these jugals. The right jugal is more complete, but is missing the tip of the postorbital ramus, the ends of both the upper and lower branches of the posterior jugal, and the ventral and anterior portions of the anterior blade. The left jugal lacks the upper one-fourth of the ascending process, nearly all of its ventral edge, all of the uppermost posterior branch, the tip of the lower branch, and the leading edge of the anterior blade. The thick, sheetlike bodies of these jugals are much deeper, when viewed from the side, than jugals of either *Allosaurus* or *Ceratosaurus*. The concave medial surface of the *Torvosaurus* jugals (fig. 6, I) is interrupted by two, low, broad ridges that start at the midpoint of the body and radiate anteriorly and dorsally. One ridge is roughly horizontal and extends forward, reinforcing the anterior blade. The other extends perpendicular to it, reinforcing the front edge of the postorbital ramus. A depression is developed behind the horizontal ridge that deepens posteriorly, producing a bifurcation of the posterior third of the jugal. This notch forms a complex scarf joint for the jugular process of the quadratojugal.

The postorbital ramus of the jugal is relatively short and stocky (fig. 6, I and J). The leading edge of this process is

FIGURE 6.—Torvosaurus tanneri *skull elements. Left quadrate, BYUVP 5110, (A–D). Right postorbital, BYUVP 9249 (E–H). Right jugal, BYUVP 4883 (I,J). Lateral (A, E, J), medial (C, F, I), posterior (B, H), dorsal (G), and ventral (D) views.*

thick and rounded, but the trailing edge tapers gradually to a much thinner margin. The anterior edge of the postorbital ramus rises abruptly and nearly perpendicular to the jugal body. Immediately anterior to the base of the postorbital ramus another curved edge rises anteriorly at a lower, but still steep, angle. This results in a narrow ventral margin for the orbital fenestra. In this respect, the jugals are similar to those of *Allosaurus*. In contrast, the base of the orbital fenestra in *Ceratosaurus* is much broader.

The posterior margin of the postorbital ramus on the *Torvosaurus* jugal forms a broad curve from a point high on the process to the tip of the upper branch of the bifurcated quadratojugal contact. Both *Allosaurus* and *Ceratosaurus* have very steep posterior margins on their postorbital ramus, which result in a much tighter arc of connection with the upper branch.

Much of the anterior blade, which forms a nonsutural contact for the maxilla and lacrimal, is incomplete on both specimens. This is not surprising, for it is the thinnest and least durable part of the jugal. Remnants of a curved horizontal ridge occur on the lower one-third of the blade's lateral side. This ridge separated the two posterior processes of the maxilla, as in *Allosaurus* (Madsen 1976b, plate 1).

The bifurcated quadratojugal contact is formed of nonoverlapping upper and lower branches. The shorter upper branch is thin, bladelike, and slopes laterally. The lower branch is like a flattened rod, much thicker than the upper branch. It tapers posteriorly and curves gently upward. The upper surface of this branch has a shallow, smooth groove on which the ventral edge of the quadratojugal rested. Although the same general structures are present in *Allosaurus*, they are quite different. The upper branch in *Allosaurus* is thin and bladelike, but it is roughly vertical, and a plane passing through it would bisect the very deep groove present on the upper surface of the branch below. Also, in medial view, the lower branch overlaps most of the lower margin of the upper branch in contrast to the clear separation in *Torvosaurus*.

The ventral margin of the jugal is fairly straight to the point below the base of the bifurcation where the ventral margin begins to curve gently upward. The same margin of *Ceratosaurus* is quite similar, but the ventral edge on *Allosaurus* jugals has a distinct lobe protruding below the rest of the ventral margin. This lobe is located below the ascending process.

Quadrate. The right quadrate, BYUVP 5110 (fig. 6, A–D), is well preserved, but most of the pterygoid blade is missing. It is massive, as are nearly all *Torvosaurus* elements. The quadrate shaft is fairly straight but has a slightly concave posterior margin (fig. 6, A and C). The head of the shaft is slightly expanded and rounded. The lower portion of the shaft expands and flairs posteriorly,

forming two convex articular surfaces that are separated by a shallow, oblique groove. The medial condyle is the most massive of the two and protrudes ventrally a greater distance than the lesser-developed lateral condyle. In ventral view (fig. 6, D), long axes of the condyles strike anteromedially, with the medial condyle protruding forward well beyond the lateral condyle. Such a marked anterior protrusion of the medial condyle does not occur in *Allosaurus* or *Ceratosaurus*.

A triangular fossa leading to a foramen 5 mm in diameter occurs on the lower medial portion of the quadrate shaft, just above the medial condyle (fig. 6, C). Neither *Allosaurus* nor *Ceratosaurus* have a foramen in this area of the quadrate. Little of the pterygoid blade is present; apparently it was lost during collecting, because a good contact is present.

The ventral contact for the quadratojugal is teardrop-shaped (fig. 6, A) with an irregular, undulatory surface, indicating a fairly strong quadrate/quadratojugal union existed. The narrow tip of the suture curves gently upward to blend into the straight quadratojugal flange of the quadrate. The same suture in *Allosaurus*, though similar in shape, has a distinct set of ridges that radiate from a common point. Having observed this suture on all available Cleveland-Lloyd *Allosaurus* elements, which span a wide ontogenetic range (Madsen 1976b, p. 2), these differences do not seem to be a product of age or individual variation.

Both *Torvosaurus* and *Ceratosaurus* lack a quadrate foramen located entirely or nearly entirely within the quadrate itself—as in many other reptiles the quadrate foramen was likely located between the quadrate and quadratojugal. In *Allosaurus*, however, there is a large, distinct foramen enclosed almost entirely by the quadrate (and to a small degree by the quadratojugal) immediately above the large, ventral quadratojugal contact (Madsen 1976b, plate 3, fig. E and F).

Mandible

Dentary. Most of the tooth-bearing portion of a left dentary, BYUVP 2003 (fig. 3, F–H), is preserved. Only the first nine alveoli and the anterior portion of the tenth alveolus are present on the dentary; therefore, the exact tooth count is unknown. It can be estimated, however, that there were approximately 13 teeth, in keeping with the estimated number of maxillary teeth, because in theropods the number of dentary teeth usually approximates the number of maxillary teeth. One complete, erupted tooth and several unerupted teeth are preserved in this element. A distinct medial symphysis is not apparent, indicating the joint was "weak." Walker (1964, p. 115) noted this is a common feature of theropods and suggested the weak symphysis allowed considerable kinesis.

The upper margin of the dentary appears to have been fairly straight (this edge is incomplete), and the lower margin is mildly convex. The ventral portion of the anterior end angles up sharply, then rounds to meet the upper margin. There is a row of foramina a few centimeters below and roughly parallel to the upper margin of the dentary along its lateral surface. Several other small foramina also dot this side of the bone, especially near the anterior end, and represent exit for arteries and terminal branches of the mandibular branch of the trigeminal nerve.

Medially, the interdental plates form the upper margin of the dentary and are clearly visible but poorly preserved. The interdental plates are firmly fused together, and the tips of unerupted teeth are commonly visible through foramina between the bases of the plates. A bladelike unerupted tooth is visible in alveolus 1, exhibiting serrated carina on both anterior and posterior margins. This tooth is quite unlike the somewhat incisiform, or D-shaped, anterior teeth of the *Allosaurus* dentary. The layer of bone medial to this tooth was removed to better expose it. The exposed surface of the tooth is smooth, unlike the anterior teeth of *Ceratosaurus*, which have strong vertical ridges on the lingual surface. The erupted and complete tooth in the dentary is bladelike, with the distal half of the crown abruptly reclining posteriorly.

The holotype of *Megalosaurus*, a left dentary, is similar to that of *Torvosaurus* but differs in several ways as noted below under the *Torvosaurus* discussion section.

The dentary of *Allosaurus* is not as deep and bears more teeth, 16 on the average (Madsen 1976b, p. 29), than *Torvosaurus*. *Allosaurus* also has a well-developed Meckelian groove, which is not in evidence on BYUVP 2003.

The dentary of *Ceratosaurus nasicornis* also has a greater number of teeth, 15 (Gilmore 1920, p. 88), than *Torvosaurus*. Though the tooth count of elements, other than the premaxilla, varies slightly within a species, tooth count is generally used as a reliable genotypic characteristic among theropods (Madsen 1976b, p. 29; Ostrom 1969, p. 17). The dentary of *Ceratosaurus* is not as deep, has interdental plates that protrude less from the dentary, and appears to be more bowed ventrally than that of *Torvosaurus*.

AXIAL SKELETON

The vertebral column of *Torvosaurus tanneri* is incompletely known; thus the vertebral formula is uncertain. But to facilitate the following descriptions of *Torvosaurus* vertebrae, the estimate is here made that the total presacral vertebral count is 23, with 9 cervical vertebrae

and 14 dorsal vertebrae. This vertebral count and formula is found in many nonavian theropods and may be the plesiomorphic theropod condition.
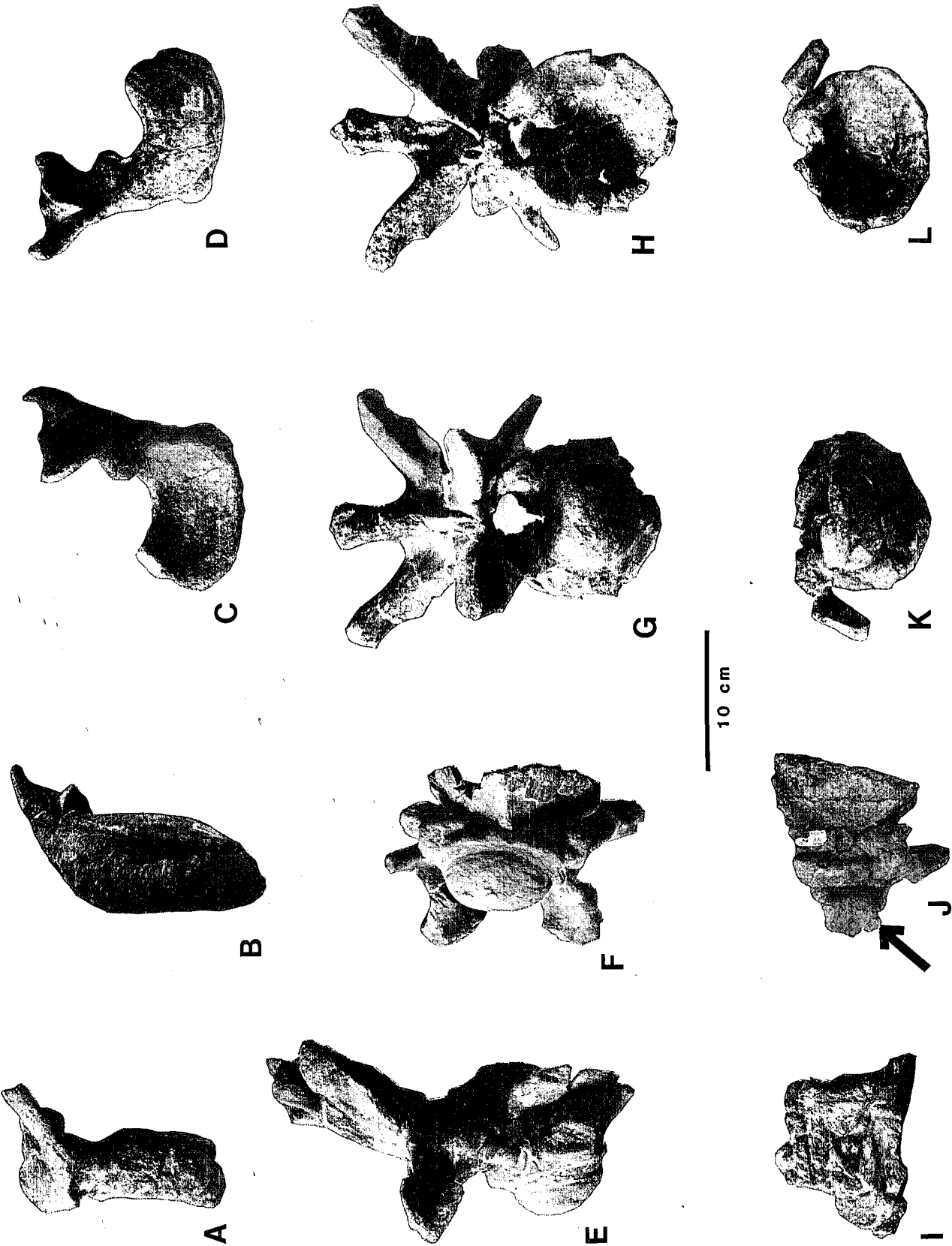
Cervical Vertebrae

Atlas-axis. Only two elements of the atlas-axis complex are known: the atlantal intercentrum and the left neurapophysis, which make up the atlas, BYUVP 4884 (fig. 7, A–D). Both elements are well preserved and firmly fused together. The intercentrum has a crescent-shaped body, like all theropods, with ventrolateral tuberosities (?parapophyses). The posterior face is a simple convex surface. The elements of *Allosaurus* and *Ceratosaurus*, however, have an S-shaped profile. Stated another way, the upper portion of their posterior faces are convex and the lower halves concave. The neurapophysis in *Torvosaurus* is triangular with a well-defined, elongate epipophysis. The neurocentral suture is fully fused and is draped with elongate bone fibers.

The most striking aspect of these *Torvosaurus* elements is their size. The intercentrum, for example, is 120 mm wide. Of necessity, the occipital condyle is smaller than the concave anterior surface of the atlas because of intervening tissues (which form the true articular surfaces). Based on comparisons with the atlas of similar-sized theropods, I estimate that the occipital condyle that articulated with this atlas was about 95 mm wide, suggesting it supported a massive skull.

Postaxial cervical vertebrae. Five *Torvosaurus* postaxial cervical vertebrae have been recovered. BYUVP 4860 (fig. 7, E–H), is well preserved and essentially complete. BYUVP 2004a–d (figs. 7, I–L, and 8, A–H) is an articulated series of four vertebrae, which are moderately to severely compressed dorsoventrally. The letters a through d have been appended to the original catalog numbers to facilitate their discussion and description. The anteriormost cervical in this series, 2004a, is represented only by a small fragment of the centrum cup (indicated by arrow in fig. 7, J). The other centra in this series are complete with one exception; BYUVP 2004b lacks the left anterior region of the centrum. Neural arch bases are present on each of these vertebrae, along with portions of the diapophyses on 2004b and 2004d. The rest of the neural arches are missing. No cervical ribs have been found.

In their preliminary description of the genus, Galton and Jensen (1979) included four cervical vertebrae in their hypodigm list. (Actually, they had five cervical vertebrae, but the small fragment making up BYUVP 2004a was not mentioned.) These were designated as cervical vertebrae numbers three, four, and five (BYUVP

10 cm

2004b–d), and cervical vertebra number seven (BYUVP 2005). Specimen BYUVP 2005 is actually an anterior dorsal vertebra.

An additional postaxial cervical vertebra, BYUVP 4860 (fig. 7, E–H), has been discovered subsequent to the original description of the genus. It is the most anterior of the *Torvosaurus* postaxial cervicals found to date and is most likely cervical number three. Based on the position of the parapophysis and diapophysis, centra length to height ratios, and the newly discovered cervical vertebra, it now appears that cervical vertebrae BYUVP 2004a–d are numbers four through seven or five through eight.

All the known postaxial cervical vertebrae are strongly opisthocoeleous. The posterior face of each centrum is deeply cupped while the anterior face has an epihemispherical central region surrounded by a sloped ledge; that is, the anterior face looks like a low derby hat with a sagging brim (fig. 7, F). The brim occupies nearly half the area of the articular surface. The anterior edge of the parapophyses are incorporated into this brim so that the functional articular surface is wider than tall. *Ceratosaurus*, though lacking the ball-like anterior face, also has a rim around the outer margin of the anterior face of the cervical vertebrae (Marsh 1884). A slight rim is sometimes evident on *Allosaurus* cervicals, but it is less well defined.

The four reasonably complete *Torvosaurus* cervical vertebrae bear large, stocky parapophyses. The concave articular surfaces of these parapophyses are vertically oriented ellipses that become increasingly deep on successive vertebrae. Only one complete diapophysis, the left of BYUVP 4860, is preserved in the cervical series. It is slender and, as is common in most theropods, extends downward at about 45° and terminates in a subrounded articular surface.

The centra are extremely hollow and were pneumatic. All known *Torvosaurus* cervical centra have well-developed pleurocoels located above and behind the parapophyses, through which the median and other internal septa of the centra are visible. As an indirect result of the deeply excavated design of the centra, all postaxial cervical vertebrae except BYUVP 4867 are dorsoventrally compressed. This distortion makes the centra, especially the weak posterior end, appear disproportionately wider than tall (fig. 8, H). This distortion resulted in a misinterpretation of the overall morphology of *Torvosaurus*

cervical vertebrae by Jensen (1985b, p. 711), who wrote that the centra were wider than tall. In *Ceratosaurus* and *Allosaurus*, the pleurocoels are located above the parapophyses, while in *Deinonychus* they are behind the parapophyses.

The ventral surface of BYUVP 4860 is a broad, obliquely angled V with a low, but distinct keel (fig. 7, F). The nature of the venter of the cervicals in BYUVP 2004a–d is difficult to ascertain because they are so crushed. It is likely that most, if not all, cervical vertebrae of *Torvosaurus* were slightly keeled, with keel size decreasing posteriorly in the cervical series.

A neural spine is intact only on BYUVP 4860. The spine is unlike the anteroposteriorly elongate, bladelike spines of most theropod anterior cervical vertebrae because its anteroposterior dimension is roughly equal to its lateral width. This is unusual because only the posterior cervical vertebrae bear anteroposteriorly narrow spines, such as those of *Allosaurus*, which facilitated dorsoflexion at the base of the S-shaped neck. Intervertebral ligament scars are prominent on the spine, especially on the posterior surface. Like the cervical neural spines of many theropods, the top of this spine is weakly bifurcate. The neural arch peduncles are broad and do not blend smoothly into the centrum because each peduncle terminates ventrolaterally in a raised edge. The epipophyses are strongly developed and extend up to 45 mm beyond the postzygapophyses. It seems that no other described theropod genus has such prominent epipophyses. Apparently, well-anchored cervical levators were required to elevate the massive skull, or perhaps the elongate epipophyses served to increase the efficiency of these muscles.

The prezygapophysial articular facets are preserved only on BYUVP 4860 (fig. 7, E–H). They are nearly circular, essentially flat, and slope gently medially and anteriorly. The cervicals of *Torvosaurus* are distinguishable from *Allosaurus* and *Ceratosaurus* by the usually well-defined brim surrounding the well-developed anterior ball, the long parapophyses and epipophyses, and a high degree of excavation of the centrum.

Dorsal Vertebrae

Four vertebrae, BYUVP 2006–2010, were identified as dorsal vertebrae five, seven, ten, and twelve by Galton and Jensen (1979) and included in their hypodigm. Their

FIGURE 7.—Torvosaurus tanneri *cervical vertebrae. Atlas, BYUVP 4884 (A–D). Third cervical vertebra, BYUVP 4860 (E–H). Fourth and fifth cervical vertebrae, BYUVP 2004a and 2004b. The former consists of a small piece of the posterior cup attached to the anterior ball of the latter and is indicated by the arrow. Lateral (A,E,I), ventral (B,F,J), anterior (C,G,K), and posterior (D,H,L) views.*
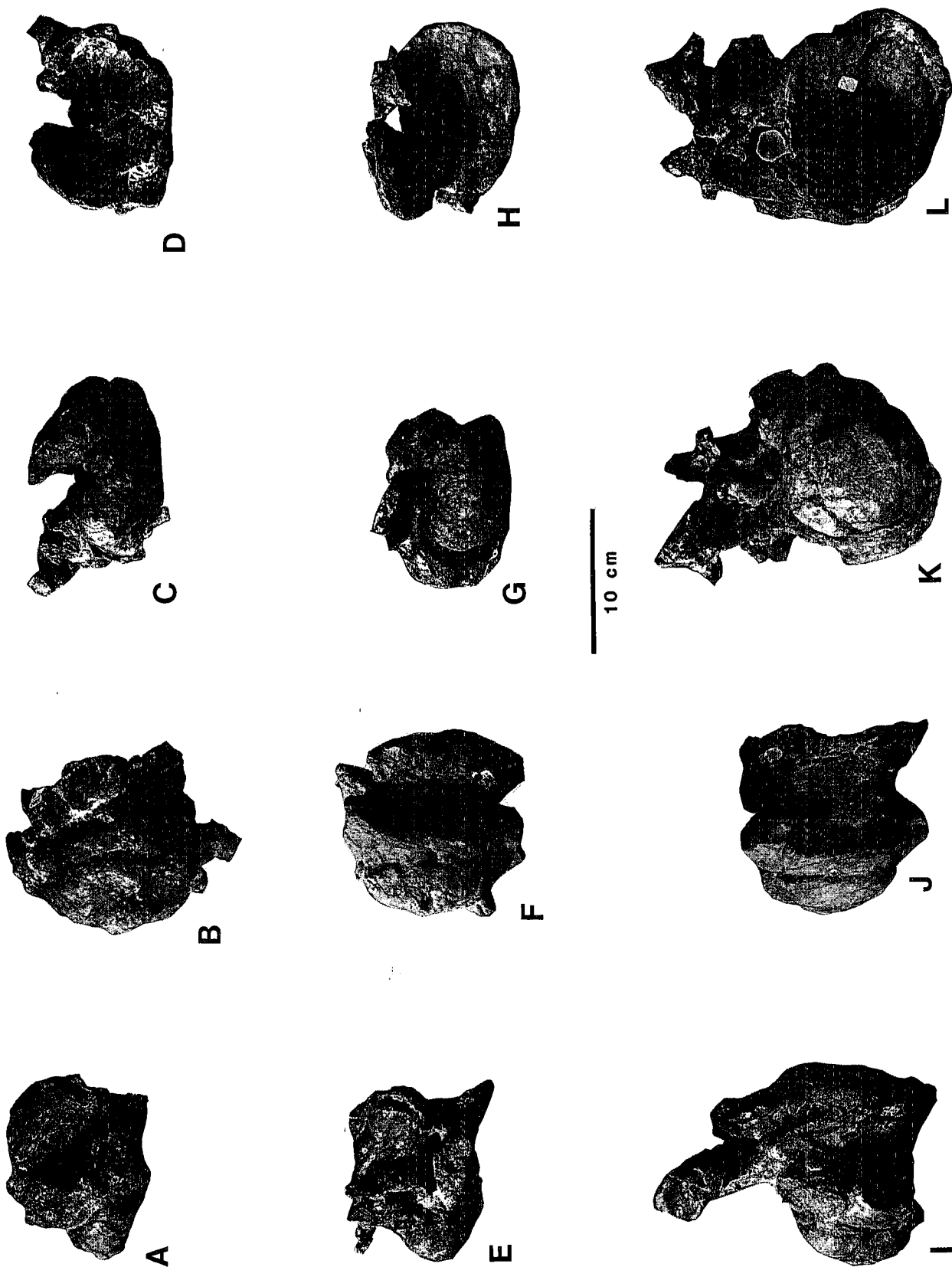
list of dorsal vertebrae, however, has two problems; 2010 is actually a left metacarpal I, and 2009 is not assigned to any specimen. While it is clear that the listing of 2010 as a dorsal vertebrae was simply a typographical error, it is not known which specimen they regarded as the twelfth dorsal vertebra because no vertebrae were figured. Galton and Jensen also included in their hypodigm BYUVP 2005 (fig. 8, I–L), which they listed as a cervical vertebra. It appears, though, that this specimen is the anteriormost dorsal vertebra, now that more *Torvosaurus* vertebrae are available.

In addition to the "original" specimens, four more *Torvosaurus* dorsal vertebrae have been found, bringing the total from the locality to nine. Most are in good condition, all have fairly intact centra and, at a minimum, the lower one-half of their neural arches are present. No dorsals were articulated, but at least two (BYUVP 9120 and 9121) were closely associated. Each bears raised, robust neural arch peduncles that are easily differentiated from the centrum body. Centra bodies are generally triangular in cross section but, in end view, the anterior and posterior articular surfaces are round. All but the posteriormost dorsal vertebra of *Torvosaurus* exhibit a cervical characteristic; they are opisthocoeleous.

Such "cervicalization" is evident on all but the most posterior centra and, like *Torvosaurus* cervical vertebrae, the anterior "ball" is surrounded by a posteriorly sloping shelf. The posteriormost centra are platycoeleous. Venters of the centra are moderately to strongly keeled except for BYUVP 2005 and BYUVP 4890, which are only weakly keeled. All have pleurocoels, ranging from well-developed foramina on anterior centra to large open cavities on posterior centra. Neural spines change gradually from short, square (in cross section) spines, anteriorly, to laterally thin spines, posteriorly. These spines have small or nonexistent supraprezygapophysial laminae.

As is often the case in theropods, it is difficult to differentiate between cervical and dorsal vertebrae, especially when dealing with disarticulated specimens. (Welles [1984] refers to these transition vertebrae as "pectorals" on *Dilophosaurus*.) However, two morphologic changes usually occur in the cervical/dorsal transition area. First, the parapophyses, which start high on the centrum in anterior cervicals, migrate ventrally so that by the ninth cervical, or first dorsal, they are at the lowest point in the

entire presacral series. The second change is related to the first. Because parapophyses and diapophyses are points of rib attachment, the transverse processes begin to "rotate" dorsally on the first dorsal vertebrae and are increasingly higher on each succeeding dorsal vertebra, except on the last two dorsal vertebrae. The posteriormost dorsals generally bear near horizontal transverse processes.

Anterior dorsal vertebrae. Four anterior dorsals are known: BYUVP 2005 (fig. 8, I–L), 4998 (fig. 9, A–D), 2006 (fig. 9, E–H), and 2007 (fig. 10, A–D). I consider them dorsals one, four, five, and six, respectively. BYUVP 2005 is probably dorsal one, as indicated by the parapophyses that are located higher up on the centrum than the parapophyses of BYUVP 2004d, which is undoubtedly a posterior cervical. The only transverse process preserved on BYUVP 2005 is depressed to a lesser degree than the transverse process on BYU 2004d. The spools of the anterior dorsal vertebrae centra are triangular in cross section with slightly concave sides and are quite hollow. The venter of most centra are V-shaped and bear a strong keel. Dorsal one (BYUVP 2005) has a weak, barely visible keel. Keels of the other anterior dorsals are sharp and well defined. The centra are strongly to moderately opisthocoeleous, becoming less so posteriorly in the vertebral column. The anterior face of each centrum is much like the equivalent face of the cervicals; the central area of the face is composed of a semihemispherical protrusion surrounded by a well-defined, posteriorly sloping shelf. The base of the hemisphere on most of these centra is separated from the shelf by a distinct constriction. The anterior end of the more posterior anterior dorsal vertebrae are less domed, but the central portion is still markedly raised above the peripheral shelf.

The posterior articular faces of the anterior dorsal vertebrae centra are simple, but deep, concavities. The smoothly curved surface gives little or no indication it articulated with the complex anterior face present on the preceding vertebrae. In life the anterior articular face of each cervical and most dorsal centra must have been covered by cartilage with a ball-like surface, bearing little resemblance to the complex topography of the bone surface beneath it. The articular faces of the cervicals and anterior dorsals of *Ceratosaurus* are even more dissimilar. Anterior faces of *Ceratosaurus* vertebrae are nearly flat with a narrow peripheral border, whereas the poste-

FIGURE 8.—Torvosaurus tanneri *cervical and dorsal vertebrae. Sixth cervical vertebra, BYUVP 2004c (A–D). Seventh cervical vertebra, BYUVP 2004d (E–H). First dorsal vertebra, BYUVP 2005 (I–L). Lateral (A,E,I), ventral (B,F,J), anterior (C,G,K), and posterior (D,H,L) views.*
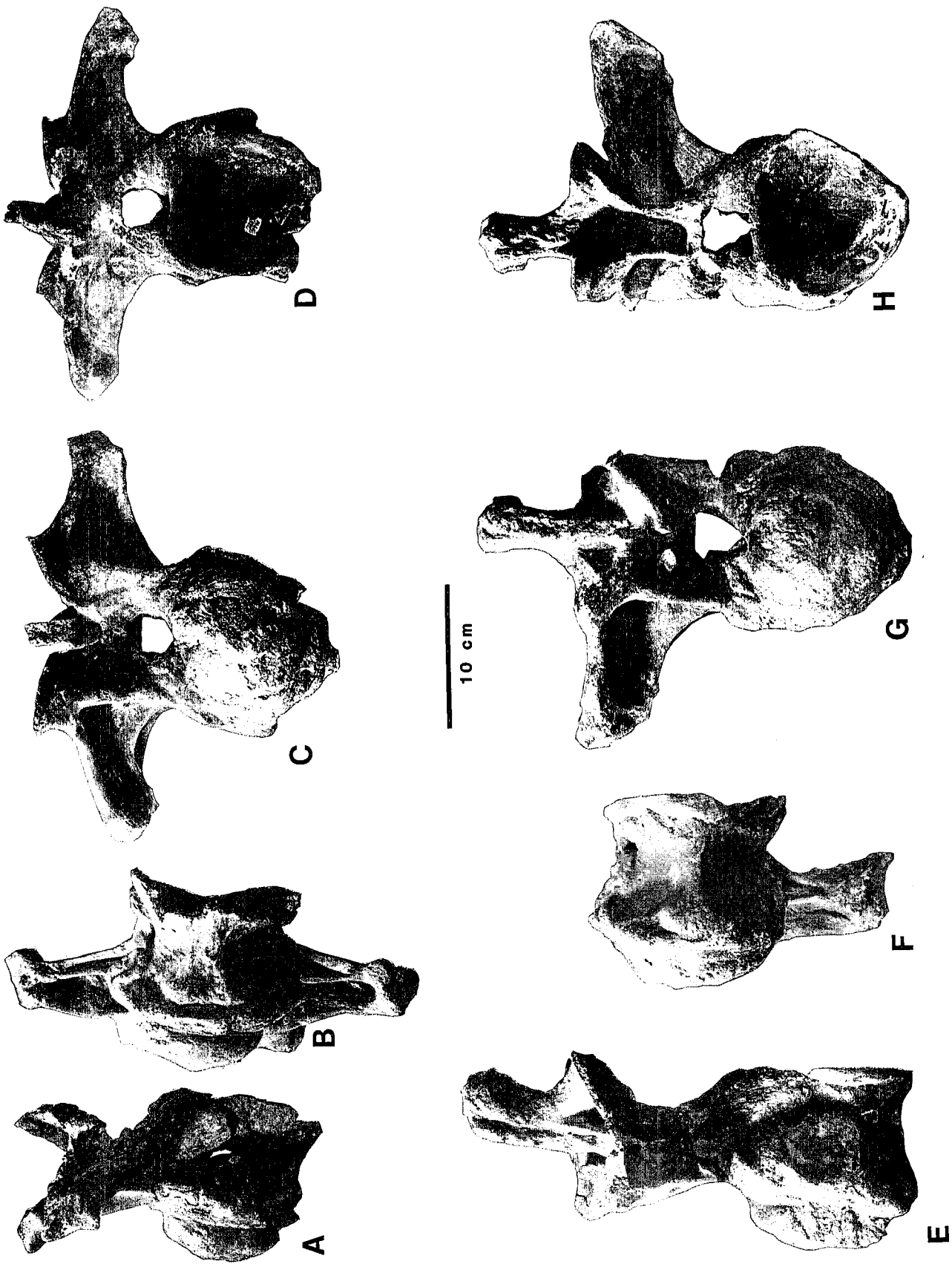
rior faces are deeply cupped (Marsh 1884). The anterior dorsal vertebrae of *Allosaurus*, while opisthocoeleous, are much less so than most *Torvosaurus* dorsal vertebrae.

As with other saurischians, the parapophyses of *Torvosaurus* dorsal vertebrae are located progressively higher on successive vertebrae. The anterior dorsal vertebrae bear short, but large, parapophyses on the centrum. The parapophyses are slightly higher than wide, strongly cupped, and are in contact with the base of the anterior neural arch peduncle. The anterior side of each parapophyses is slightly flattened because it forms part of the articular rim of the anterior centrum face.

The lateral openings of the pleurocoels are irregular ovoids. Deep to these openings the cavities invade the ventral portions of the centra. The lateral openings are located above and behind the parapophyses in the most anterior dorsal vertebrae and gradually shift to a position directly behind the parapophyses in more posterior vertebrae. The upper border of the pleurocoel opening is formed by the ventral margin of the neural arch peduncle.

Of the presently known anterior dorsal vertebrae, only the fifth dorsal vertebra has a complete neural spine (fig. 9, E, G–H). Spinous bases are present on the other two anterior dorsal vertebrae, and a fair summary of their characteristics can be made. The spines appear to have been short and square in cross section. There are no supraprezygapophysial lamina on anterior dorsal vertebrae (fig. 9, G). Intervertebral ligament scars are well developed and protrude markedly from the anterior face of the spine but only slightly from the posterior face (fig. 9, E).

Large, ventrolaterally sloping facets are borne at the tips of the diapophyses. The facets are triangular in outline with rounded corners. The diapophyses are supported ventrally by a pair of laminae that rise up from the anterior and posterior portions of the neural arch peduncle and converge below the transverse process to form a single supporting plate. Prezygapophyses and postzygapophyses are moderately spaced. Their facets are conspicuously wider than long and slope medially. No anterior dorsals, with the exception of number six, bear a hyposphene—the infrapostzygapophysial laminae, which form the hyposphene in posterior dorsals, being widely separated.

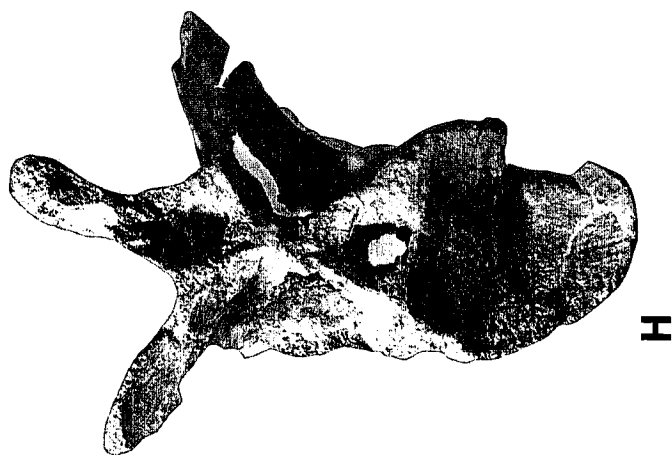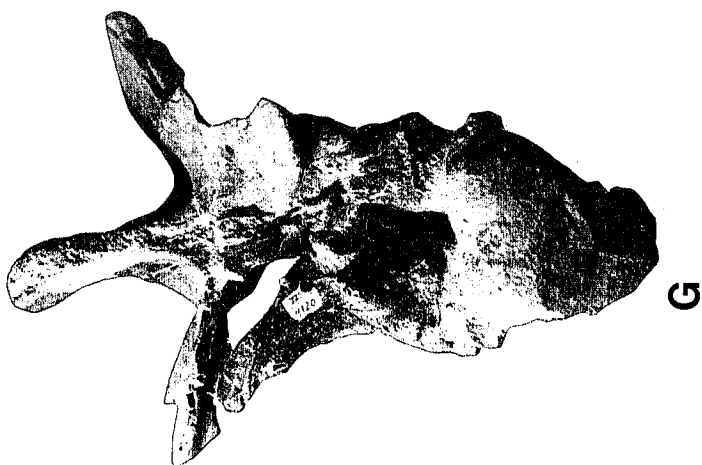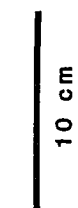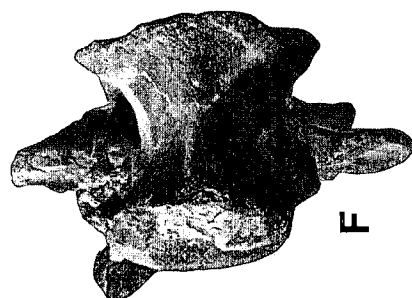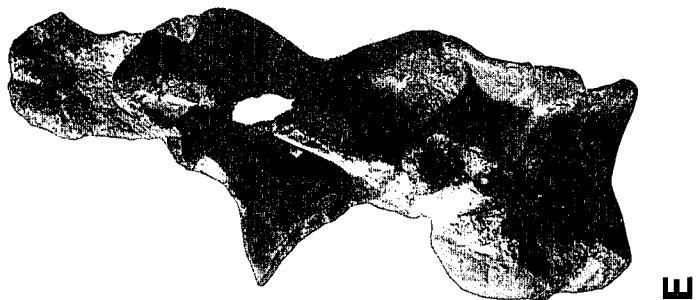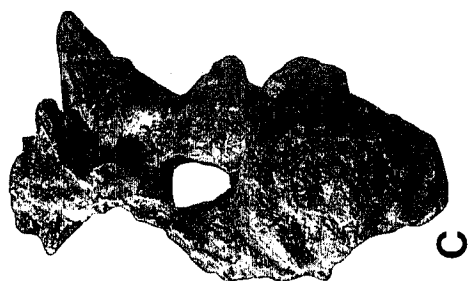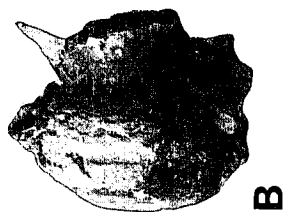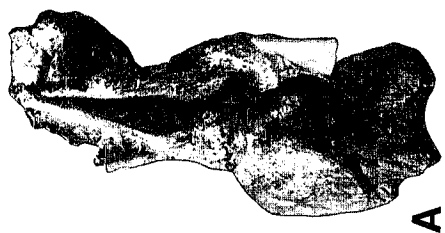*Posterior dorsal vertebrae.* Five posterior dorsal vertebrae are known: BYUVP 9120 (fig. 10, E–H), 9121 (fig. 11, A–D), 9090 (fig. 11, E–H), 2008 (fig. 12, A–D), and 4890 (fig. 12, E–H). They appear to be dorsal vertebrae seven, nine, ten, twelve, and fourteen, respectively.

The parapophyses of all posterior dorsals are located mainly on the base of the neural arch with the lowest portion of the articular surface overlapping the centrum. The parapophyses of numbers six and seven are about one-third higher than long (fig. 10, A and E). The remainder of the parapophyses are narrow along the horizontal axis but very elongate along the vertical axis. This vertical elongation occurs first on dorsal nine, though it probably also occurred on eight, which has not been found. The most pronounced example of this vertical elongation of the parapophyses is exhibited by dorsal ten, which has parapophyses over 80 mm high but only 28 mm wide (fig. 11, E).

BYUVP 2007 (fig. 10, A–D) has a comparatively wide, rounded keel (fig. 10, B) that does not closely match the general pattern of the balance of the dorsal series. Other morphologic characters of this specimen, however, clearly indicate it is a *Torvosaurus* dorsal vertebra. Otherwise, with the exception of the last dorsal vertebra, fourteen, which has a more cylindrical centrum with a flat venter (fig. 12, F), the posterior dorsal vertebrae have triangular centra (in transverse section) with a prominent keel on the venter.

Posterior dorsal vertebrae grade from opisthocoelous, anteriorly, to the amphiplatyan, posteriorly. The last three or four dorsal vertebrae are amphiplatyan. The anterior face of dorsal ten, BYUVP 9090 (fig. 11, G), is shallowly convex and is the last dorsal to exhibit the *Torvosaurus* "derby hat" type anterior face. The posterior face of the same specimen is planar (fig. 11, H). The anterior and posterior faces of the remaining posterior centra are also planar, with one exception. The posterior face of the centrum of dorsal fourteen, BYUVP 4890 (fig. 12, H), is warped along a horizontal axis with a trough near the top and a crest near the bottom. The last dorsal vertebra of *Allosaurus* is similarly curved. BYUVP 4890 (fig. 12, E–H) is the last dorsal vertebra as evidenced by its "warped" posterior face, horizontal transverse processes, and parapophyses, which must have been located just below the transverse processes. The parapophysial location is not positively known because the area where they must have been located, the proximal leading edge of the transverse processes, is missing.

FIGURE 9.—Torvosaurus tanneri *dorsal vertebrae. Fourth dorsal vertebra, BYUVP 4998 (A–D). Fifth dorsal vertebra, BYUVP 2006 (E–H). Lateral (A,E), ventral (B,F), anterior (C,G), and posterior (D,H) views.*

The pleurocoels of *Torvosaurus* anterior posterior dorsal vertebrae are similar to those of the anterior dorsals. However, by dorsal nine, BYUVP 9121, the pleurocoels are much larger (fig. 11, A), and they continue to increase in size posteriorly in the series. Unlike the pleurocoel foramina of the more anterior dorsals, which were small compared to the internal sinuses or fossae they led to, the pleurocoel openings of dorsals nine to fourteen become increasingly larger until the outer rim is as large as the fossa they lead to. On dorsal fourteen (fig. 12, E) the outer margin of the cavity is wider than the basal portion of the fossa.

The transverse processes of the more anterior posterior dorsal vertebrae are generally longer than those of the anterior dorsals, are angled slightly posteriorly, and have a strong dihedral angle. Dorsals nine, ten, and twelve have a dihedral angle of approximately 35°. The transverse processes of the most posterior dorsal vertebrae, fourteen, have a much lower dihedral angle of about 20°. It is expected the dihedral angle of dorsal thirteen, which has not been found, would be closer to that of dorsal fourteen than dorsal twelve because the transverse processes of dorsal vertebrae thirteen and fourteen in *Allosaurus* are nearly horizontal and angle slightly forward (Madsen 1976b, p. 34).

The transverse processes of *Torvosaurus* posterior dorsal vertebrae, except for twelve and fourteen, are supported ventrally by a pair of laminae originating on the anterior and posterior neural arch peduncles and converging near the ventral surface of the transverse process. In the most anterior posterior dorsal vertebrae these laminae converge before intersecting the transverse process, but farther back in the posterior dorsal series the laminae do not intersect one another except near the distal portion of the transverse process. The anterior lamina decreases in size on the more posterior dorsals until on dorsal twelve, BYUVP 2008, it consists of a small ridge running the length of the ventral anterior edge of the transverse process (fig. 12, A and B). There is no trace of the anterior lamina on dorsal fourteen (fig. 12, E and F).

The neural canals are taller than wide throughout the posterior dorsals and gradually decrease in size on succeeding vertebrae. The bladelike neural spines of the posterior dorsal vertebrae increase in size posteriorly in the series. The apexes of all these spines are slightly

thicker than the body of the blade. Both the anterior and posterior intervertebral ligament scars are obvious. The anterior intervertebral ligament scar tends to protrude from the spine, especially distally, while its posterior component protrudes only on the anterior posterior dorsals. The anterior intervertebral ligament scar on dorsal fourteen (fig. 12, G), BYUVP 4890, is thin and much less developed than the same scar on the balance of the posterior dorsals. The posterior intervertebral ligament scar of the same dorsal vertebrae is essentially restricted to the distal one-third of the neural spine (fig. 12, H).

Suprapostzygapophysial laminae are present on all *Torvosaurus* dorsals. Supraprezygapophysial laminae, however, are not present except on dorsal twelve, BYUVP 2008, and dorsal fourteen, BYUVP 4890, but they are short and do not extend far up the neural spine. The virtual lack of supraprezygapophysial laminae on *Torvosaurus* dorsal vertebrae contrasts sharply with *Allosaurus*, where they are prominent and extend high up the neural spine. On *Torvosaurus* the aforementioned laminae are significant, however, because they, in conjunction with the leading edge of the transverse processes, brace the prezygapophyses with a footlike contact that is not fused to the prezygapophyses. The same basic feature is also present on *Allosaurus*, but the "foot" is barely visible. On BYUVP 4890 (fig. 12, E–H) the prezygapophyses have been broken off, leaving the footlike base of the supraprezygapophysial laminae (fig. 12, E and G), making them look like postzygapophyses.

Prezygapophysial facets are ovoid on all posterior dorsal vertebrae except those on dorsal twelve, BYUVP 2008, and presumably all dorsals posterior to it, though this cannot be confirmed because dorsal thirteen is not known and dorsal fourteen lacks prezygapophyses. The prezygapophysial facets of dorsal twelve, BYUVP 2008, are wider than long. The preserved postzygapophyses of all posterior dorsals are wider than long and slope medially. This slope decreases posteriorly in the series.

A hyposphene first appears on dorsal six, BYUVP 2007, and is found on all subsequent dorsal vertebrae. The hyposphene increases in size posteriorly in the series. A feature that is apparently unique to *Torvosaurus* is a large fenestra, located anterior to the hyposphene. This fenestra passes completely through the neural arch, leaving the hyposphene complex as a pillar connecting the posterior

FIGURE 10.—Torvosaurus tanneri *dorsal vertebrae. Sixth dorsal vertebra, BYUVP 2007 (A–D). Seventh dorsal vertebra, BYUVP 9120 (E–H). Lateral (A,E), ventral (B,F), anterior (C,G), and posterior (D,H) views.*

10 cm
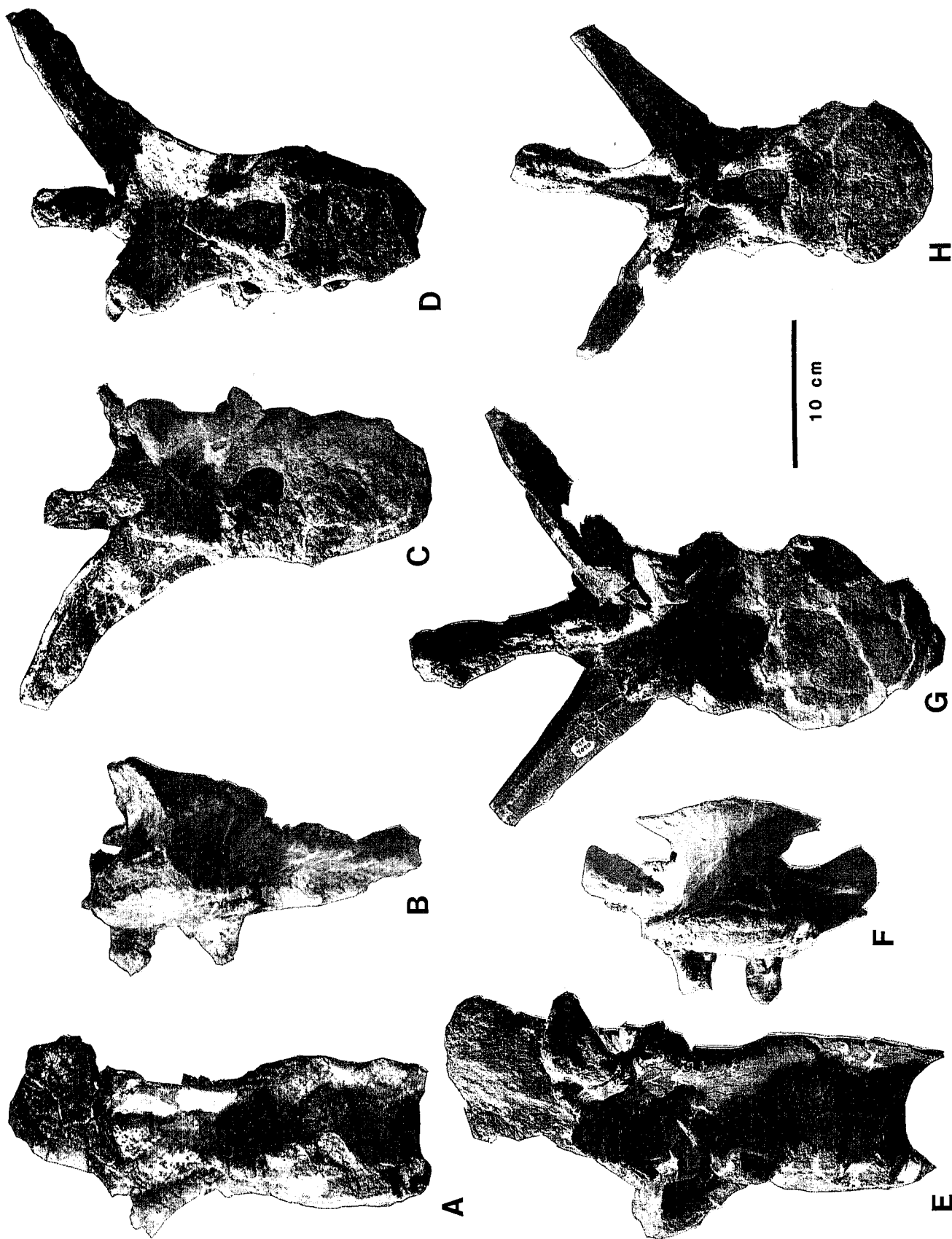
neural arch peduncles and postzygapophyses. This fenestra is shown well on BYUVP 9120 (fig. 10, E) and is definitely not an artifact of preservation.

Sacral Vertebrae

No *Torvosaurus* sacral vertebrae have been found, but they were probably similar to those of *Megalosaurus* as figured by Owen (1856). This assumption is made because the genera have very similar ilia and because of the similarity of these two genera in general. As discussed in the *Torvosaurus* ilium section of this paper, it is difficult to discern the sacral rib scars on either of the ilia. It is clear, however, that the sacral vertebrae count was at least four, based on observable scars, and probably five, the number of sacrals commonly found in theropods.

Caudal Vertebrae

No *Torvosaurus* caudal vertebrae were known when Galton and Jensen (1979) described the genus. Jensen (1985b) mentioned and figured several caudal vertebrae, but did not describe them in detail. Fifteen caudal vertebrae assignable to *Torvosaurus* have been found in the Dry Mesa Quarry collection. Eleven of these, BYUVP 4976 A–K (figs. 16–19), form an articulated series. All known *Torvosaurus* caudals in the collection came from the anterior half of the tail and represent "pretransition point" caudals in the sense of Russell (1972, p. 378); that is, they bear transverse processes. It is difficult to assign position numbers to vertebrae in this series, but they appear to represent caudal vertebrae eight through nineteen. The total number of caudal vertebrae in this genus is unknown, but there is no reason to suspect the count differs significantly from the "normal" theropod caudal count of roughly 50 (or less), the caudal count given for *Allosaurus* by Madsen (1976b, p. 35) and *Ceratosaurus* by Gilmore (1920, p. 98).

Two nonconsecutive caudals, BYUVP 5086 (fig. 13, A–D) and 5004 (fig. 13, E–H), are from a position anterior to those represented by the articulated series. Specimen 5086 is caudal vertebra two or three, a determination based on its compound curved, concave anterior face, broad based transverse processes, and an anteroposteriorly long neural spine with intervertebral ligament scars

from its base to its tip. All these characters indicate a strong union, in the vertical plane, with adjacent vertebrae. BYUVP 5004 is caudal four or five and has features similar to BYU 5086, but the chevron facets are better defined.

BYUVP 9135 (fig. 18, E–H) is the most distal *Torvosaurus* caudal vertebra in the collection and is estimated to be caudal twenty three. Its size suggests it could have belonged to the same individual represented by the articulated caudal series. BYUVP 9013 (fig. 18, A–F) clearly represents another, slightly smaller, individual because it is smaller than an equivalent vertebra in the articulated series, which it duplicates. It is approximately caudal vertebra twelve.

In general, the caudal centra are spool-shaped, with concave sides and venter. The spool of the most anterior caudal vertebra is similar in shape to *Torvosaurus* dorsals. The centrum is V-shaped in cross section, the sides of the V being nearly flat surfaces. The venter proper has a narrow, but shallow, groove along its length. The depth of this groove is variable, but in general it tends to be shallower on the more posterior centra. Subtle radiating ridges decorate the proximal surfaces of the flanges on both ends of the centrum.

Anterior and posterior faces of the centra are round in outline. *Torvosaurus* caudal centra are amphicoeleous with the posterior face being less concave than the anterior one. This is especially evident in the more anterior caudals. This relationship is found in most theropods.

There is a striking difference between the small, barely discernible anterior chevron facets and the large posterior facets. Some of the anterior facets have two pits into which a fingerlike protrusion of the articular surface on the chevron inserted (see fig. 15, F). Occurrences of these pits and protrusions appears to have been quite variable from one centra to another on the same individual, even in the articulated series.

BYUVP 5086, 5004, and 4976a–b (fig. 14, A and F) exhibit fossae immediately below the neurocentral suture. If position assignments given to the vertebrae in the articulated series are correct, the first 10 or so caudal vertebrae had fossae. The narrow and shallow fossae are axially elongate. While the fossae do not occur farther back in the series, a shallow depression exists just below

FIGURE 11.—Torvosaurus tanneri *dorsal vertebrae. Ninth dorsal vertebra, BYUVP 9121 (A–D). Tenth dorsal vertebra, BYUVP 9090 (E–H). Lateral (A,E), ventral (B,F), anterior (C,G), and posterior (D,H) views.*
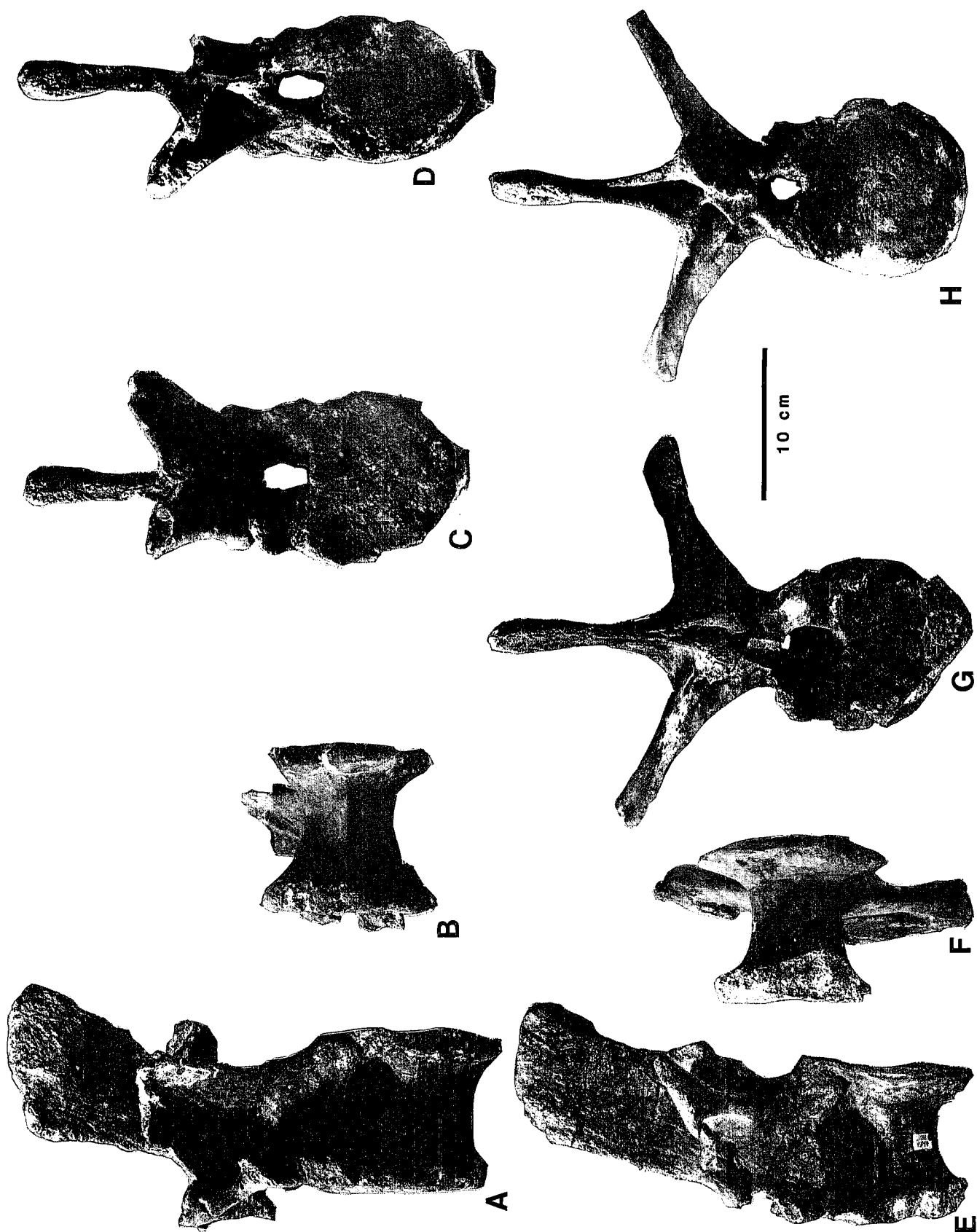
the neurocentral suture in all known *Torvosaurus* caudal vertebrae. The swollen peduncular bases aid in associating them with the dorsal series.

Torvosaurus caudal vertebrae transverse processes are thin, backswept blades with the trailing edge of the lateral margin posteriorly elongate. The blades have a flat to nearly flat dorsal surface and a biconvex to convex ventral surface. The processes are swept back at an angle of about 35°. This angle increases slightly in the more posterior elements of the series, BYUVP 4976a–k (figs. 16–19), and there is a slight dihedral angle to the transverse processes. The dihedral angle decreases posteriorly in the series until about the sixteenth caudal, BYUVP 4967i, where the transverse processes are nearly horizontal.

The transverse processes are supported below by a pair of ridgelike buttresses, one immediately behind the leading edge, the other just in front of the trailing edge. These buttresses terminate ventrally on their respective areas of the neural arch peduncle. Differentiation of the supporting ridges lessens posteriorly in the caudal vertebrae series so that by the last caudal preserved in the BYUVP 4976 series, the ventral surface of the transverse process is convex with no buttress below.

Pre- and postzygapophyses are short, with articular faces that slope medially at about 40° and anteriorly at about 20°. The articular facets are round to slightly anteroposteriorly elongate in outline. Articular facets of the postzygapophyses do not extend above the plane defined by the upper surface of the transverse process. While this generalization holds true for anterior caudal vertebrae, it may not apply in the unknown posterior caudal vertebrae.

Neural spines of *Torvosaurus* caudal vertebrae are unusual. As a whole, the spines are laterally thin (fig. 14, C and D) anteroposteriorly narrow blades that recline posteriorly (fig. 14, A). However, the more anterior caudal vertebrae bear laterally thin, nearly vertical, neural spines (fig. 13, A). Apparently these broad blades served to restrict the dorsoventral motion of the anterior part of the tail in conjunction with the intervertebral ligament that was located along the entire length of the anterior and posterior edges. Both the anterior and posterior edges of all *Torvosaurus* caudal vertebrae spines are subparallel

(they converge slightly distally) along their complete length with no distal expansion in any direction. This feature clearly sets *Torvosaurus* caudals apart from those of *Ceratosaurus* and *Allosaurus* because the spines of the latter genera are distally expanded anteroposteriorly. The intervertebral ligament scar in *Torvosaurus* is restricted to the base of each spine, except on the anterior four or five caudal vertebrae, indicating most of the tail had potential for considerable vertical mobility.

A well-defined circular pit occurs at the intersection of the anterior edge of the neural spine and the neural arch body. It penetrates up to 15 mm into the vertebra spine in some cases. These foramina are the insertion point for the interspinous ligament and are common on theropod caudal vertebrae. Neural canals are slightly elongate, vertically, and teardrop-shaped in cross section. The narrowest portion is located ventrally and invades the centrum to some degree.

In summary, *Torvosaurus* caudal vertebrae have several features that serve to distinguish them from those of all other known Morrison theropods:

(1) narrow, backswept transverse processes with flat but slightly anteroposteriorly expanded distal ends;

(2) tall, thin, anteroposteriorly narrow, bladelike neural spines, excepting the anteriormost vertebrae, which have anteroposteriorly broad spines;

(3) a nearly straight, filletlike contact is formed at the intersection of the transverse process/zygapophyses and neural spine;

(4) transverse processes on at least the anterior half of the tail are supported ventrally by two buttresses, one near the leading edge and one near the trailing edge of each process;

(5) a striking difference exists between the small, almost nonexistent, anterior chevron facets and the large posterior chevron facets on each centrum; and

(6) subneurocentral suture fossae occur on the anterior one-third of the caudal series.

Chevrons

Ten *Torvosaurus* chevrons were found attached to vertebrae in the caudal series, BYUVP 4976 A–K (fig. 19).

FIGURE 12.—Torvosaurus tanneri *dorsal vertebrae. Twelfth dorsal vertebra, BYUVP 2008 (A–D). Fourteenth dorsal vertebra, BYUVP 4890 (E–H). Lateral (A,E), ventral (B,F), anterior (C,G), and posterior (D,H) views.*
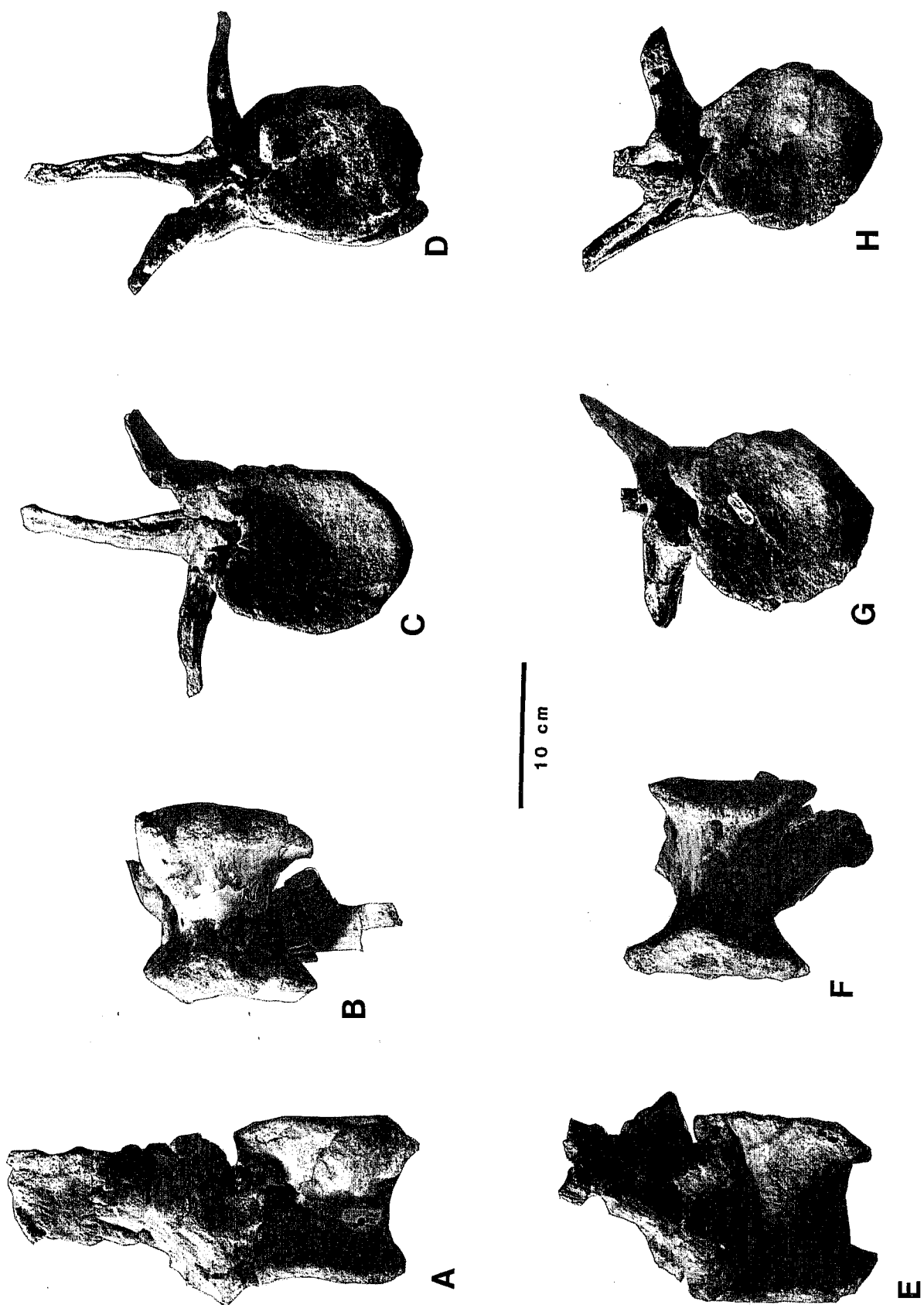
No other *Torvosaurus* chevrons have been found in the quarry. *Torvosaurus* chevrons are briefly discussed by Jensen (1985b), and one is figured.

The shaft of each chevron is nearly straight, and the distal one-third is somewhat laterally flattened. Thin carinae project anteriorly and posteriorly from the flattened portion. Posterior carinae project farther beyond the shaft than the anterior ones, making the shafts appear slightly bowed. In cross section the middle third of the shaft has rounded sides while the anterior and posterior surfaces are marked by a shallow, concave groove.

Haemal canals in *Torvosaurus* chevrons are large in comparison to the length of the chevrons, noticeably larger than those of *Allosaurus* or *Ceratosaurus*. Each haemal canal is covered dorsally by a concave bridge on complete elements (fig. 19, N and Q). Most of the laterally wide, anteriorly posteriorly short, ovoid articular surface of the bridge (fig. 19, L and O) contacted the posterior chevron facet of the centrum. Fingerlike processes extend anteriorly from each side of the bifurcated proximal end of the chevron (fig. 19, B–D).

A cross section of the *Torvosaurus* tail is similar to that of *Allosaurus*, as figured by Madsen (1976b, p. 36). However, in *Torvosaurus*, the lengths of the chevrons are subequal to the height of the vertebrae, whereas in *Allosaurus* the chevrons are noticeably shorter than the vertebrae.

Ribs

No ribs of *Torvosaurus* have been found, or at least none have yet been identified. Because ribs are generally comparatively fragile by nature, they tend to be badly broken, and, hence, there may be collecting bias. Also, due to their relatively long length, ribs are frequently "intertwined" with several bones in the quarry, and during the collection of seemingly more important bones, ribs tend to suffer. According to Voorhies (1969), ribs are among the first elements to be separated from a carcass. However, *Torvosaurus* vertebrae, phalangeal elements, and pelvic elements are also listed by Voorhies (1969) as being among the most readily transported elements relatively common in the east end of the quarry. Therefore, it

seems reasonable that the lack of *Torvosaurus* ribs in the quarry is, in fact, a sampling bias.

Even though no ribs of *Torvosaurus* are known, two statements on their morphology are justified. First, in keeping with the large overall size and robustness of the vertebrae to which they were attached, the ribs are probably rather massive in comparison with other Morrison Formation theropods. Second, the ribs that articulated with the posterior dorsal vertebrae must have born narrow, but very tall, capitular faces to match the narrow, vertically elongate parapophyses of these vertebrae. In addition, it is probable that the ribs were pneumatic and possessed fair-sized pneumatopores. This hypothesis is based on the occurrence of similar structures in *Ceratosaurus* ribs (Madsen personal communication 1985) and the extreme pneumaticity of the cervical and dorsal vertebrae.

APPENDICULAR SKELETON

Pectoral Girdle

Scapula and Coracoid. No scapula or coracoid assignable to *Torvosaurus tanneri* has been found. However, it seems plausible that the scapula would be relatively short and robust—two characters that typify the forelimbs of this genus. Because of the large hands, which may have borne four digits, the coracoid was probably large. The scapula and coracoid of *Torvosaurus* will probably prove to be morphologically similar to those of *Megalosaurus bucklandi*, as figured by Walker (1964, p. 109), because of the many similarities these genera share.

Forelimb and Manus

All known elements of the forelimb and manus (left metacarpals I, II, and III, BYUVP 2010–2012; left first phalanx of digit I, BYUVP 2018; left and right humeri, left and right ulnas, and right radius [cataloged as BYUVP 2002]) have been well figured and described by Galton and Jensen (1979) and need not be redescribed here. Also, Galton and Jensen (1979) have made an extensive comparison of *Torvosaurus* forelimbs with those of other genera.

FIGURE 13.—Torvosaurus tanneri *caudal vertebrae. Second or third caudal vertebra, BYUVP 5086 (A–D). Fourth or fifth caudal vertebra, BYUVP 5004 (E–H). Lateral (A,E), ventral (B,F), anterior (C,G), and posterior (D,H) views.*

10 cm
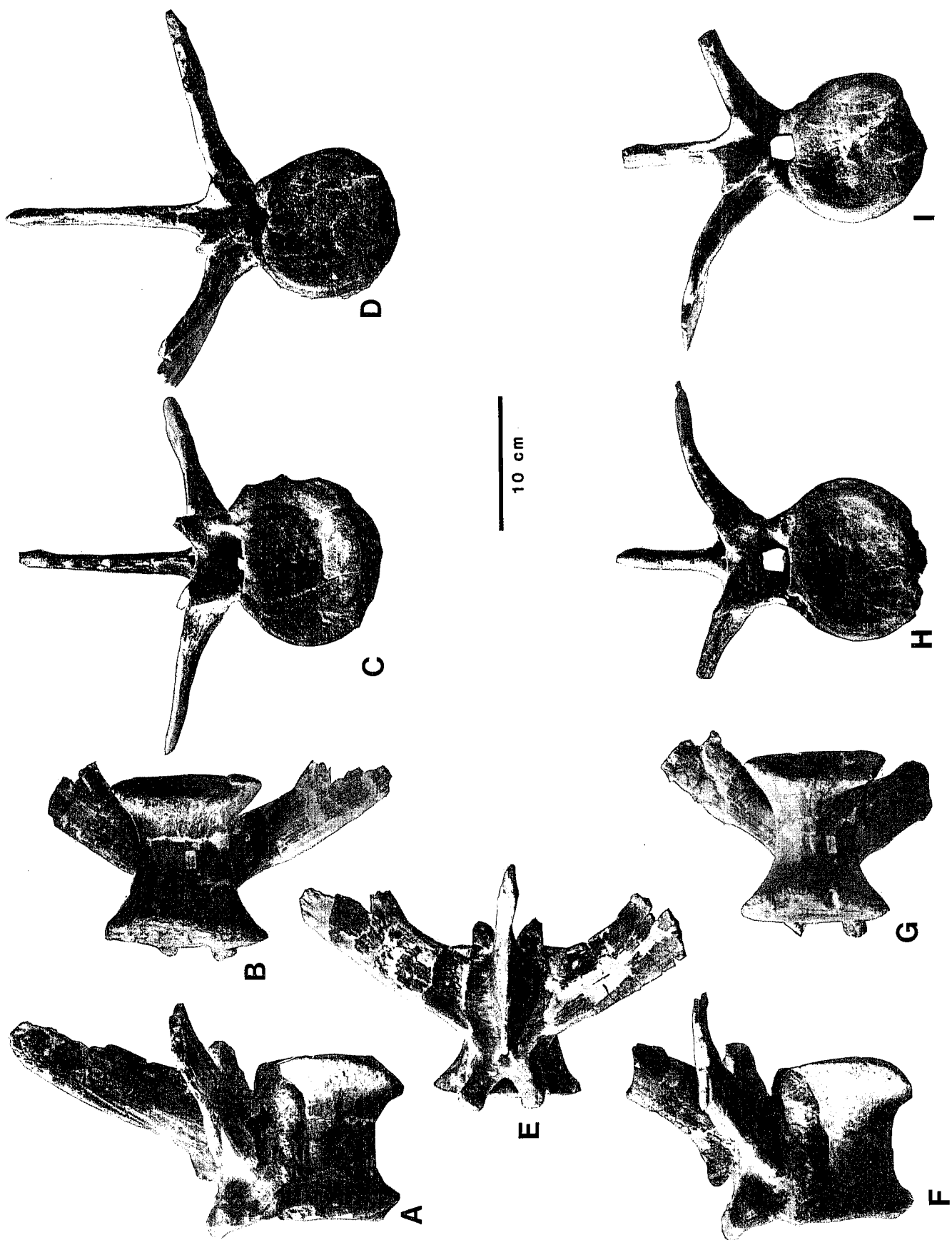
The long bones of both the left and right forelimbs are designated as the type of *Torvosaurus* by Galton and Jensen (1979). However, on page 4 (Galton and Jensen 1979), they wrote that none of these bones were found in articulation. They also wrote that only one *Torvosaurus* individual was found in the quarry, yet included two right tibiae in their hypodigm. This means their holotype may consist of elements from more than one individual. For this reason it is best to consider the well-preserved left humerus, BYUVP 2002, as the type specimen. Further compounding the problem, it is now known that at least three individuals of this genus have been recognized in the quarry: two large individuals indistinguishable from each other, and a smaller one—possibly a juvenile. It was also indicated (Galton and Jensen, p. 4) that the holotype consists of six elements, inferring left and right pairs of all forelimb long bones had been found. However, a left radius of *Torvosaurus* is not known. It should also be noted that Galton and Jensen (1979, p. 2) show several views of a left radius. Since no left radius is known to me, it seems that reversed drawings of the right radius were used without explanation.

Pelvic Girdle

Ilium. A right ilium, BYUVP 2013 (fig. 20), was made a paratype of *Torvosaurus tanneri* by Galton and Jensen (1979). The paratype includes several other pelvic elements, a pair of pubes, and a right ischium. Unfortunately, the ilium is badly distorted dorsoventrally, making the blade appear lower than it should. Also, the ilium was substantially restored with plaster and painted. The resulting restoration gives an inaccurate representation of the true shape of the ilium in the figures of Galton and Jensen (1979, p. 3, 9, 10, and 11). For the present study the paint and plaster were removed and the repositioned portion restored to its original, but distorted position (fig. 20, A and E) makes it evident that the anterior portion of the medial blade is incomplete. Also, only the bases of the pubic and ischiac peduncles are preserved (fig. 20).

Fortunately, a *Torvosaurus* left ilium, BYUVP 4977 (fig. 21), has been collected. It is in better condition than the right ilium in that it is more nearly complete and

essentially undistorted. Only a small portion of the leading edge of the anterior blade and part of the medial surface of the pubic peduncle are missing. The two ilia are similar in size and could represent the same individual. Their relationship to each other in the quarry, however, is unknown, except that they may have been from the same general area.

Initially, the gross morphology of *Torvosaurus* ilia does not appear to differ much from those of *Allosaurus* and *Ceratosaurus*. They have, however, several significant characters distinguishing them from other Morrison Formation theropods. *Torvosaurus* ilia have a low profile with a height to length (H:L) index of 29. *Ceratosaurus* has a similarly shaped ilium body with a H:L index of approximately 28 (see Gilmore 1920). The measurements for *Ceratosaurus* were taken from Marsh's illustration of USNM 4735 (which first appeared in Gilmore 1920, plate 21) with estimates made to compensate for missing/restored portions. In contrast, *Allosaurus* ilia have a H:L index of 34 based on measurements of seven ilia. This similarity of *Torvosaurus* and *Ceratosaurus* is in general harmony with the comparisons of other elements of these genera, but I suspect the similarities are plesiomorphic and, therefore, of little phylogenetic significance. It implies, however, that the mode of locomotion in these two genera was similar, but an analysis of locomotion style is beyond the scope of this paper.

The preacetabular notch, formed by the ventral border of the anterior blade and the dorsal border of the pubic peduncle, is narrower in both *Torvosaurus* and *Ceratosaurus* than in *Allosaurus*. This notch on *Ceratosaurus* is narrower than that of *Torvosaurus*. The intersection of the anterior blade, ventral border, and pubic peduncle is simple and rounded in *Torvosaurus*. However, in *Allosaurus* the same zone of the blade is very wide, consisting of two ridges arising from the front edge of the pubic peduncle and converging to form the simple rounded ventral border of the anterior blade. The basal ridges are separated by a concave or flat surface. Twenty-three *Allosaurus* ilia, from the Cleveland-Lloyd and Dry Mesa quarries, were observed to confirm this as a diagnostic *Allosaurus* feature; none of the specimens had simple rounded intersection zones. The posterior end of the

FIGURE 14.—Torvosaurus tanneri *caudal vertebrae. Eighth caudal vertebra, BYUVP 4976a (A–E). Ninth caudal vertebra, BYUVP 4976b (F–I). Lateral (A,F), dorsal (E), ventral (B,G), anterior (C,H), and posterior (D,I) views.*

10 cm
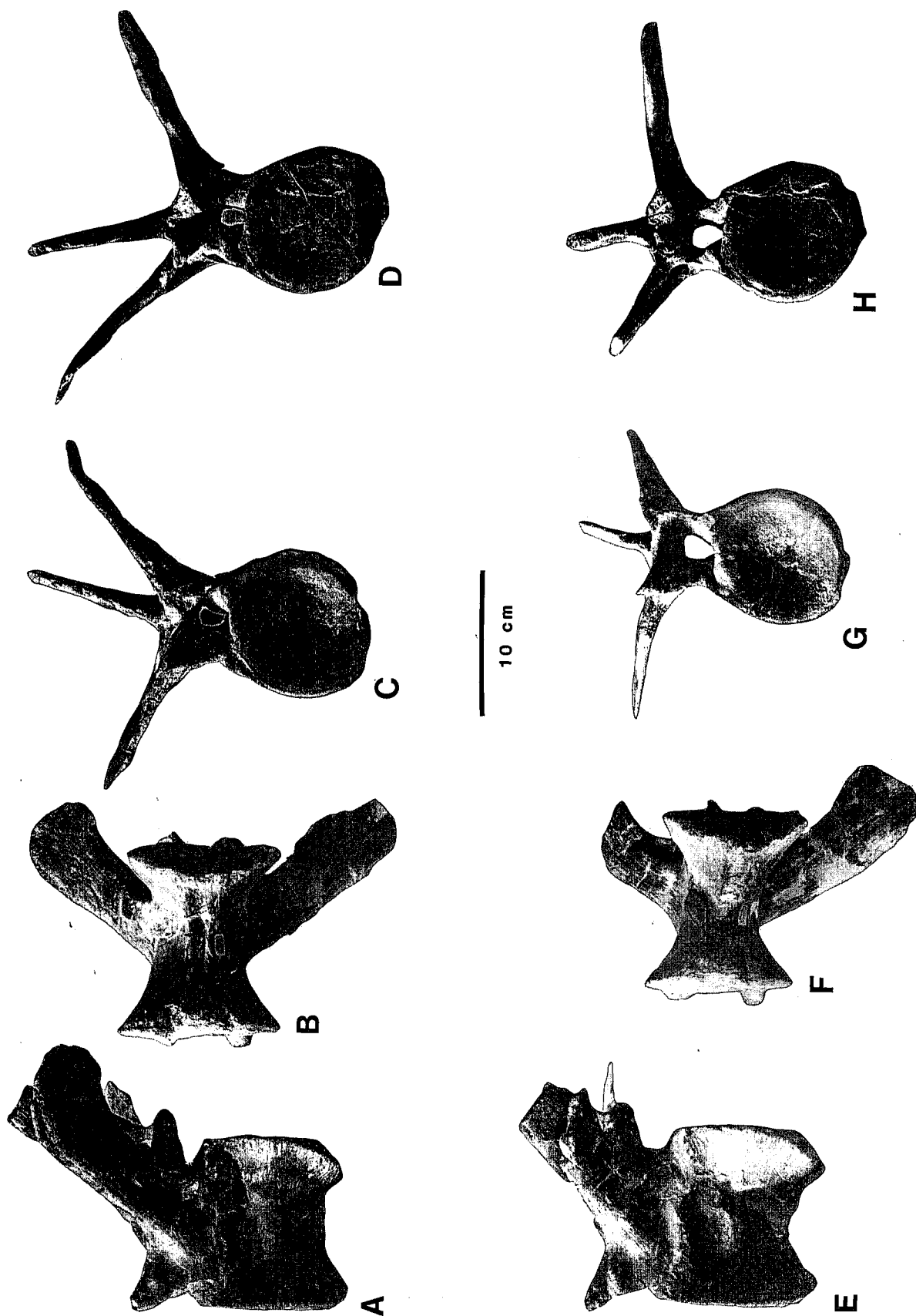
undistorted *Torvosaurus* ilia is relatively smaller in the dorsoventral direction than *Allosaurus*. The nature of the intersection of the anterior blade and pubic peduncle of *Ceratosaurus* is not readily apparent in Marsh's 1844 illustrations, but it appears to be simple and rounded, as in *Torvosaurus*.

Of the described Morrison theropods, *Torvosaurus* ilia are most similar to *Ceratosaurus* ilia, but the likelihood that the ilia identified as belonging to *Torvosaurus* could actually be misidentified *Ceratosaurus* ilia is small for several reasons. Again, the preacetabular notch of the *Ceratosaurus* is narrower than that of *Torvosaurus*. Another difference between these two genera is that the peduncles of *Ceratosaurus* are considerably longer and more slender than those of *Torvosaurus*. (Compare Gilmore 1920, plate 23, with fig. 21, A, of this paper.) Finally, considering the facts that both ilia were associated with all the other *Torvosaurus* elements and that all the *Ceratosaurus* elements recovered from the Dry Mesa Quarry are from much smaller individuals, it seems the assignment of these ilia to *Torvosaurus* is justified.

Galton and Jensen (1979, p. 7) compared *Allosaurus* and *Torvosaurus* on five iliac characters. After removing the plaster from BYUVP 2013, taking into account distortion and the discovery of the left ilium, it is apparent that only the first point, that the body of *Allosaurus* ilia are deeper and have a deeper acetabulum than *Torvosaurus*, is valid. Point two reads "(the) postacetabular process (the posterior ends of the medial and posterior blades) is squared off posteriorly with rounded corners" (words within parentheses are mine). The left ilium shows this is also true of *Torvosaurus*. Point three says the pubic peduncle of *Allosaurus* is more massive than is the case with *Torvosaurus*, which is true. However, it was also noted the pubic peduncle of *Allosaurus* has "a transverse width greater than anteriorposterior thickness." The opposite of this statement is true. Apparently this was a simple inversion of a supposed *Torvosaurus* character with that of *Allosaurus* because the distorted *Torvosaurus* ilium, BYUVP 2013, has a severely deformed pubic peduncle that matches the description given under point three. Point four notes *Allosaurus* has a "relatively weak ischiadic peduncle." With the new ilium at hand it appears

Allosaurus and *Torvosaurus* have about equally developed ischiadic peduncles. Finally, point five notes *Allosaurus* has a "narrow acetabulum and brevis shelf in ventral view." However, these features are similar on both genera. The ischiac peduncle on the left ilium is complete. In general this feature is similar to *Allosaurus*, with the medial-lateral dimension being greater than the anteroposterior dimension. The distal end is bluntly rounded to fit the matching depression on the ischium.

Though incomplete even on the good (left) *Torvosaurus* ilium, the pubic peduncle appears to have been relatively larger than that of *Allosaurus*. The articular surface of the peduncle on the left ilium is only partially preserved but exhibits moderate rugosity. A distinct ridge on the acetabular surface of the ischiac peduncle is a feature common to both *Torvosaurus* ilia. The ridge roughly parallels the long dimension of the ilia. Its function is unknown, but it may be a diagnostic feature.

The brevis shelf of the right ilium, BYUVP 2013, appears very wide (fig. 20), as noted by Galton and Jensen (1979, p. 7), but this is due to the dorsoventral shortening and resultant widening of both the acetabulum and brevis shelf. The left ilium (fig. 21) clearly shows the brevis shelf to be of the same relative width as on *Allosaurus*.

Sacral rib attachment scars are visible on the medial surface of the ilium blade, but not all are clearly defined. From the scars it is apparent that at least four sacral vertebrae attached to the ilium, and the actual count was undoubtedly five as in *Megalosaurus*, *Ceratosaurus*, and *Allosaurus*. But as is sometimes the case, not all points of transverse process and sacral rib attachment are visible on the ilium.

The *Megalosaurus* ilium figured by Owen (1856) is similar to that of *Torvosaurus*. A more detailed comparison of these genera is presented in the discussion of affinities below and will not be considered further at this point.

Pubis. A pair of *Torvosaurus* pubes, BYUVP 2014, have been figured and described in detail by Galton and Jensen (1979, figs. 2, 6 and 7). Recent observations support their description and conclusions regarding these elements, with one exception. In figure 2E of their paper, the pubes are shown in the anterior view, articulated,

FIGURE 15.—Torvosaurus tanneri *caudal vertebrae. Tenth caudal vertebra, BYUVP 4976c (A–D). Eleventh caudal vertebra, BYUVP 4976d (E–H). Lateral (A,E), ventral (B,F), anterior (C,G), and posterior (D,H) views.*
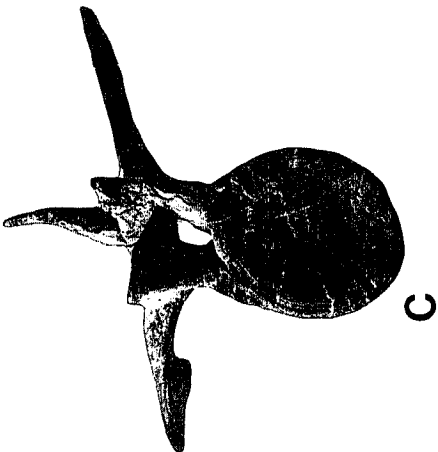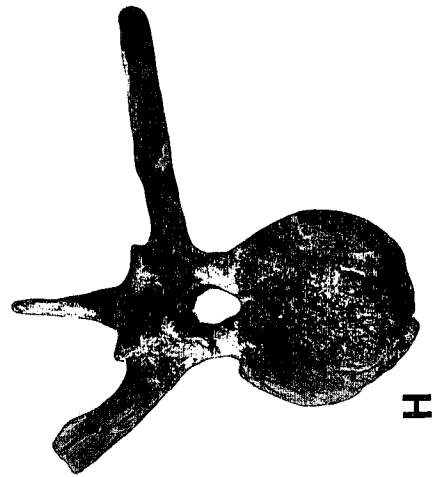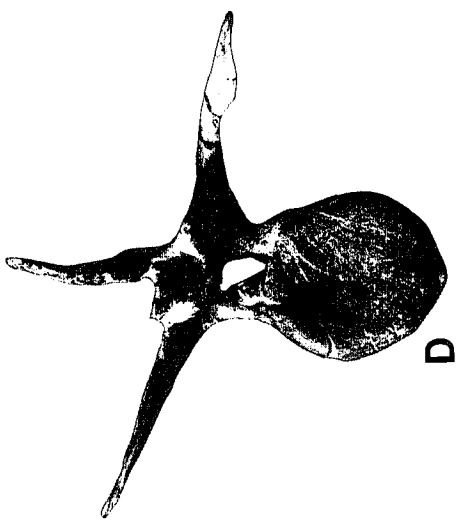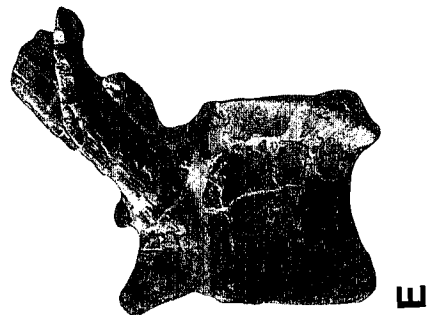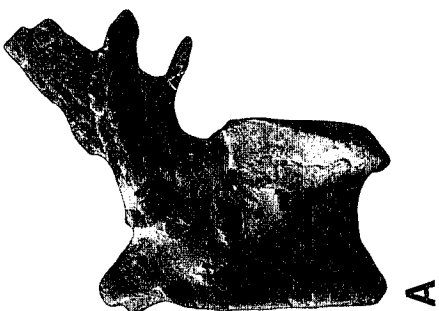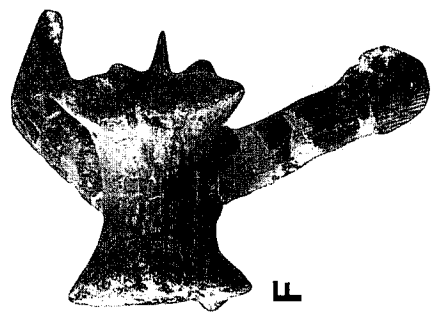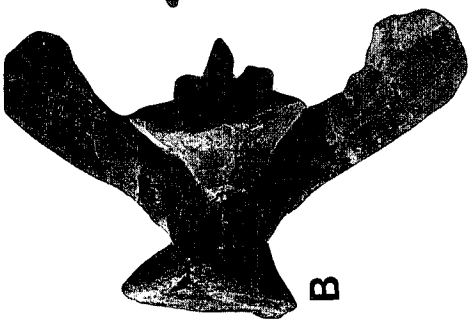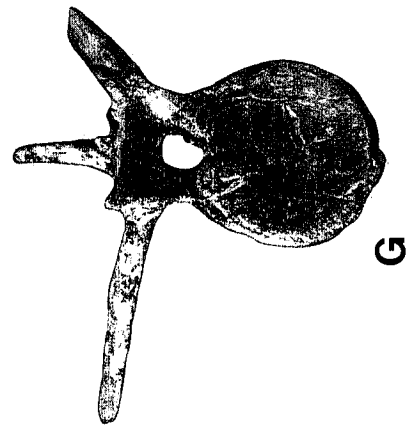
with a fenestra between the distal ends of the bones. Detailed observations of this region show no fenestra existed in life. A slight postdepositional widening of the distal ends apparently accounts for the "pseudo-fenestra."

Ischium. A right ischium, BYUVP 2015, is listed as a paratype by Galton and Jensen (1979). They also presented and illustrated the differences between *Torvosaurus* ischia and those of other saurischians. For a graphic comparison of saurischian pelvic girdles with the *Torvosaurus* pelvis, see Galton and Jensen (1979, fig. 8).

Since the publication of Galton and Jensen's (1979) paper on *Torvosaurus*, the distal half of a *Torvosaurus* left ischium, BYUVP 4881, was discovered. Though slightly distorted, it matches well the right ischium, and it is likely the two elements belong to the same individual. It appears that the other *Torvosaurus* pelvic elements also came from a single individual because they fit together so well. Despite the distortion, the distal end of the left ischium is more complete than that of the right and indicates that approximately 50 mm is missing from the distal end of BYUVP 2015. The left ischium also confirms that the distal end of *Torvosaurus* ischia are rounded when viewed laterally, and in this respect they resemble *Allosaurus*. The distal ends of *Ceratosaurus* ischia are unknown.

The shaft of the right ischium is noticeably curved, convex up, as illustrated by Galton and Jensen (1979, fig. 7), but most of this curvature may be due to postmortem deformation. The shaft of the left ischium is straight, as is true for most theropods, supporting the present claim that the right ischium shaft is distorted.

The articular surface of the iliac contact is concave with a slight, but distinct, depression posteromedially. The iliac articulation is slightly larger than the acetabular border. The ischia were in contact over most of their length along the thin medial flange and distal expansion, but were not fused. Madsen (1976b, p. 42) stated that none of the *Allosaurus* ischia from the Cleveland-Lloyd Quarry are ankylosed, and in life the ischia must have been joined by a ligament. This appears to have been true for *Torvosaurus* ischia as well.

Galton and Jensen (1979, fig. 2) illustrated the distal ends of the ischia diverging because BYUVP 2015 was used in their reconstruction of the pelvic girdle. The lateral flexure of the distal end of BYUVP 2015 is due to postdepositional deformation, and BYUVP 4881 confirms the distal ends of the ischia were closely appressed in life.

Of the known theropods, *Torvosaurus* ischia most closely resemble those of *Megalosaurus*. Unlike the ischia of *Torvosaurus*, however, the outline drawing of the *Megalosaurus* pelvis in Huene (1926), reproduced in Galton and Jensen (1979, fig. 8), shows an ischium with a distal, footlike, expansion bearing a posterior extension. The ischium figured by Owen (1856, plate 26, fig. 4), from the Stonesfield Slate of Oxfordshire, England, was probably the source illustration for Huene's (1926) ischium drawing because they are so similar. However, Huene's drawing makes the ischium appear more robust, showing a proportionately larger distal expansion and larger medial flange. The most reliable drawing of the two was the original illustration, and *Torvosaurus* ischia differ from it in several ways. The distal end of *Torvosaurus* ischia are more rounded and do not have the significant posterior protrusion that *Megalosaurus* does. Also, while *Torvosaurus* has a well-developed flange extending medially from the shaft of the ischium, *Megalosaurus* appears to have a weakly developed medial flange. Finally, *Megalosaurus* appears to have a large node on the upper surface of the middle portion of the ischium shaft, but there is no node on the shaft of *Torvosaurus*.

Megalosaurus has become somewhat of a catchall ("ragbag" according to Charig 1973) genus hosting a great assortment of reptiles, but Owen's (1856) figured ischium should probably be regarded as a co-type according to John McIntosh (personal communication 1984). Because of the confused status of the genus *Megalosaurus*, few comparisons have been made between it and *Torvosaurus* in the descriptive portion of this paper. However, a general comparison of *Megalosaurus* and *Torvosaurus* is given later in the phylogenetic section.

Hind Limb and Pes

Femur. No femur assignable to *Torvosaurus* has been found. Interestingly, the femora of *Allosaurus* and *Ceratosaurus* are very similar and are differentiated mainly

FIGURE 16.—Torvosaurus tanneri *caudal vertebrae. Twelfth caudal vertebra, BYUVP 4976e (A–D). Thirteenth caudal vertebra, BYUVP 4976f (E–H). Lateral (A,E), ventral (B,F), anterior (C,G), and posterior (D,H) views.*
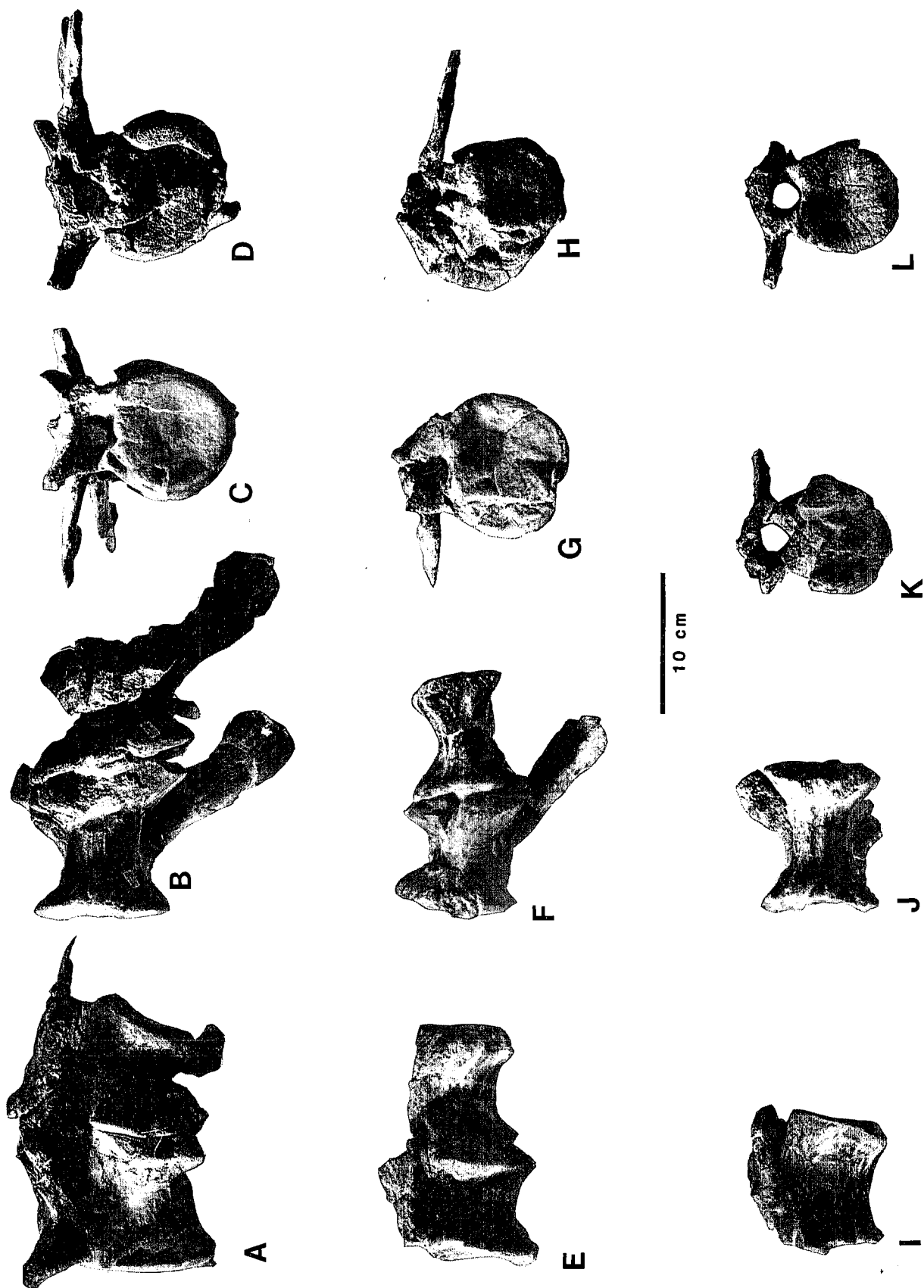
on the relative sizes of the lesser trochanters. The lessor trochanter of *Ceratosaurus* is relatively smaller than that of *Allosaurus*. It seems reasonable to assume the femur of *Torvosaurus* would have a form like that of *Ceratosaurus*, though more robust.

Tibia. Two right *Torvosaurus* tibiae were reported by Galton and Jensen (1979), and they are listed as paratypes but not figured. Jensen (1985b) neither figured nor mentioned the tibiae. Both tibiae are in excellent condition and about the same size. BYUVP 2016 (fig. 22) is complete, but BYUVP 2017 (not figured), the larger of the two specimens, is incomplete and consists of only the distal two-thirds of the bone.

Galton and Jensen (1979) designated four right elements as BYU 2016: a tibia, fibula, astragalus, and calcaneum. None of these elements were found articulated, although they may have been associated. To more accurately reflect the uncertain relationship of these elements, all but one of them have been recataloged. Since a right *Torvosaurus* tibia was the first specimen they mentioned that bears the BYUVP 2016 catalog number, this assignment shall remain unchanged. The other paratypes originally included in BYUVP 2016 have been recataloged as *Torvosaurus*: right fibula = BYUVP 9620, right astragalus = BYUVP 5029, and right calcaneum = BYUVP 9622.

Torvosaurus tibiae are robust with a circumference:length index of 45 for BYUVP 2016 and an estimated 47 for BYUVP 2017. The same index for *Allosaurus* averages 34 and for *Ceratosaurus* is 37 to 38, based on UUVP 5681 and 5682, according to Madsen (1976b, p. 44). (The circumference used in these calculations are the minimum circumference, which in the case of these tibiae happens to be at midshaft.)

The stocky shaft of the tibia is curved very slightly posterolaterally. The lower half of the anterolateral surface of the shaft is flattened where it contacted the fibula. The long, low fibular ridge is located high on the shaft, and the most proximal portion of the ridge extends almost to the proximal articular surface of the tibia. The proximal articular surface is slightly depressed in the middle.

The cnemial crest is robust (fig. 22, A and C), even more so than in *Allosaurus*. A very shallow groove occurs immediately lateral to the crest, whereas in *Allosaurus* and *Ceratosaurus* the same groove is deeper and better defined. The posterior notch of the proximal articular surface is narrow and continues down onto the shaft as a shallow but distinct channel (fig. 22, B and E). *Allosaurus* exhibits no similar channel. Also, the proximal articular surface is wider and more massive in *Torvosaurus* than *Allosaurus*.

Distally the tibia flares lateromedially (fig. 22, A). The broad lateral flange receives the astragalus, and a ridge marks the dorsomedial contact of the astragalus. This ridge slopes medially at about 35° from the shaft's long axis. The angle of the same ridge on *Ceratosaurus* is nearly identical, but on *Allosaurus* it is much greater, being approximately 55°. This feature alone is sufficient to differentiate tibiae of *Torvosaurus* and *Ceratosaurus* from those belonging to *Allosaurus*. In ventral view (fig. 22, F), the distal articular surface of the tibia is roughly wedge-shaped, with the apex of the wedge pointing laterally. This surface is considerably more rounded on the medial portion than are *Allosaurus* tibiae.

Fibula. There are three *Torvosaurus* fibulae in the Dry Mesa collection: two right, BYUVP 9620 (fig. 23, A–D), formerly cataloged as BYU 2016 and BYUVP 5136; and one left, BYUVP 5129. BYUVP 9620 was listed as a paratype by Galton and Jensen (1979) but was neither figured nor described. Both BYUVP 9620 and BYUVP 5136 are complete. BYUVP 5136 is badly distorted due to postdepositional deformation. James Jensen (personal communication 1985) stated BYUVP 9620 was found near, and parallel to, a *Torvosaurus* tibia, BYUVP 2016, but they were not in articulation.

Torvosaurus fibulae are significantly more robust than those of any other known theropod from the Morrison Formation. The average index of minimum circumference (= circumference at midshaft): length is about 20. The proximal end is approximately three times as wide as the shaft (fig. 23, A and D) in the anteroposterior direction. The circumference of the shaft is essentially constant

FIGURE 17.—Torvosaurus tanneri *caudal vertebrae. Fourteenth and fifteenth caudal vertebrae, BYUVP 4976g and 4976h (A–D). Sixteenth and seventeenth caudal vertebrae, BYUVP 4976i and 4976j (E–H). Eighteenth caudal vertebra, BYUVP 4976k (I–L). Lateral (A,E,I), ventral (B,F,J), anterior (C,G,K), and posterior (D,H,L) views.*
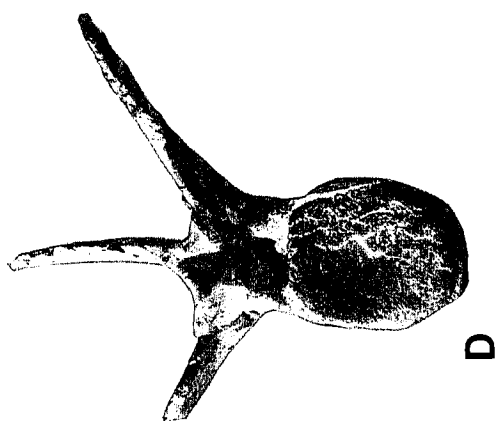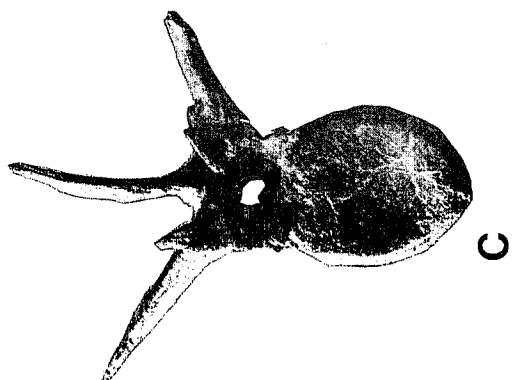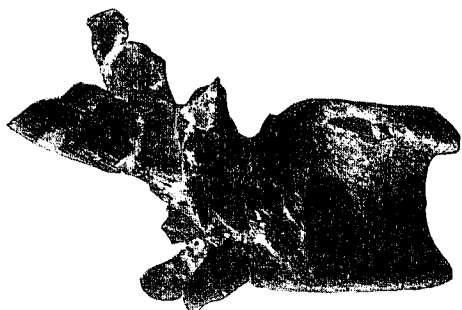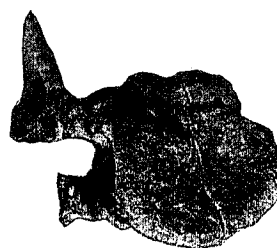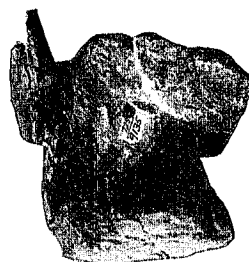
below the expanded proximal end and above the distal end. The distal end is slightly expanded but is not much broader than the shaft (fig. 23, A and C).

The distal end is ellipsoidal in outline (fig. 23, C), being shaped like a high camber airfoil. The lateral surface is strongly convex, the thickest portion being near the middle of its proximal-distal length, and the medial surface is slightly convex. The proximal-distal length: medial-lateral width index is a useful comparison aid. This index for all three *Torvosaurus* fibulae is about 22. The same index for *Allosaurus* ranges from 13 in small individuals to 16 in large individuals, as determined for all Cleveland-Lloyd allosaur fibulae in the Brigham Young University collection. The indices for the Cleveland-Lloyd *Ceratosaurus* are 50 and 52.

Astragalus. A right astragalus was listed as a paratype by Galton and Jensen (1979). Originally numbered BYU 2016, it was briefly described, but not figured, nor was it figured later by Jensen (1985b). Because it was not articulated with the other elements originally assigned this specimen number, it has been recataloged as BYUVP 5029. An additional right *Torvosaurus* astragalus, BYUVP 9621 (fig. 23, I–N), has recently been discovered.

The first described *Torvosaurus* astragalus, BYUVP 5029, has a height:breadth (H:B) index of 68, while the recently discovered astragalus, BYUVP 9621, has an index of 81. Madsen (1976b, p. 45) noted the H:B index for *Allosaurus fragilis* ranges from 100 in juveniles to 85 in old individuals. In the same paper Madsen listed the H:B index of two *Ceratosaurus* astragali from the Cleveland-Lloyd Quarry, UUVP 5682 and 5681, as 74 and 71, respectively. Therefore, the astragali of *Torvosaurus* can probably be easily differentiated from *Allosaurus* but not from *Ceratosaurus* on the basis of the height/breadth index.

The ascending process of the two *Torvosaurus* astragali have slightly different orientations. Some of the differences are due to individual variation but most, as is apparent when articulating astragalus BYUVP 5029 with its (?)matching tibia, BYUVP 2016, was caused by post-burial deformation. In anterior view, the ascending process has a distinct lateral cant (fig. 23, J). The same process

in *Allosaurus* is nearly vertical. The lateral edge of the ascending process is either nearly vertical or slightly laterally reclined, and the medial edge of the process slopes laterally at a low angle. The ascending process is about 20 mm thick, much thicker than the same process of a large *Allosaurus,* which is about 10 mm thick. The dorsal tip of the process is bluntly rounded and has an expanded fibular contact on its lateral edge.

In anterior or posterior view the ventral border of the *Torvosaurus* astragali is less concave than that on *Allosaurus* astragali, and in this respect they resemble *Ceratosaurus* astragali. The calcaneum sulcus (fig. 23, K) is simply a slight indentation, quite unlike the deep calcaneum notch of *Allosaurus.* The lower horizontal groove (fig. 23, J), in the sense of Welles (1984), is shallower than the same groove of *Allosaurus.* While these features allow the astragali of these genera to be differentiated from each other, no explanation is offered here to account for the differences.

In posterior view (fig. 23, L), a ridge runs parallel to, and slightly inset from, the medial edge of the ascending process. A deep, vertically elongate pit is located at the base of the tibial surface of the ascending process. Pits in the same location on *Allosaurus* are characteristically round, and Madsen (1976b, p. 44) considers this a diagnostic feature. It seems that no one has addressed the function of these pits in the literature.

In lateral aspect (fig. 23, K), the fibular sulcus is shallow and broad. *Allosaurus* has a deep and narrow fibular sulcus. The nature of the same sulcus of *Ceratosaurus* has never been described because the tarsal elements of all known specimens are fused to the tibia, preventing close comparison. The posterior edge of *Torvosaurus* astragali (fig. 23, K and N) do not curve up around the posterior surface of the tibia nearly as much as in *Allosaurus.*

Calcaneum. Two *Torvosaurus* calcanea have been recovered from the Dry Mesa Quarry. A right calcaneum, BYUVP 9622, formerly cataloged as BYU 2016, was listed as a *Torvosaurus* paratype by Galton and Jensen (1979). It fits well onto astragalus BYUVP 9621, which in turn articulates with tibia BYUVP 2017. All are probably from the same individual. Recently, a left calcaneum, BYUVP

FIGURE 18.—Torvosaurus tanneri *caudal vertebrae. Twelfth caudal vertebra of small individual, BYUVP 9013 (A–D). ?Twenty-second caudal vertebra, BYUVP 9135 (E–H). Lateral (A,E), ventral (B,F), anterior (C,G), and posterior (D,H) views.*
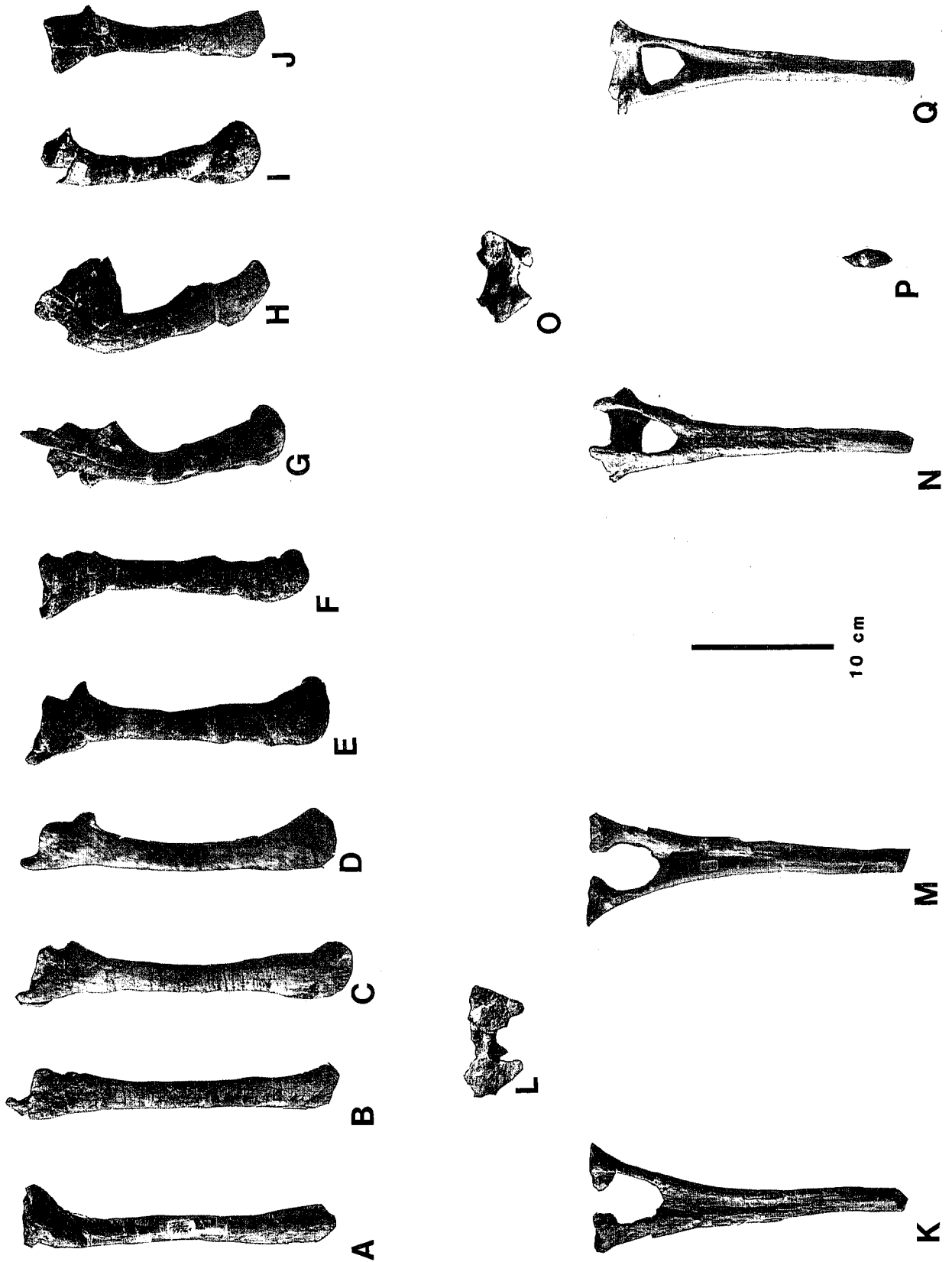
5020 (fig. 23, E–H), was prepared. It is slightly smaller than BYUVP 9622, but could easily have come from one of the individuals represented by either of the *Torvosaurus* tibiae.

In lateral view (fig. 23, H), the calcanea are roughly triangular in shape with a slightly concave surface. The margin of this concave surface is encompassed by a low ridge. In the same view, the dorsolateral border, which is the lateral expression of the fibular contact, is essentially a straight line.

In medial view (fig. 23, F), the calcanea are blocky with no large flange to contact the lateral margin of the fibula as in *Allosaurus*. The fibular contact (fig. 23, E) is broad and shallowly concave. The morphology of their nonarticular surfaces is more similar to that on *Ceratosaurus* calcanea except that the dorsolateral border on *Ceratosaurus* is distinctly concave.

Metatarsals. A total of nineteen metatarsals of medium to large theropods from the Dry Mesa Quarry have been discovered. Of the nineteen, twelve are assignable to *Torvosaurus*, two are assignable to a very large *Allosaurus*, and two to *Ceratosaurus*. I can offer no explanation for the preponderance of *Torvosaurus* metatarsals except that their large size alone would increase their preservation potential.

Four examples of *Torvosaurus* metatarsal II are in the Dry Mesa collection: two left, BYUVP 5147 (fig. 24, G–L) and 5281, and two right, BYUVP 5077 and 5276. The shafts are straight with subequal expansion of lateral and medial surfaces on the distal end, the lateral side being slightly more prominent. The same elements of *Ceratosaurus* and *Allosaurus* differ from *Torvosaurus* because the distal portion of the shafts are noticeably angled mesially. This, along with the unconstricted proximal end of metatarsal III and the very slightly deflected distal end of metatarsal IV, indicates the metatarsals of *Torvosaurus* were oriented with their shafts essentially parallel in life, radiating distally only slightly. Unlike *Ceratosaurus* and *Allosaurus* there are no deep pits at the point of origin of the collateral ligaments, but there are moderately deep, broad concavities. The distal end of this bone is broader than that of *Allosaurus*, but similar to that of *Ceratosau-*

rus. Likewise, the proximal articular surface (fig. 24, K), viewed end on, is more similar to *Ceratosaurus*, by virtue of the nearly flat medial surface and simple convex lateral surface, than *Allosaurus*.

Five examples of *Torvosaurus* metatarsal III have been collected: three left, BYUVP 5005, 5241, and 5280 (fig. 24, A–F), and two right, BYUVP 5009 and 5277. Based on the number of left metatarsal III, the minimum number of *Torvosaurus* individuals represented in the quarry is three. Like the *Torvosaurus* tibiae, these metatarsals indicate the presence of two large individuals of the same size but, additionally, one of the metatarsals, BYUVP 5005, is from a slightly smaller individual.

Torvosaurus metatarsal III has a thick, nearly straight shaft (fig. 24, A) and lacks deep lateral pits (fig. 24, C and D). The proximal end of metatarsal III (fig. 24, E) has a flatter dorsal surface, a more angular indentation on its lateral surface (which is the contact for metatarsal IV), and a flatter medial surface than *Allosaurus* (Madsen 1976b, p. 48). The overall design of this end of the bone is more similar to the latter genus than *Ceratosaurus*, which has a much more trapezoidlike outline illustrated by Gilmore (1920, plate 24).

The distal articular surface of metatarsal III (fig. 24, F) is broader and has a less pronounced inverted, obtuse V-shaped ventral surface than *Allosaurus*. The ventral surface of the distal end of *Ceratosaurus* is a concave arch rather than an inverted V like that of *Allosaurus* or *Torvosaurus*. The dorsoposterior margin of the cartilage-bearing articular surface of both *Torvosaurus* (fig. 24, D) and *Ceratosaurus* is located significantly higher above the dorsal surface of the shaft than is the case with *Allosaurus*.

Three *Torvosaurus* metatarsals of the fourth digit, two left, BYUVP 5279 and 8966, and one right, BYUVP 5278 (fig. 24, M–R), are present in the Dry Mesa collection. Like all *Torvosaurus* metatarsals, they are readily distinguished from *Allosaurus* and *Ceratosaurus* by their stockiness and their relatively straight shafts. The proximal end lacks the prominent, ventrally pointing medial process found on *Allosaurus* metatarsal IV. The proximal end of the same element on *Ceratosaurus* is much more rectangular in outline than either *Torvosaurus* or *Allosaurus*.

FIGURE 19.—Torvosaurus tanneri *chevrons. These chevrons were articulated with the posterior end of the eighth (A,K–M), ninth (B), tenth (C,N–Q), eleventh (D), twelfth (E), thirteenth (F), fourteenth (G), fifteenth (H), sixteenth (I), and seventeenth (J) caudal vertebrae, BYUVP 4976a–j, respectively. Lateral (A–J), anterior (K,N), posterior (M,Q), proximal (L,O), and distal (P) views.*

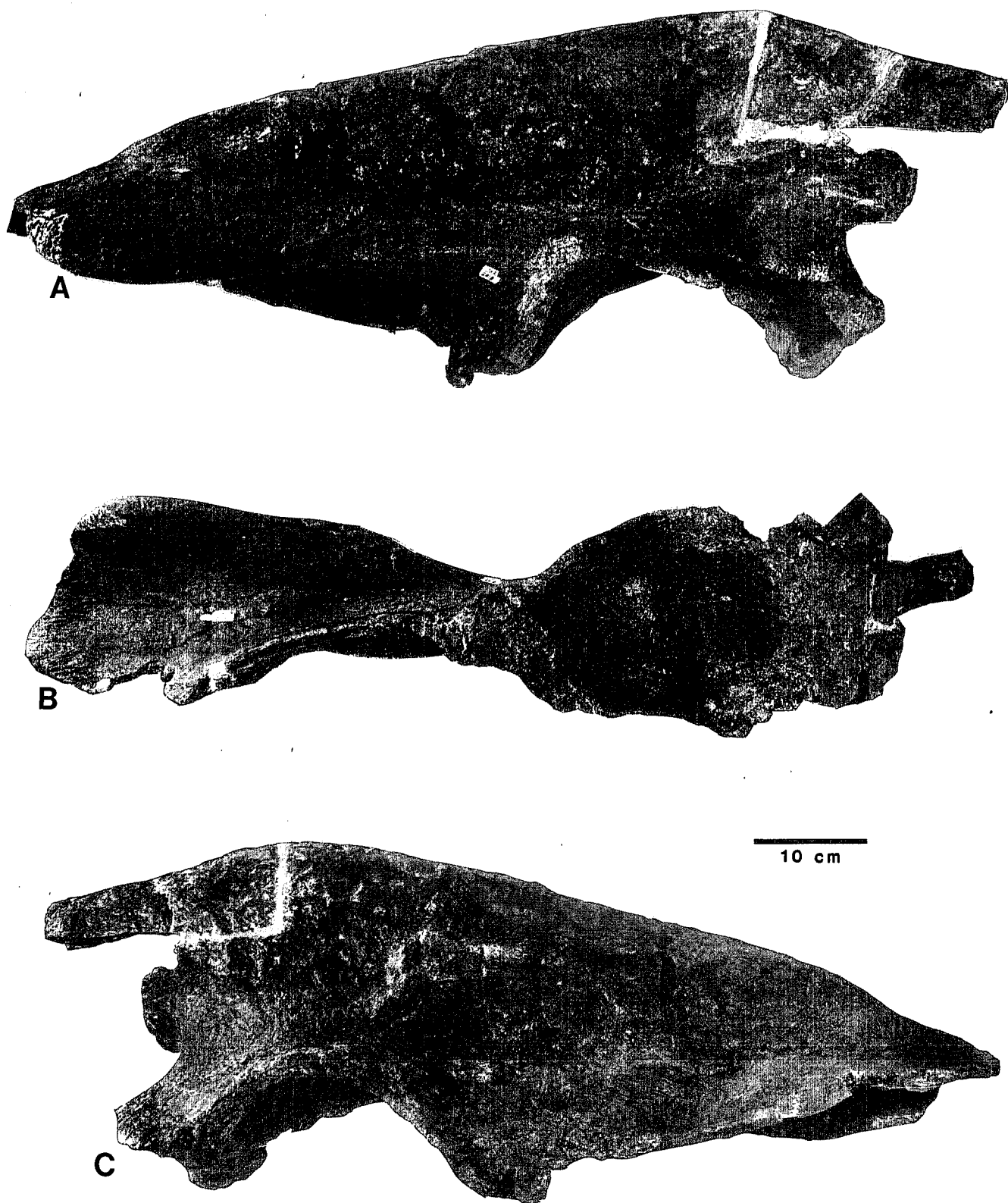FIGURE 20.—Torvosaurus tanneri *right ilium, BYUVP 2013 (A–C). Lateral (A), medial (C), and ventral (B) views.*
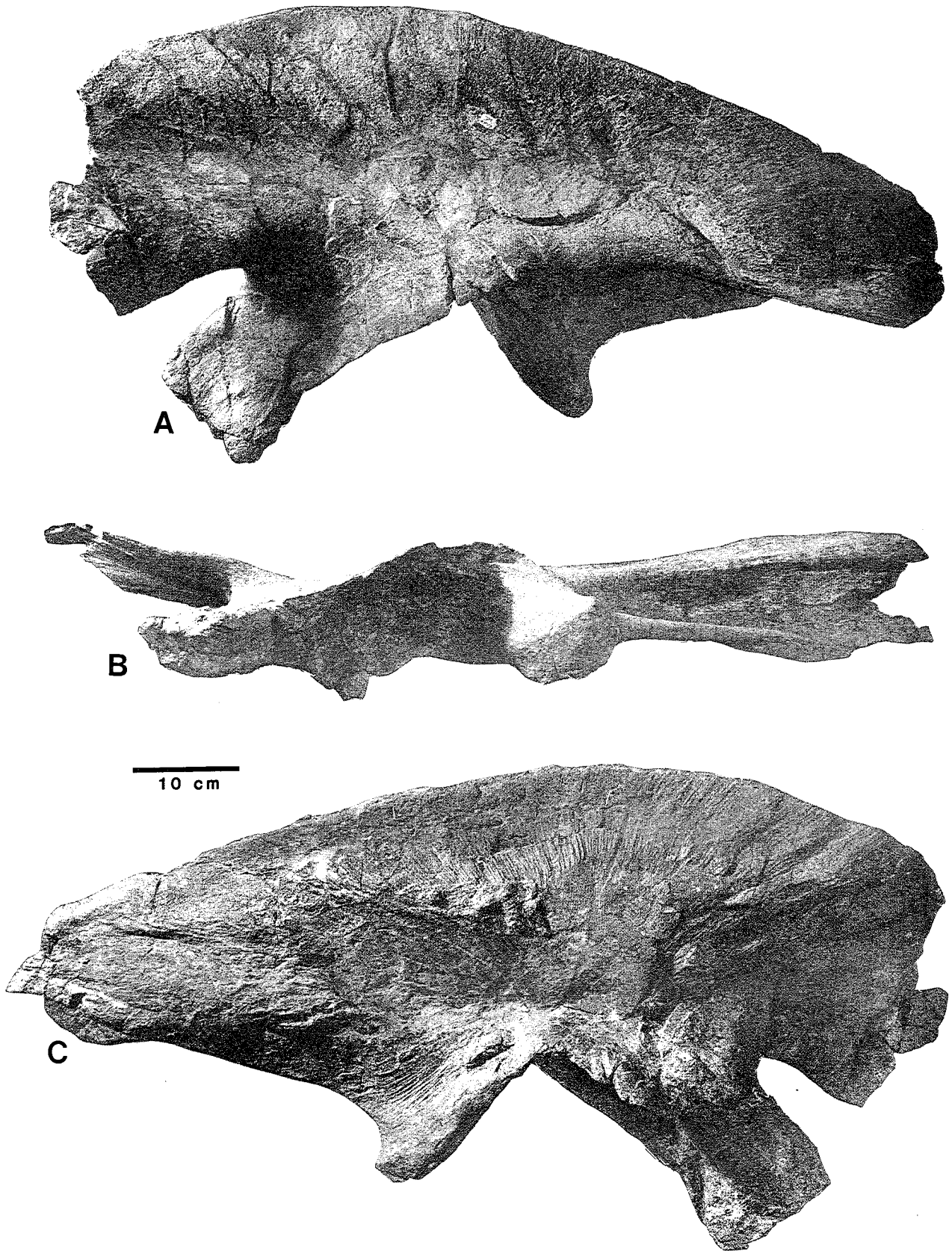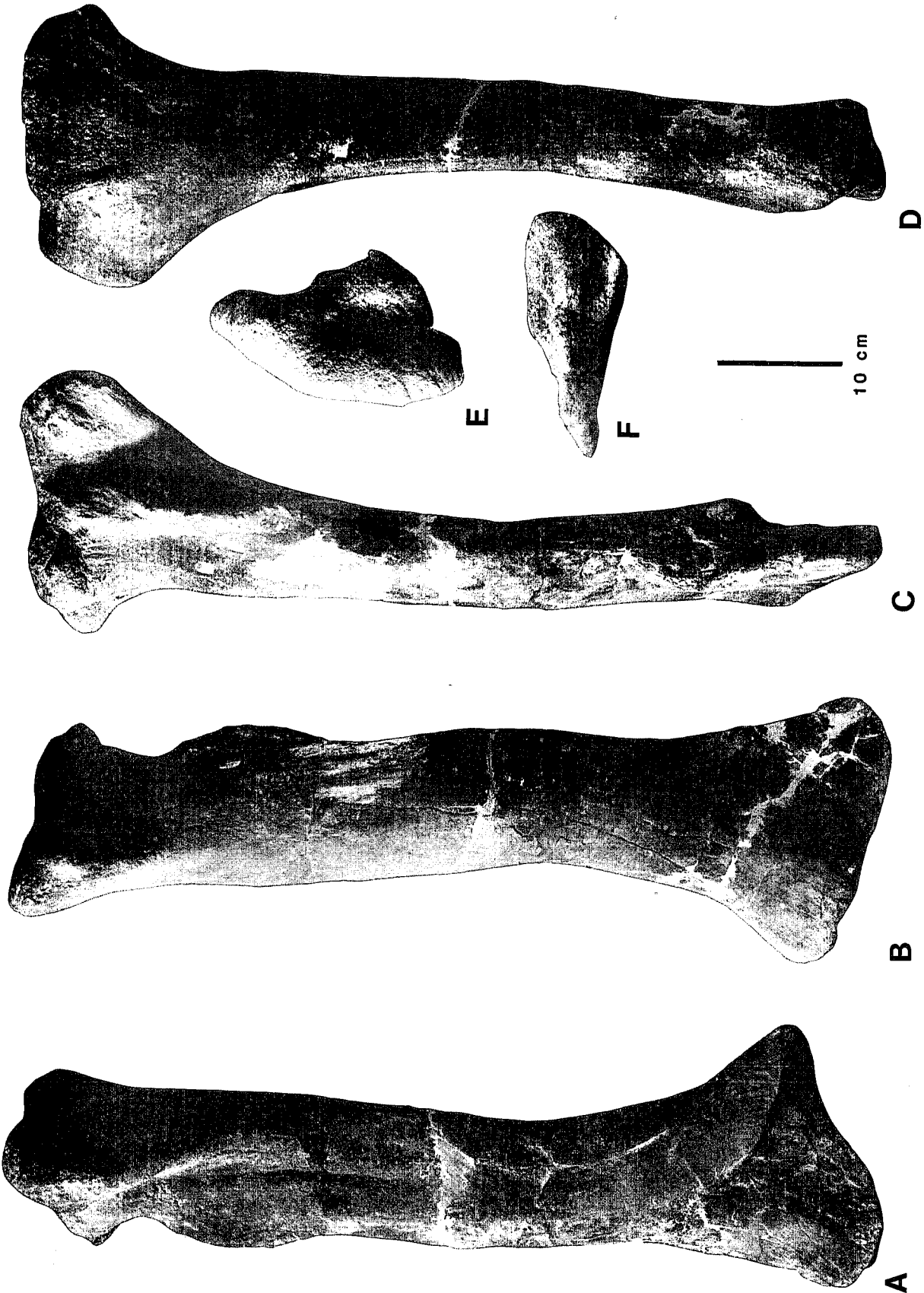
FIGURE 21.—Torvosaurus tanneri *left ilium, BYUVP 4977 (A–C). Lateral (A), medial (C), and ventral (B) views.*

The distal end of this element in *Torvosaurus* (fig. 24, R) is noticeably lower in height, and the inverted V-shaped outline on the ventral surface of the same end is more obtuse than either *Allosaurus* or *Ceratosaurus*. No collateral ligament pit is present, but there is a broad fossa on the medial surface of the distal end (fig. 24, O).

DISCUSSION

The phylogenetic history of *Torvosaurus* is not well understood at present. Nevertheless, it seems *Torvosaurus* is closely related to *Megalosaurus bucklandi*. As originally suggested by Galton and Jensen (1979), *Torvosaurus* belongs in the Megalosauridae. However, Paul's (1984) statement that *Torvosaurus*, *Poikilopleuron*, and *Megalosaurus* are congeneric is in error. For, though *Poekilopleuron* and *Torvosaurus* are vaguely similar, they are clearly separate taxa. For example, *Torvosaurus* differs significantly from *Poekilopleuron* in the form of the humerus, radius, and ulna as noted in Galton and Jensen (1979, p. 4), as do the other major elements known for *Poekilopleuron* (i.e., tibia, fibula, astragalus, caudal vertebrae, and chevrons; compare figs. 24, 25, 15–20, and 21 with Eudes-Deslongchamps 1838, plates 6, 7, and 2). No skull material of *Poekilopleuron* has been described. Since essentially all the conjunct postcranial elements of these two genera differ, it is clear that *Torvosaurus* and *Poekilopleuron* are not assignable to the same genus.

The only elements that positively belong to the ubiquitous *Megalosaurus* are those collected from the original locality in the Stonesfield Slate of Oxfordshire, England. The type of *Megalosaurus* is the anterior half of a dentary figured on plate 33 by Owen (1856). The other elements collected from the same locality are: a partial dentary (Owen 1856, plate 34), a right ilium, a set of sacral vertebrae, and a partial right ischium. These should be regarded as co-types, according to John S. McIntosh (personal communication 1984).

The ilium of *Megalosaurus* is similar to that of *Torvosaurus*, with height to length indices of 27 and 28, respectively. The *Megalosaurus* ischium is also similar to that of *Torvosaurus* but is more robust and has a sharper ventral

deflection at midshaft. The dentary of *Megalosaurus* has a straight ventral margin, a pronounced Meckelian groove, and has a height:length index of 34 for the first 9 alveoli, assuming the presence of 11 alveoli. In contrast, the dentary of *Torvosaurus* has a curved ventral margin and shows no apparent evidence of the groove, indicating it must have been extremely shallow on the distal half of the bone, and has a height:length ratio of 37 (using the total preserved length, which contains nine complete alveoli).

The overall similarity of these three elements of *Torvosaurus* and *Megalosaurus* are here interpreted as being indicative of a close phylogenetic relationship. There is a remote possibility that these two genera are indeed congeneric as Paul (1984) thought, but they differ significantly from *Poekilopleuron*. Unfortunately, a more thorough comparison of *Torvosaurus* with *Megalosaurus* is not possible because the holotype of the latter consists of so few elements and a direct comparison is not possible at this time. Through the years a large number of specimens have been referred to *Megalosaurus*, however, making it a "catch all" genus for many fragmentary European theropods (Charig 1973, Romer 1966). An extensive comparison of the European megalosaurs would prove very enlightening, especially with the data now available on the osteology of *Torvosaurus*.

The middle Jurassic, Chinese theropod *Xuanhanosaurus qilixiaensis* described by Dong (1984) also appears to be a true megalosaur. It is incompletely illustrated, but the figure of its cervical vertebra shows that it has a strongly keeled venter, like some of the cervical, and nearly all of the dorsal, vertebrae of *Torvosaurus*. Also, like *Torvosaurus* and other megalosaurids, it has a straight-shafted humerus. Like *Ceratosaurus*, however, its elements are more slender than those of *Torvosaurus*.

Jensen (1985b) proposed a monogeneric family, Torvosauridae, for *Torvosaurus*, but this is probably unwarranted because the genus shares so many characters with *Megalosaurus* and thus should be considered a member of Megalosauridae. The Torvosauridae was defined by Jensen so as to contain all genera with the following characters: short skull; very short forelimbs; lachrymal with the anterior and ventral processes separated by 90°;

FIGURE 22.—Torvosaurus tanneri *right tibia, BYUVP 2016 (A–F). Anterior (A), posterior (B), lateral (C), medial (D), proximal (E), and distal (F) views.*
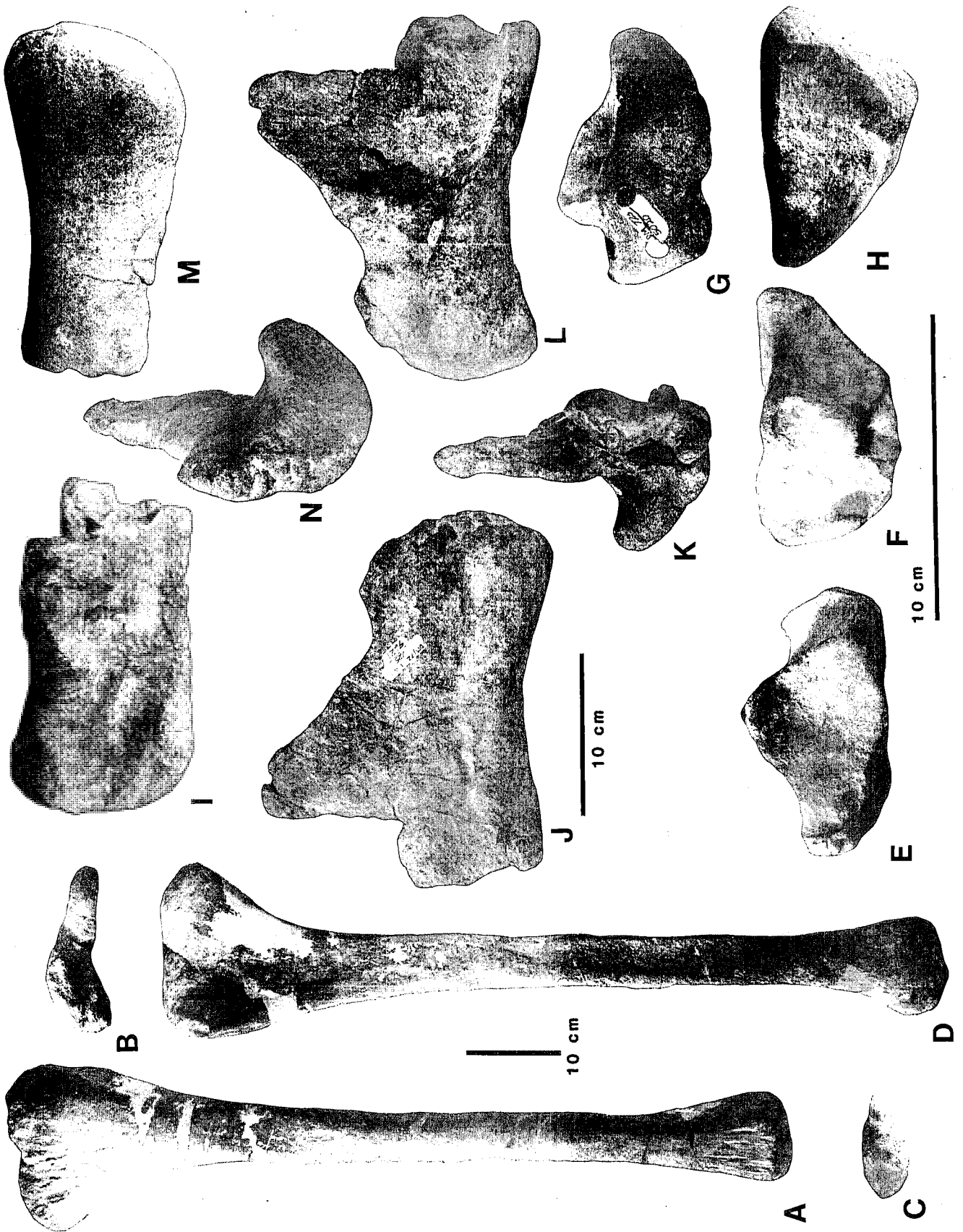
dolichoiliac ilium, brachyiliac pubis, and ischium each with a continuous median symphysis; and pubis with closed obturator foramen and small distal expansion. The problems with basing the family on these characters are: the skull of *Torvosaurus* is relatively long, not short; the forelimbs are stout but not small in relation to the size of the animal, and they are the same size in relation to the body as in *Poekilopleuron* as noted by Galton and Jensen (1979); the combined dolichoiliac/brachyiliac type pelvis is also found on *Megalosaurus* (Galton and Jensen 1979, Huene 1926, Owen 1856); a closed obturator foramen is a primitive character also found on *Ceratosaurus* (Gilmore 1920), *Megalosaurus* (Huene 1926), *Piatnitzkysaurus*, a primitive allosaurid (Bonaparte 1986), as well as primitive theropods in general (Romer 1956); and, finally, a small distal expansion on the pubis is found on *Plateosaurus*, *Coelophysis*, *Megalosaurus*, and *Eustreptospondylus*, not just *Torvosaurus*.

Torvosaurus is similar to *Ceratosaurus*, both in the form of some skull elements and ilium as noted in the descriptions of these skeletal members of *Torvosaurus*. However, I suspect, but cannot verify, that the characters they share are symplesiomorphic and therefore are not indicative of a close relationship. *Ceratosaurus* is frequently placed in the Megalosauridae (Dodson and others 1980, Ostrom and McIntosh 1966, Romer 1966). In this regard it is interesting to note that Cope (1892) wrote that *Ceratosaurus* is probably the same genus as *Megalosaurus* and that they differ only at the specific level. Other authors, however, have placed *Ceratosaurus* in its own family, the Ceratosauridae (Gilmore 1920, Marsh 1884, Olshevsky 1978, Russell 1984), a scheme I agree with because of the unusual nature of the vertebrae. Gauthier (1986, p. 9) proposed a new combination of the taxon Ceratosauria to encompass the late Triassic to late Jurassic theropods *Ceratosaurus*, *Syntarsus*, *Coelophysis*, *Segisaurus*, *Sarcosaurus*, and *Dilophosaurus*. However, he tentatively placed "megalosaurs" in his new combination of the Carnosauria because of a lack of data. The similarity of *Ceratosaurus*, *Megalosaurus*, and *Torvosaurus* as demonstrated in this paper indicate that the latter genera fall within Gauthier's definition of Ceratosauria.

Genus *Ceratosaurus ?nasicornis* Marsh 1884

DESCRIPTION

Six dorsal vertebrae, seventeen caudal vertebrae, and two metatarsals found in the Dry Mesa Quarry are referred, and tentatively referred, to *Ceratosaurus* as noted below.

Dorsal Vertebrae

Six dorsal vertebrae found in the Dry Mesa Quarry collection are referred to *Ceratosaurus*. Two of them, BYUVP 4951 and 4952 (fig. 25), have most of their neural arches intact and were found closely associated with each other. The remaining *Ceratosaurus* dorsal vertebrae (BYUVP 8907, 9143, 9142, and 9144) consist of centra only and are not figured. All these dorsal vertebrae may be from the same individual because the centra are similar in length, ranging from 83 to 96 mm long. However, the possibility that these vertebrae are from two or more individuals of the same size cannot be ruled out, in part because of a lack of information about their relative positions in the quarry. One of the centra, BYUVP 9144, is highly distorted and is only 70 mm long; the "shortness" is obviously due to postdepositional anterior-posterior compression.

It is extremely difficult to determine the exact position of dorsal vertebrae that consist of centra only. However, because they do not bear parapophyses, they must be from the middle or posterior region of the dorsal series. BYUVP 4951 and 4952 are clearly posterior dorsals. Unfortunately, their exact positions cannot be judged with accuracy because this genus is incompletely known.

The centra and neural arches are extremely hollow, the centra walls being about 5 mm thick. The walls of the neural arch vary in thickness and in some places are less than 0.5 mm thick. Such thin-walled bone is generally considered to be a characteristic of the infraorder Coelurosauria and is one of the features that led Romer (1956) to speculate that *Ceratosaurus* was from coelurosaurian stock. All these centra have fine striae on the inner surface of the centrum flanges. The posterior dorsal vertebrae

FIGURE 23.—Torvosaurus tanneri *right fibula, BYUVP 9620 (A–D). Right astragalus, BYUVP 9621 (I–N). Right calcaneum, BYUVP 5020, (E–H). Anterior (J), lateral (A,H,K), medial (D,F,N), proximal (B,E I), and distal (C,G,M) views.*
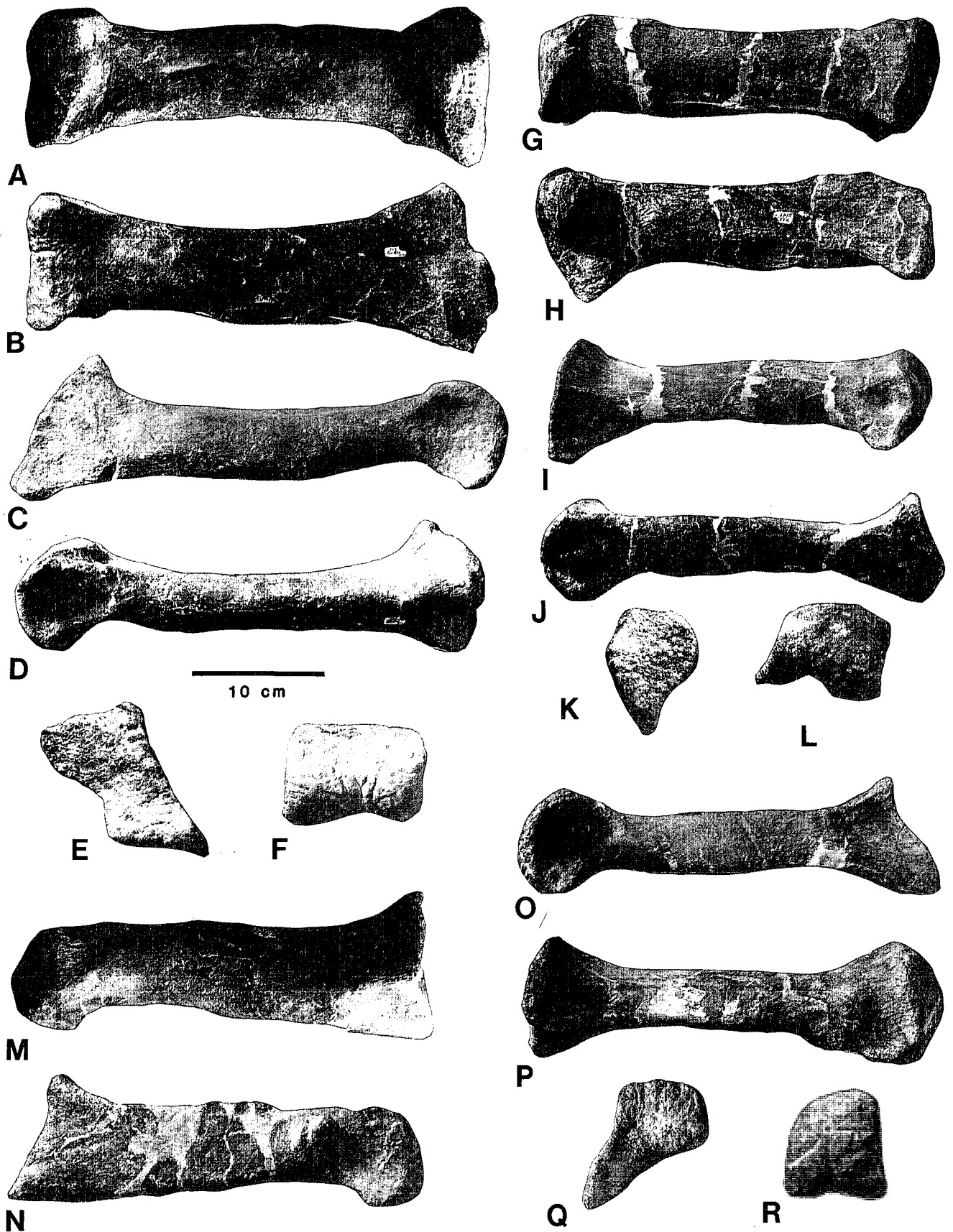
FIGURE 24.—Torvosaurus tanneri *left metatarsals II, BYUVP 5147 (G–L); III, BYUVP 5280 (A–F); and IV, BYUVP 5278 (M–R). Dorsal (A,G,M), ventral (B,H,N), medial (C,I,O), lateral (D,J,P), proximal (E,K,Q), and distal (F,L,R) views.*
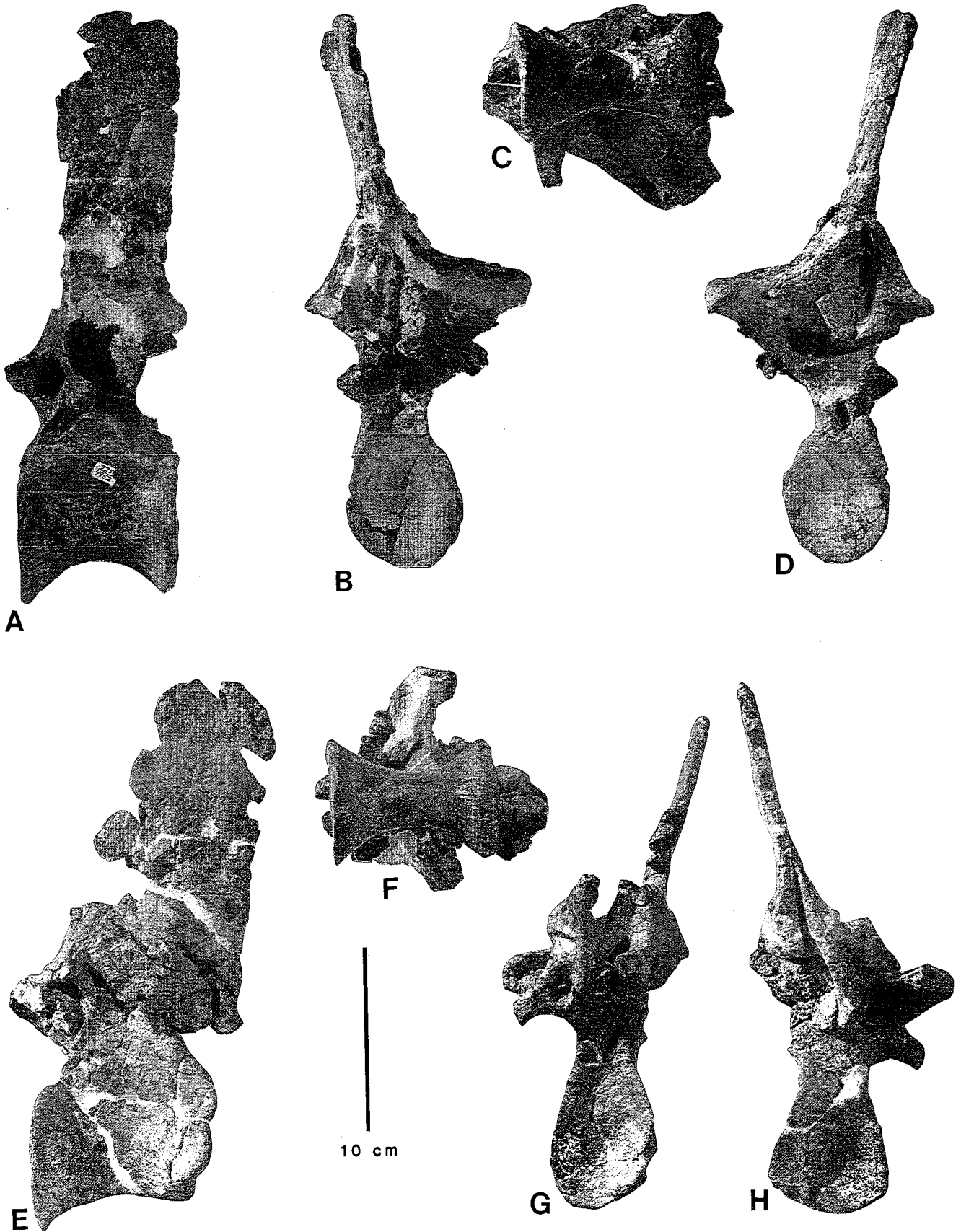
FIGURE 25.—Ceratosaurus ?nasicornis, *BYUVP 4952 (A–D) and BYUVP 4951 (E–D). Lateral (A,E), ventral (C,F), anterior (B,G), and posterior (D,H) views.*

bore hyposphenes in life, as evidenced by the presence of hypantra, but the hyposphenes themselves are missing on both specimens.

Ceratosaurus characteristics evident on these vertebrae are:

(1) parapophyses borne on long, slender stalks (Gilmore 1920, p. 97);

(2) hollow centrum (Madsen 1976b, p. 49, fig. 26);

(3) tall neural spine (Gilmore 1920, p. 97);

(4) simple, spool-shaped centrum (this paper);

(5) centrum longer than high (this paper);

(6) ends of centrum not flangelike (Gilmore 1920, p. 96);

(7) articular surfaces of centrum moderately amphicoeleous (Marsh 1884);

(8) extremely thin bone on the basal neural arch and centrum (this paper); and,

(9) they are of a gracile build.

Because of their size (particularly the length to height aspect), morphology, and preservation, it is likely these dorsal vertebrae belong to the same individual as the group of 15 caudal vertebrae assigned to *Ceratosaurus* below.

Caudal Vertebrae

The anterior caudal vertebra, BYUVP 4853, is identified as *Ceratosaurus* because it has a well-developed hyposphene with a small "accessory" hyposphene developed below it, and strongly backswept transverse processes. It also has a well-developed anteroposteriorly oriented ridge on the proximal dorsal surface of the transverse process, a definitive *Ceratosaurus* character (Madsen personal communication 1986). A more posterior, but still pretransitional caudal vertebra, BYUVP 8910, is recognized as *Ceratosaurus* because of the narrow, but deep, groove on the venter. In addition, the small nodelike postzygapophyses, the vertical neural spine, and the upwardly concave base of the transverse processes are all *Ceratosaurus* characters (Gilmore 1920, Madsen personal communication 1986).

An additional 15 caudal vertebrae, BYUVP 4838, 4908, 5092, 8937, 8938 (fig. 26, A–E), 8974, 8982 (fig. 26, F–J),

9099, 9108 (fig. 28, P), 9141, (fig. 28, Q), 9152, 9161, 9162, 9163, and 9165, are morphologically similar and seem to represent one taxon, probably *Ceratosaurus*. They are thought to be from a single individual because the more anterior caudal vertebrae are similar in length, and the more posterior caudal vertebrae regress in length at a rate expected for an individual. The 15 here discussed range from 70 to 95 mm in length and 60 to 75 mm in width (across the proximal face).

The centra are moderately amphicoeleous, slightly taller than wide, and laterally constricted at midsection, accentuating their height to width difference. Both articular ends exhibit about the same degree of concavity. The ends of all 15 centra are less concave than the ends of any of the numerous *Allosaurus* caudal vertebrae observed in the UUVP and BYUVP collections. Chevron articular facets are about equally developed on both ends of the centra, but several have a posterior contact noticeably larger than the anterior. A bulbous protrusion is present just above the chevron facet on both ends of the centra. The sides of the centra are moderately constricted under the transverse processes on the pretransitional caudal vertebrae and less constricted and more slab-sided on the posttransitional caudal vertebrae. In lateral view, the ventral surfaces of the caudal vertebrae appear as a straight line under the bulk of the centra but curve down near either end to meet the lower surface of the chevron facets. The venter is V-shaped with no trace of a ventral groove.

The prezygapophyses of the *Ceratosaurus* caudal vertebrae are short to moderate in length, increasing slightly in size posteriorly in the series. Postzygapophyses are very small, leaf-shaped (chordate), pointed distally, and protrude a short distance beyond the posterior end of the centrum. Each vertebra in this group bears, or bore, a simple neural spine. The thin spines slope posteriorly at 20 to 30° from vertical and distally are slightly anteroposteriorly expanded. There is no increase in lateral thickness at the tip of the spine. Unlike the middle caudals of *Allosaurus*, no anterior neural spine blade is present, but a small conical protrusion located between the bases of the prezygapophyses with an apical depression marks the

FIGURE 26.—Ceratosaurus ?nasicornis, *BYUVP 8938 (A–E) and BYUVP 8982 (F–J); indeterminate theropod caudal vertebra BYUVP 9012 (K–N). Lateral (A,F,K), dorsal (C,H), ventral (B,G,L), proximal (D,I,M), and distal (E,J,N) views.*
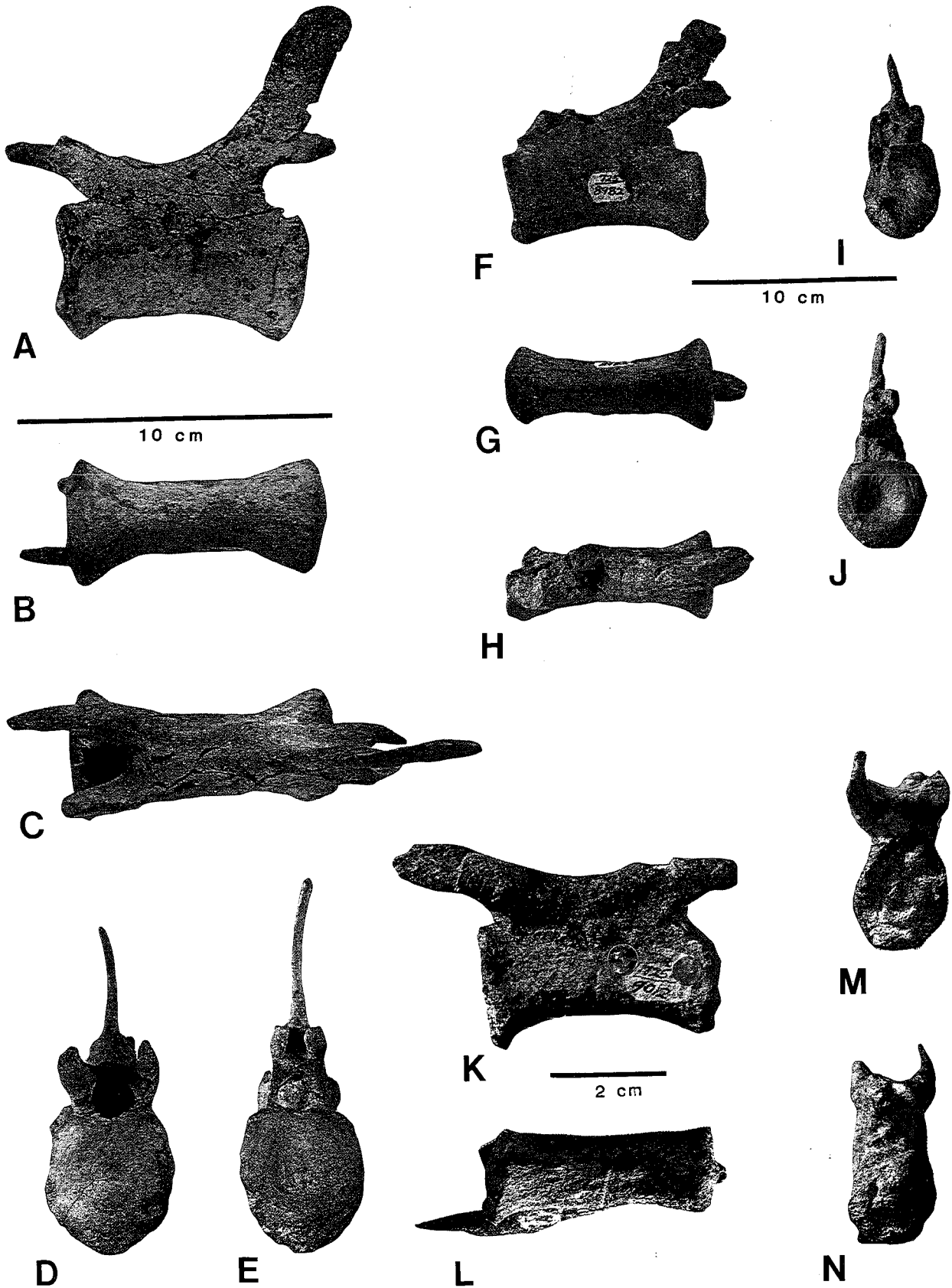
insertion of the interspinous ligament. The neural spines are very persistent and are well developed on posttransitional vertebrae that lack transverse processes.

Of the 15 caudal vertebrae, 10 are posttransitional forms. The remaining five are pretransitional, most with incomplete transverse processes. BYUVP 4908 is a proximal caudal vertebra, probably one of the first four. Such a position is indicated because the posterior end is clearly downset from the anterior end. Though incomplete, the transverse processes were located well up on the neural arch. These processes are backswept at about 30° and appear to have been slightly anteroposteriorly expanded distally. The dorsal surface of the transverse process bases are convex to very slightly concave.

The caudal vertebrae are hollow (fig. 28, P and Q) but could not have been pneumatic because they lack pneumatopores. Most likely they were filled with marrow, as is the case with the caudal vertebrae of most extant birds (Paul Bühler personal communication 1986).

These 15 caudal vertebrae are only tentatively referred to *Ceratosaurus* because they differ from the caudal vertebrae of the holotype in the following aspects: the neural spines are relatively taller and very persistent beyond the point of transition, the postzygapophyses apparently protrude beyond the centra, the venters are V-shaped with no groove, there is no thickening of the apex of the neural spines, and the spines are more reclined than those of *Ceratosaurus*. It is possible that these vertebrae may belong to an as yet unrecognized Morrison Formation genus or species.

Metatarsals

Left metatarsal III, BYUVP 5010 (not figured), is tentatively identified as *Ceratosaurus* because the distal end is subrectangular in outline. Also, the outline of the concave ventral surface of the distal articular end is a gentle arc, making it similar to a *Ceratosaurus* metatarsal III figured by Gilmore (1920).

Left metatarsal III, BYUVP 5008 (not figured), has been found in the Dry Mesa collection and is here tentatively assigned to *Ceratosaurus*. It is complete but slightly distorted with some crushing apparent, especially on the proximal end. The slender shaft is fairly straight with no great medial expansion of the mediodorsal surface. On the lateral surface, just proximal to the expanded distal end, is a distinct depression against which laid metatarsal IV. The distal half of the medial surface of the shaft has a well-developed groove that slopes distally toward the ventral surface. A protrusion of metatarsal II was appressed into this groove. All observed *Allosaurus* metatarsals of the third digit have a flattened area at this point of contact, but no groove.

In distal view, the articular surface is trapezoidal in outline. In this respect it is very similar to *Ceratosaurus*, but narrower. Unfortunately, it is not clear whether this narrowness is due to a taxonomic difference or to crushing. The articular surface exhibits a shallow convex ventral margin typical of *Ceratosaurus*. It also has a pair of vertical grooves on the distal surface like those shown on metatarsal III of *Ceratosaurus* by Gilmore (1920, plate 25), but these are probably of little significance. The collateral fossae are deep, particularly the medial one. The great depth of the latter may be attributed, at least in part, to distortion. The depression visible on the dorsal surface of the shaft immediately behind the articular surface of the distal end is due entirely to crushing. This specimen, while generally similar to *Ceratosaurus*, is more slender overall than the *Ceratosaurus* metatarsal elements figured by Gilmore (1920); hence, I have only tentatively assigned the element to *Ceratosaurus*.

DISCUSSION

Ceratosaurus, an uncommon, medium- to large-sized Upper Jurassic theropod, is moderately well represented in the Dry Mesa assemblage. Its occurrence at Dry Mesa Quarry is significant because it is known, though not necessarily reported in the literature, from only five other North American localities—all in the Morrison Formation. These localities are: Garden Park (Canon City) Quarry #1, Colorado (Marsh 1884); Fruita, Colorado (currently under study by James Madsen); Como Bluff Quarry 9, Wyoming (Bakker 1986); Dinosaur National Monument Utah (White 1964); and Cleveland-Lloyd Quarry, Utah (Madsen and Stokes 1963). Based on a set of ankylosed metatarsals, Stovall (1938) reported that *Ceratosaurus* had been found at an Oklahoma locality. Wann Langston (personal communication 1986), however, has never been able to locate the referred material and seriously doubts the identification.

Dodson and others (1980) noted *Ceratosaurus* was rarely found in the Morrison Formation. But while the genus was undoubtedly a comparatively uncommon component of Morrison faunas, it is probably more widespread than its reported occurrences would seem to indicate, an observation made by James Madsen, cited in Dodson and others (1983). Almost certainly there are many isolated *Ceratosaurus* bones lying in specimen drawers either unidentified or misidentified because medium- to large-sized theropod bones from the Morrison Formation are frequently assumed to be *Allosaurus*. In addition to the localities listed above, *Ceratosaurus* has been reported from the Tendaguru beds of Africa (Janensch 1925). In addition, some recently described Chinese theropod taxa appear to be *Ceratosaurus*, not

new genera (Olshevsky 1978). To my knowledge, no other occurrences of *Ceratosaurus* have been reported. If the six dorsal and nineteen caudal vertebrae are from a single individual, the individual is estimated to have been 4.5 m in length.

The presence of two left metatarsals and a possible duplication of caudal vertebrae indicate that a minimum of two *Ceratosaurus* individuals were present in the quarry, if the generic identifications for the elements described above are correct. The size and general morphology of the vertebral elements, particularly the dorsal vertebrae, are more similar to the holotype of *Ceratosaurus* in size and morphology than they are to the CLDQ elements of *Ceratosaurus*.

<center>Family ?Tyrannosauridae
Genus cf. *Stokesosaurus*</center>

DESCRIPTION

Caudal Vertebrae

Three non-allosaurid, non-ceratosaurid caudal vertebrae, BYUVP 5073 (fig. 28, G–K), 5103, and 8908 (not figured), have been recovered from the Dry Mesa Quarry. They appear to be from a singe individual. All are from a position immediately anterior to the transition point because they have small transverse process bases— most of the processes having been broken off during collection. The prezygapophyses remaining are short for such posterior caudal vertebrae and terminate in a point, a feature that seems to be unknown on any figured caudal vertebrae of theropods from the Morrison Formation. No postzygapophyses are preserved. The centra are amphicoeleous and slightly wider than tall. The flat sides of the centra converge ventrally on the venter, which is laterally broad with a wide but shallow groove along its length. Madsen (1974) tentatively referred *Stokesosaurus* to the Tyrannosauridae because of the vertical ridge on its ilium and the fact that it bore four premaxillary teeth.

DISCUSSION

It is possible these vertebrae belong to either *Stokesosaurus* or *Marshosaurus* because of their similarity to vertebrae in the Cleveland-Lloyd Collection. They are here tentatively referred to *Stokesosaurus*. If BYUVP 5201 (see p. 110) is *Stokesosaurus*, then these could be *Marshosaurus*, or vice versa—or they may represent a new genus.

<center>Family Allosauridae
Genus *Allosaurus fragilis*</center>

DISCUSSION

Allosaurus is the most abundant theropod in the Dry Mesa quarry with a total of nearly 200 identified elements having been recovered thus far. The osteology of this genus has been comprehensively covered in Madsen's (1976b) monograph and will be only superficially discussed in this paper.

Nearly all the *Allosaurus* elements from Dry Mesa Quarry differ to some degree from those collected at the Cleveland-Lloyd Quarry. This is not unexpected because the quarries may differ in age by roughly 11 million years. The age of the Dry Mesa Quarry is about 127 Ma (a debatable age) while the Cleveland-Lloyd Quarry is between 152 Ma and 146 Ma (Bilbey-Bowman 1986). Most appendicular elements of *Allosaurus* from Dry Mesa are considerably more robust than bones of equal length from Cleveland-Lloyd. Also, the only *Allosaurus* lacrimal, BYUVP 5125 (fig. 27, I and J), from the Dry Mesa Quarry has a distinct, sharply pointed apex, which matches perfectly the lacrimal on USNM 4734, figured by Gilmore (1920, p. 8). In contrast, the lacrimals figured for AMNH 666 (Gilmore 1920), as well as the Cleveland-Lloyd and UUVP 6000 specimens figured by Madsen (1976b), have a blunt, rounded apex. All 18 available lacrimals from the Cleveland-Lloyd Quarry have been observed, and though they exhibit individual variation, none have a high, distinct apex like BYUVP 5125 or USNM 4734. While more research is required to confirm this observation, it appears that there are at least two species of *Allosaurus* in the Morrison Formation. The older, from the Cleveland-Lloyd, Dinosaur National Monument, and perhaps quarries of similar age, has slender limb bones and bluntly rounded lacrimals. The younger, from Dry Mesa, Garden Park, and perhaps quarries of similar age, has comparatively robust limb bones and sharply pointed lacrimals. From this admittedly brief analysis it seems that the two allosaur morphs were roughly the same length, but the Cleveland-Lloyd/Dinosaur National Monument form was more gracile with a long, low skull as compared to the Dry Mesa/Garden Park form, which was noticeably more robust with an unusually short, high skull. A more detailed analysis of this problem is beyond the scope of this paper.

<center>Family Incertae sedis
Genus cf. *Marshosaurus*</center>

DESCRIPTION

Caudal Vertebra

BYUVP 5201 (fig. 28, L–O) is a caudal vertebra from the anterior third of the tail and is the only one of its type in the Dry Mesa collection. It consists of a complete centrum and lower portion of the right side of the neural arch including the basal transverse processes and prezygapophysis. The centrum is laterally constricted with a

rounded, but slightly V-shaped venter and bears a very slight median groove. The anterior end of the centrum is more concave than most theropod caudal vertebrae, but the posterior end is only slightly concave, almost flat. The anterior chevron facet was small, but it is not distinguishable because a small portion of the centrum in this area is missing. The posterior chevron facet is well developed and is dorsoventrally convex.

DISCUSSION

This caudal vertebra does not match that of any figured Morrison Formation dinosaurs, but does match several as yet unfigured specimens from the Cleveland-Lloyd Dinosaur Quarry. These caudal vertebrae from the CLDQ are part of the collection of *Marshosaurus/Stokesosaurus* postcranial material currently being studied by James H. Madsen. While it is clear that these vertebrae do belong either to *Marshosaurus* or *Stokesosaurus*, it is not yet absolutely clear which vertebrae belong to which genus. The caudal vertebra in question, however, is here tentatively referred to *Marshosaurus* by a process of elimination because the other set of caudal vertebrae equivalent to those in the CLDQ are, in this paper, referred to *Stokesosaurus*. BYUVP 5201 apparently belongs to the same genus as UUVP 99, 441, 5247, 5780, and similar caudal vertebrae from Cleveland-Lloyd Quarry.

Genus Indeterminata

DESCRIPTION

Caudal Vertebra

BYUVP 9012 (fig. 26, K–N) is a distal caudal vertebra of unknown theropod affinity. The neural spine, right postzygapophysis, and anterior half of the left prezygapophysis are missing. The centrum is 54 mm long, and the anterior end is 23 mm wide. The anterior and posterior articular ends are covered with rugae, indicating they have been eroded or were never well ossified or are pathologic. The anterior end of the centrum is significantly taller than the posterior end. The sides of the centrum are nearly planar and vertical. The venter is broad with a narrow furrow on either side of a low median ridge. The neural arch, especially the anterior half, is large for the size of centrum upon which it sits. The prezygapophyses are robust but short. The lateral surface of the prezygapophyses are smooth and convex. The lower medial surface of the prezygapophyses have a prominent ridge extending nearly to the tip of the process.

DISCUSSION

BYUVP 9012 compares favorably with a specimen, also unidentified, in the *Stokesosaurus/Marshosaurus* postcranial collection from the Cleveland-Lloyd Quarry currently under study by Madsen. The two specimens may be pathologic caudals, but the possibility of two such specimens from different quarries and ages pathologically developing so many equivalent features is improbable. At present this caudal cannot be assigned to a genus.

DESCRIPTION

Ischia

A pair of theropod ischia, BYUVP 4862 (fig. 27, A–H), were found in articulation. They differ from described Morrison theropod ischia and cannot be assigned to a genus at this time. Both ischia were distorted after permineralization, resulting in the shafts, particularly the left one, being bent posteriorly just below the proximal bladelike expansion of the ischia (fig. 27, E and H). The blade ventral to the pubic articulation on the right ischium has also been dislocated posteriorly. The ischia were separated while being prepared, though the distal ends were firmly co-ossified over a short distance. At the zone of fusion the two bones parted along a nonmedial fracture, causing some difficulty in determination of the exact distal outline of the ischia (fig. 27, B and F).

The ischia are lightly built with a slender shaft. Viewed from the side, the proximal ends are triangular in outline (fig. 27, A and E). No obturator process, as described for ischia of *Tyrannosaurus* (Osborn 1905 and 1906), Gorgosaurus (Lambe 1917, Matthew and Brown 1923), and *Allosaurus* (Madsen 1976b) is present. In fact, most theropods do not have a well-differentiated obturator process. The obturator process is here interpreted to be a derived feature formed of only the more ventral portion of the thin plate of bone spanning from the pubic articulation to the upper end of the shaft. The obturator flanges of BYUVP 4862 meet along the sagittal plane.

The ischia were in close contact along their entire length. In life they were united by a ligamentous union except at the conjoined distal end. A particularly rugose area is located on the medial contact at midshaft (fig. 27, D and H) and may represent an incipient osseous connection. The balance of the shaft's symphysial surfaces have small striations parallel to the shafts. Such striae were interpreted by Romer (1956) to represent a ligamentous union. Viewed distally (fig. 27, B and F), the ischia seem to have had a subrounded, triangular outline, with the low apex of the triangle pointing laterally. Viewed from the side, the distal ends, or feet, of the ischia are asymmetrically expanded with the bulk of the expansion in the posterior direction (fig. 27, A and H).

The "body" of the pubic peduncle is rodlike and terminates in a triangular, concave "articular" surface (fig. 27, C). The iliac contact consists of a very deep posterior

concavity and a small, slightly concave surface that lies somewhat anterolaterally to the deep concavity (ibid.). The inner rim of the cuplike cavity is covered with small rugae. The surface on most of the cavity has no easily recognized surface boundary but is lined with spongy bone, apparently indicating the cavity was lined with cartilage undergoing calcification. The angle of descent of the better-developed bony surface of the rim indicates the cavity was not filled with cartilage but was a deep articular cavity in life. The acetabular margin of the ischium is a short, fairly thin ridge. In this aspect it is similar to *Dilophosaurus* (Welles 1984, fig. 3) and *Deinonychus* (Ostrom 1969b, p. 112).

DISCUSSION

The ischia of *Marshosaurus* and *Allosaurus* differ from BYUVP 4862 because the distal foot of these genera are, in comparison, subsymmetrically developed and the acetabular portion of the bone in these genera is a well-developed shelf, rather than a ridge. The latter genus also differs in having a well-developed obturator process. The only known ischium of *Elaphrosaurus*, though incomplete, has a deeper acetabular area, an unusual flange on the posterior edge, and the distal end is expanded more anteriorly than posteriorly.

The ischia of *Ceratosaurus* have a larger pubic peduncle "shaft," which is at least three times as broad dorsoventrally than that of BYUVP 4862, and the shaft narrows noticeably more at midlength than BYUVP 4862. The nature of the distal end of the *Ceratosaurus* ischium is not known for certain because the ends of both the pubis and ischium of USNM 4735 were lost sometime after their collection and before Gilmore's (1920) redescription of the genus. The illustration of the *Ceratosaurus* ischium in Marsh's (1884) original description of the genus shows a prominent anterior projection on the distal foot. Gilmore (1920, p. 108) noted that though the distal end of the bone was missing, it was apparent that "there was an abrupt forward expansion of the enlarged distal end." If this is true, *Ceratosaurus* ischia differ significantly from BYUVP 4862. The only other ischia with a similar fossa in the iliac peduncle are those of a tyrannosaurid, possibly *Albertosaurus*, TMP 81.10.1, from the Upper Cretaceous Horseshoe Canyon Formation of Alberta. Thus the ischia cannot be presently assigned to any Morrison theropod for which ischia are known. This leaves *Stokesosaurus* or perhaps an as yet undiscovered/described genus as possible alternatives.

DESCRIPTION

Fibula

BYUVP 4876 (fig. 28, A–F) is a slender left fibula. It is well preserved, except for a lateroposterior distortion of the distal end of the shaft caused by postdepositional distortion. A small ridge originates on the posteromedial surface of the proximal end and continues one-fourth of the way down the length of the medial surface of the shaft. A similar ridge is found on the fibula of *Allosaurus*. When viewed medially or laterally, the shaft initially narrows only slightly on the proximal one-third but tapers considerably on the middle one-third. The deep, medial depression, just below the triangular proximal portion of the bone (fig. 28, B), is accentuated distally by crushing. The distal end has a subrounded triangular outline with the anterior edge being the largest and most rounded (fig. 28, F). The distal articular surface is strongly convex.

Pes

Several bones of small theropods, possibly of *Coelurus*, *Ornitholestes*, or juvenile theropods, have been found at the Dry Mesa Quarry. BYUVP 4841 (not figured) is a complete, small, 50-mm-long, first metatarsal. The laterally reduced proximal half is very thin, being less than 1 mm thick and has no articular surface. The distal half of the metatarsal is more shaftlike with a diameter of approximately 5 mm. The first metatarsal of theropods could not have been a weight-bearing element because it has no proximal articular surface and probably functioned as a dew claw (Madsen 1976b). The articular surface of the distal end is somewhat rounded. Ventral to the distal articular surface are a pair of poorly developed, lateral, longitudinal ridges representing rudimentary condyles.

DISCUSSION

The slender nature of the fibula indicates an adaptation to a cursorial habit as discussed by Coombs (1978). Though slender in comparison with *Ceratosaurus*, *Torvosaurus*, and *Allosaurus* fibulae, it is not as slender as the fibulae of *Deinonychus* or *Ornitholestes*. The fibula could belong to either *Stokesosaurus* or *Marshosaurus* because it is of the correct size. However, no fibulae of the latter two genera are described at the present time, so a morphological comparison is not possible. Only the proximal end of a left fibula of *Ornitholestes*, AMNH 619, is known, but Ostrom (personal communication 1985) stated BYUVP 4876 is too robust and long for *Ornitholestes*. However, Ostrom (ibid.) also mentioned the possibility cannot be ruled out that it may be an ontogenetically older individual. The identification of this bone, beyond belonging to a moderate-sized "coelurosaurian" theropod, remains tenuous.

Even though *Coelurus* and *Ornitholestes* were described around a century ago, *Coelurus* by Marsh (1879) and *Ornitholestes* by Osborn (1903), only a few bones of each have been adequately figured, as noted by Ostrom
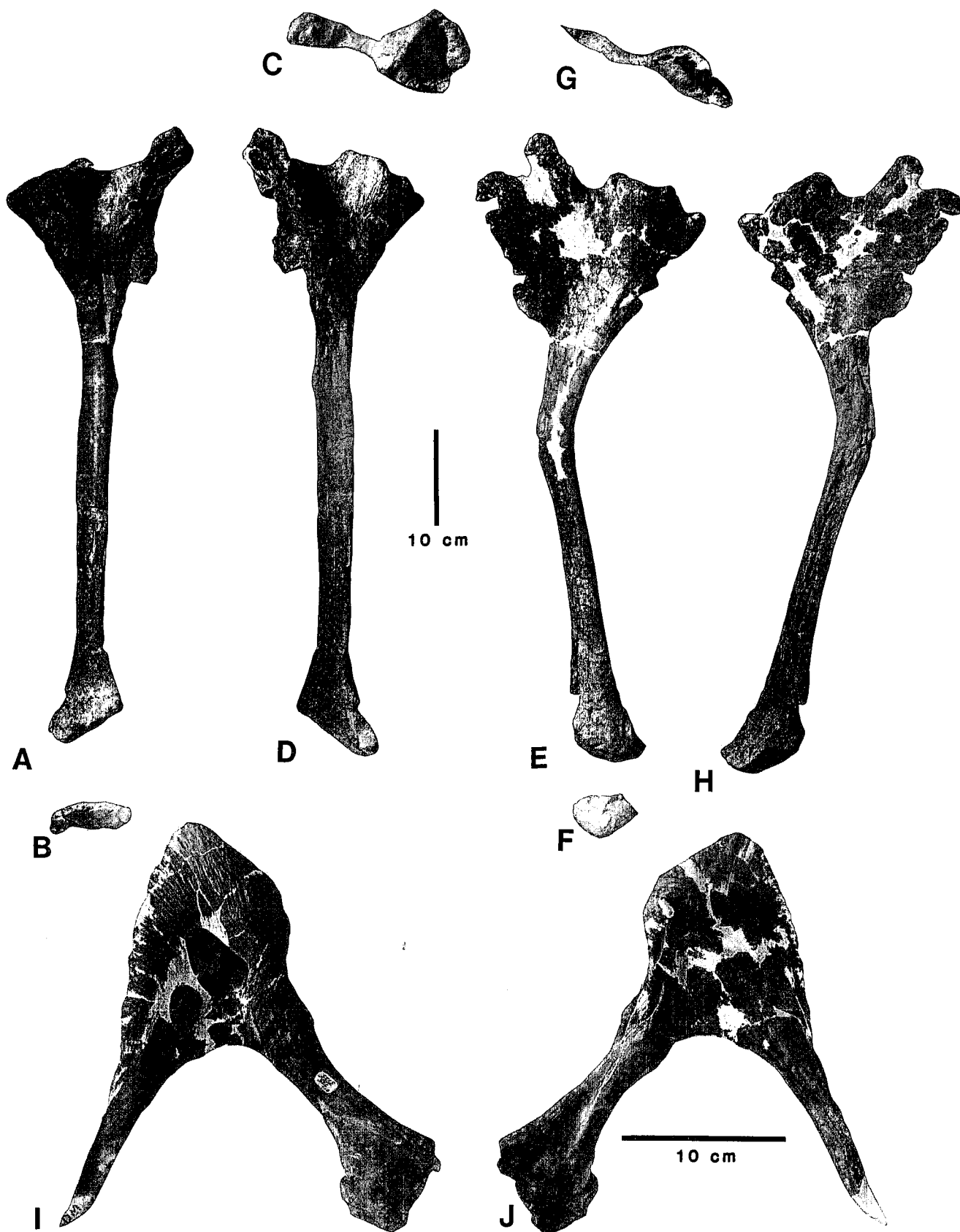
(1980). Osborn (1917) figured the known elements of *Ornitholestes* in a reconstruction, but the particulars of individual bones are not illustrated. Ostrom is currently describing these genera in detail, but at this time no figures are available to aid in the generic identification of the "coelurosaur" bones described above.

Genus Indeterminate

DESCRIPTION

Teeth

Four tooth crowns of a small theropod have been recovered. BYUVP 9605 (unfigured) is the largest of the two with a nearly complete crown measuring 12 mm high with a 7-mm-long base. The posterior edge is serrated along its entire preserved length, with approximately 16 denticles per 5 mm, the denticles being separated from each other by a small but distinct gap. The tip and anterior edge are worn, and no denticles are visible on the anterior carina. It seems that either no denticles were present on the anterior carina or they were considerably smaller than those on the posterior carina and have been worn off.

The second tooth, BYUVP 9611 (unfigured), is only 7 mm tall and 4 mm long. The posterior edge is serrated with about 17 denticles per 5 mm. The denticles of the posterior carina appear identical to those of BYUVP 9605. The tooth is less laterally compressed than 9605 and is presumably from the anterior end of the dentary or premaxilla. No denticles are visible on the anterior edge, and there is no sign of wear in this area. However, it is possible that minute denticles were present but not discernible because the anterior edge is slightly crushed. Both teeth (BYUVP 9605 and 9611) may belong to the same genus of very small theropod.

The two remaining tooth crowns, BYUVP 9597 and 9603 (fig. 5, E–F and G–I, respectively), are of the same general size and form as those just described.

DISCUSSION

All four of these teeth are dromaeosaurid in form, particularly BYUVP 9603. Ostrom (1969b) described the teeth of *Deinonychus* as having much larger and more persistent denticles on the posterior carina than on the anterior carina. He also notes *Velociraptor* and, perhaps, *Saurornithoides* teeth have considerably fewer denticles on the anterior carina than the posterior. Ostrom (1969b) suggested the unequal anterior/posterior denticle count "may be of phyletic as well as taxonomic significance." Interestingly, Barsbold (1977) included *Deinonychus*, *Velociraptor*, and *Saurornithoides* in the infraorder Deinonychosauria, which tends to support Ostrom's (1969b) suggestion. Carpenter (1982) noted the dromaeosaurid teeth included in his study are nearly as long in the anteroposterior direction as they are tall. The same is true of BYUVP 9603. Because the small teeth just described had either very small anterior denticles, or none at all, as well as anteroposteriorly elongate bases, it seems reasonable to suggest the four small theropod teeth from the Dry Mesa Quarry are from a dromeosaurid or, perhaps, *Marshosaurus*. BYUVP 9603 compares very well with UCM 39502, the tooth of a Late Cretaceous dromaeosaurid illustrated by Carpenter (1982, p. 128). The numbers of serrations differ, however, probably because the Late Cretaceous specimen is from a very young individual and it has been shown by Farlow (1987) that the density of serrations decreases with increasing tooth size.

Ostrom (1969b) showed that *Deinonychus* and later dromaeosaurids could have been derived from an *Ornitholestes*-like ancestor because of shared characters of the manus and pes. If this is true, it is possible that these teeth came from *Ornitholestes*. The teeth just described, however, are considerably larger than those of *Ornitholestes* and considerably broader based. Osborn (1903) stated that at least the maxillary teeth of *Ornitholestes* are unserrated, though he may have been in error on this point, which means the teeth are probably not equivalent. A positive generic identification for the dromaeosaurid-like teeth from Dry Mesa will not be possible until the small Morrison theropods are better known.

CONCLUSIONS

A few observations on the taphonomy and paleoecology of the Dry Mesa Quarry are appropriate, though a

FIGURE 27.—*Indeterminate theropod right (A–D) and left (E–H) ischia, both BYUVP 4862, and* Allosaurus *?*atrox *left lachrimal, BYUVP 5125 (I–J). Lateral (A,E,I), medial (D,H,J), proximal (C,G), and distal (B,F) views.*
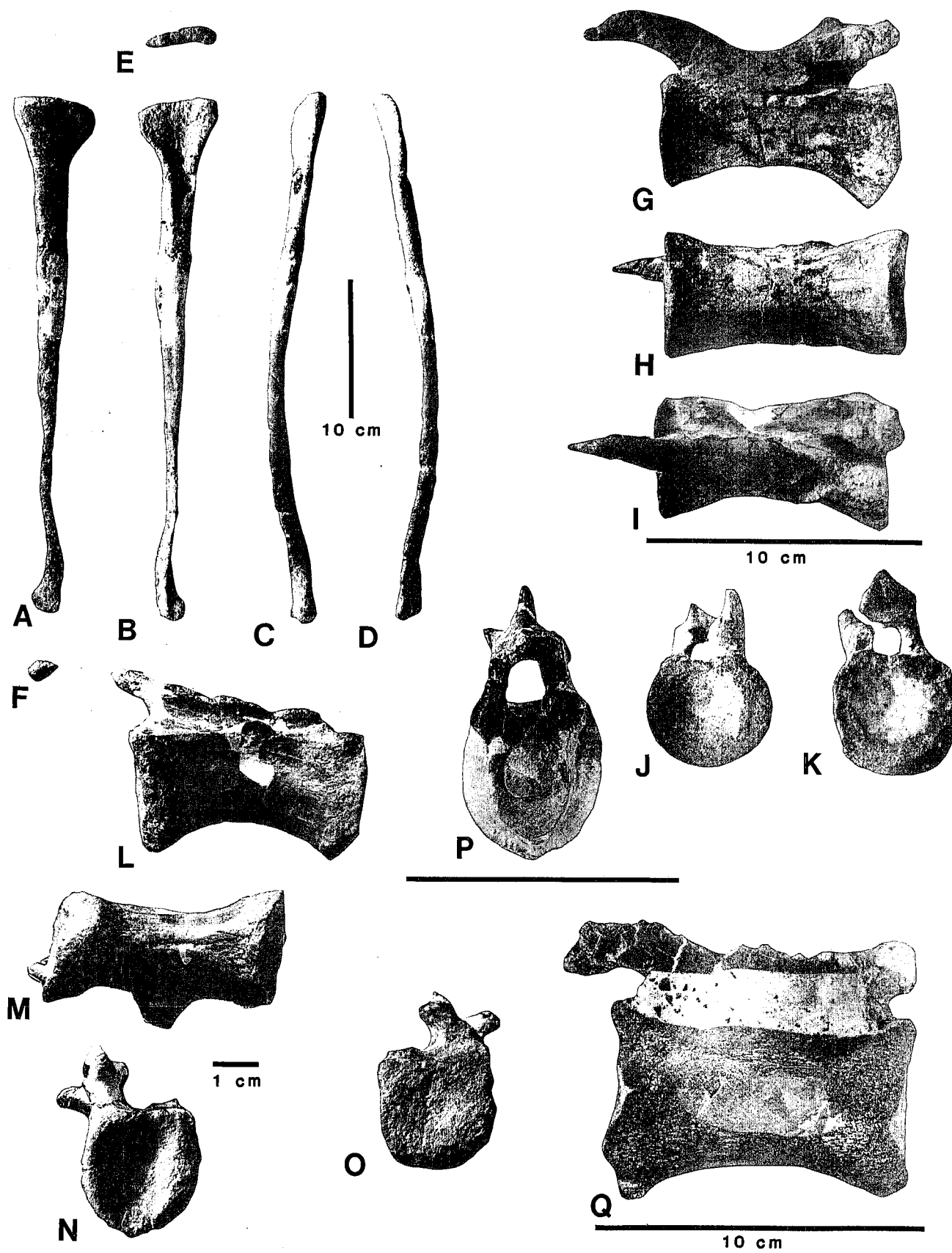
detailed analysis is beyond the scope of this study. For an in-depth consideration of these topics the reader is referred to the studies by Dodson and others (1980 and 1983), which deal exclusively with the Morrison Formation.

The paleoecology of the Morrison Formation is still a matter of debate (compare Dodson and others 1980 and 1983 with Tidwell 1990). The formation is interpreted by many authors (Dodson and others 1980; Mook 1916; Stokes 1944, 1985) to have been deposited on a lowland plain following the retreat of the epicontinental sea far to the north into what is now Alberta. The pebbles in the conglomeratic sandstones of the quarry suggest a relatively close clastic source. However, the paleogeographic map by Imlay (1956, plate 9) indicates the central Colorado high was no longer a factor in the Late Jurassic, and the area was a flood, or alluvial, plain with sediments being derived from the west, in Utah, and the south, in New Mexico. In light of the fact that no large channels are known in the Morrison Formation (Dodson and others 1980, Stokes 1944), the coarse clastic wedges of the Morrison in Utah and New Mexico are too distant to be a significant source of the chert pebbles. It seems most likely, then, that the pebbles were not derived directly from highlands but from the reworking of slightly older intraformational sediments by medium- to small-size streams. The streams flowed over the shallow slope of the floodplain, constantly reworking the sediments, resulting in the vast, but thin, Morrison Formation as postulated by Stokes (1944).

Plants are the best paleoclimatic indicators, but macro- and microplant fossils, other than petrified wood, are generally considered rare in the Morrison Formation (Dodson and others 1980, p. 229; Stokes 1944, p. 976). However, Tidwell (1990) noted that over 34 macroplant form-genera occur in the formation and reported 16 localities with abundant plant fossils. Similarly, Hansley (1987, p. 669) stated that "carbonized and silicified plants are locally abundant" in the formation. With the exception of a few suspect carbonaceous films, no macroplant fossils have been recovered from the quarry area.

Two samples of gray green mudstone were processed for palynomorphs by the author but proved to be barren, except for small organic (oxidized plant?) fragments, which is not surprising because Morrison palynomorphs are relatively rare according to Tschudy and others (1981) and Dodson and others (1980). The green mudstones may be secondarily reduced oxidized red mudstones, thus explaining the lack of palynomorphs. Palynomorphs are similarly uncommon in some Tertiary formations, which, like the Morrison Formation, are characterized by red, green, and maroon mudstones (Retallack 1984). These Tertiary formations provide ample evidence of plants in the form of root traces and herbivorous mammals, but Retallack (1984) stated that "other than isolated finds of fossil wood and the fruits and hackberry endocarps, plant fossils are surprisingly rare. No pollen and spores were found despite numerous attempts to prepare them." He hypothesized that the paucity of plant fossils in the Tertiary formations he studied is due to unfavorable Eh and pH states (see Krumbein and Garrels 1952), as well as other conditions, that existed during, and shortly after, deposition. Similar conditions unfavorable to plant preservation may have existed during Morrison time.

Because no micro- or macroplant fossils have been found in the quarry locale, nothing can be stated about the flora of the Morrison Formation in the quarry region. Tidwell (1990), however, wrote that the Morrison flora appears to have been dominated by conifers, ferns, cycads, and, to a lesser degree, sphenophytes. Seed ferns and ginkgos are also known to occur, but have only been reported from localities in Montana (Brown 1972 and 1975). Based on the flora, Tidwell (1990) concluded the climate was warm and humid. By far the greatest percentage of Tidwell's Morrison Formation flora consists of petrified wood, cones, and seeds. In contrast to Tidwell's interpretation, Hotton (1986) concluded the climate was arid to semiarid based on palynomophs—despite the abundance of fern and fernlike spores, as well as cycad spores, in her samples. Hotton (1986) cited the occurrence of *Ephedripites*, interpreting it to be of gnetalian origin and therefore indicative of aridity. However, this

FIGURE 28.—*Indeterminate left fibula, BYUVP 4862 (A–F);* ?*Stokesosaurus caudal vertebra, BYUVP 5073 (G–K);* ?*Marshosaurus caudal vertebra, BYUVP 5201 (L–O); transverse-section through middle of* Ceratosaurus ?*nasicornis caudal vertebra, BYUVP 9108 (P), showing calcite-filled central cavity; and saggital-section of caudal vertebra, BYUVP 9141 (Q), showing calcite-filled central cavity. Lateral (A,G,L), medial (B), anterior (C,J,N), posterior (D,K,O), proximal (E), distal (F), dorsal (I), ventral (H,M), transverse-section (P), saggital-section (Q).*

genus is also known from the Judith River Formation in Alberta (Dennis Braman personal communication 1987), which was probably not deposited under arid conditions. Therefore, the frequent assumption that *Ephedripites* is indicative of an arid climate is not always a valid one. Also, pollen referred to *Ephedripites* may be of coniferalean, not gnetalean, origin (Ash 1972; see also Pocock and Vasanthy [1988] for a discussion of the *Ephedripites* problem). Dodson and others (1980) concluded the climate was semiarid with strongly seasonal precipitation, resulting in a sparse vegetative cover that forced dinosaurs to migrate long distances for food.

The archosaurian assemblage of the Dry Mesa Quarry is very diverse (table 2). Of the eight valid theropod genera previously known to occur in the Morrison Formation, only one, *Elaphrosaurus*, has not been at least tentatively identified in the Dry Mesa assemblage. *Elaphrosaurus* has been reported from only one Morrison Formation locality (Yale Peabody Museum Quarry 1, Garden Park, Colorado, by Galton [1982]), and the identification is based on a single element, a humerus. The Dry Mesa Quarry has at least five genera of theropods including *Allosaurus, Torvosaurus, Ceratosaurus, Marshosaurus,* and *Stokesosaurus,* which have been positively identified at this time. In addition, a theropod caudal vertebra, which is not assignable to any described Morrison Formation genus, is also present. Four small theropod teeth that either lack or had very small serrations on the anterior carinae are questionably considered to be of dromaeosaurid origin. No Jurassic members of the Dromaeosauridae have been described so the teeth cannot be referred to a genus at this time. It should be pointed out, however, that Ostrom (1969b) suspected that *Ornitholestes* may be related to the Dromaeosauridae, but since the teeth of this genus lack serrations (Osborn 1903, Ostrom 1980) and are more peglike than bladelike, with narrow bases, the dromaeosaurid-like teeth in question are not referred to this genus.

The miscellaneous elements of indeterminate, small theropods may represent *Coelurus* and/or *Ornitholestes* because they are the smallest theropod taxa reported to date from the formation. Admittedly, size alone is hardly justification for identification, but these taxa have not been adequately figured, thus making a complete comparison impractical at this time. It is hoped that direct comparison with the original specimens of these two taxa will be possible at a future date.

The most common theropod taxa in the Dry Mesa Quarry are *Allosaurus,* represented by a minimum of six individuals (nearly 200 elements) and *Torvosaurus,* represented by a minimum of three individuals (75 elements). Partial, articulated caudal vertebrae of both genera and two partial crania of *Allosaurus* have been found in the quarry. Twenty-five elements, including two

closely associated dorsal vertebrae representing a minimum of two individuals of *Ceratosaurus,* have been found in the quarry. Because these genera are represented by several individuals and numerous elements, they are assumed to be proximal components of the paleocommunity.

The elements of indeteminate small theropods, possibly ?*Coelurus* and ?*Ornitholestes,* are few, consisting of a fibula, a phalanx, and a metatarsal. All of these bones are very fragile, but show no evidence of abrasion. These genera are rare (Dodson and others 1980). Because the bones show no evidence of significant fluvial transportation, the genera represented by these elements are considered to have been rare components of the proximal community.

The remainder of the Dry Mesa theropod assemblage, *Stokesosaurus, Marshosaurus,* and the indeterminate theropod (represented by the caudal vertebrae with a pair of ventral grooves), are thought to have been transported in because the elements are incomplete and worn. Therefore, they could represent members of a separate, but proximal, community that were transported to the area by fluvial action. However, the possibility that they were members of the proximal community cannot be ruled out. No interpretation of a proximal or distal community origin is given for the small theropod represented by the dromaeosaurid-type teeth because enamel is more resistant to abrasion than bone, so teeth can be transported farther without showing signs of abrasion. These four teeth are significant because no true Jurassic dromaeosaur is yet known, though *Ornitholestes* is suspected of being a primitive dromaeosaurid (Ostrom 1969b). The dromaeosaurid *Deinonychus* is known from the overlying Cloverly Formation in Montana, so it is probable that older, more primitive members of the family were present in Jurassic strata.

Of the five described ornithischian genera known to occur in the Morrison Formation, four have been found in the Dry Mesa collection. The most common, *Dryosaurus,* is represented by an assortment of elements from several individuals. The bones of *Camptosaurus* found in the quarry are: a cranium, a caudal vertebra, a dorsal vertebra, and an ulna. *Stegosaurus* is represented by a distinctive caudal neural arch. *Othnelia* is questionably represented by an ilium, which could be that of a small *Dryosaurus.* Ornithischian elements have not been purposely selected for preparation and hence are underrepresented. Additional ornithischian elements await preparation and will shed new light on this group of the Dry Mesa assemblage.

At least three families of sauropods are present in the quarry (table 2). The sauropod genera positively identified at this time are *Apatosaurus, Diplodocus, Barosaurus, Supersaurus, Brachiosaurus,* and *Camarasaurus*

(John McIntosh personal communication 1986). Two other sauropod taxa, *Ultrasaurus macintoshi* and *Dystylosaurus edwini,* recently described by Jensen (1985a), based on specimens from the quarry, may be congeneric and assignable to *Brachiosaurus.*

Both in terms of numbers of elements and volume, sauropods constitute the vast bulk of the bones collected from the quarry; however, relatively few have been prepared. As additional specimens are readied for study, new genera may come to light. In the past, elements identified in the field as belonging to known sauropod genera were selected against on the preparation priority list in favor of elements that hopefully belonged to new taxa.

Dodson and others (1980) reported that 18 valid dinosaurian genera were known to occur in the Morrison Formation. Since the compilation of that report, several other Morrison genera have been described or discovered: *Torvosaurus* (Galton and Jensen 1979), *Elaphrosaurus* (Galton 1982), *Supersaurus* (Jensen 1985a), *Ultrasaurus* (Jensen 1985a), and *Dystylosaurus* (Jensen 1985a). Counting *Torvosaurus, Elaphrosaurus,* and *Supersaurus,* the total number of dinosaur genera now known to occur in the Morrison is 21. Of these 21 valid genera, 17, or about 80% of the total Morrison dinosaur assemblage, are now known to occur in the Dry Mesa Quarry, and the ornithischians and sauropods have yet to be studied in detail. This makes the Dry Mesa Quarry the most prolific of all Morrison Formation quarries in terms of archosaur genera. By way of comparison, the next most prolific Morrison Formation localities are Dinosaur Na-

tional Monument, with 11 genera (counting *Torvosaurus* [this paper] and a small theropod, probably either *Marshosaurus* or *Stokesosaurus*), and the Cleveland-Lloyd Quarry, with about 12 genera, including a recently discovered specimen that appears to have nodosaurid affinities (James H. Madsen personal communication 1986). The genus count of DNM, less *Torvosaurus,* is from Dodson and others (1980, p. 222) and Daniel Chure (personal communication 1987). The genus count of CLDQ is from Madsen (1976b and personal communication 1987) and Stokes (1985). The unusual caudal vertebra, BYUVP 9012, and the dromaeosaurid-like teeth may represent additional genera, but more evidence is needed before reaching a conclusion on these points.

At this time no complete explanation can be offered to account for the great generic diversity of the Dry Mesa assemblage. However, in part, the diversity can be explained by taking into account the large sample size, a sample that is from an enormous mass accumulation consisting almost exclusively of disarticulated bones. And, as pointed out by Badgley (1986), bones concentrated by fluvial systems better represent the original community than concentrations developed by other means. It is plausible the bones from the Dry Mesa Quarry may be from several different communities within the drainage system. In fact, *Stegosaurus,* which is represented by a single abraded element, may have been transported in from some distance up the drainage system. The balance of the genera, however, presumably represents the "local" drainage community.

APPENDIX

The "equivalent" symbol (~) preceding a number indicates a portion of the bone is missing but is complete enough for a reasonable estimate to be made. The measurement given represents a reasonable estimate.

Blank cells indicate that the specified dimension of the bone is too incomplete to permit a reasonable estimate to

be made, or that the measurement is not applicable to that element.

The "greater than" symbol (>) indicates the element is incomplete for the specified parameter and that the bone's original dimension would have been greater than the number given.

TORVOSAURUS TANNERI ELEMENTS

SKULL AND MANDIBLE ELEMENTS

BYUVP Number	Side	Element	Length	Width	Height	Distal Width
2003	L	Dentary			125	
4883	L&R	Jugal				
5286	L	Lacrimal				
9249	R	Postorbital	>115		260	
4882	R	Premaxilla	145		149	
5110	R	Quadrate	273			119

CERVICAL AND DORSAL VERTEBRAE

BYUVP Number	Element	Centrum Length	Max. TVP Total Width	Centrum Anterior Height	Centrum Proximal Width	Centrum Distal Width	Neural Arch Height
4884	Atlas Cervical 1	50		61	>113	101	
4860	Cervical 3	90	180	63	~95	108	160
2004a	Cervical 5						
2004b	Cervical 6	115	NA	~60	~128	110	NA
2004c	Cervical 7	123	NA	>60	~120	<133	NA
2004d	Cervical 8	121	NA	>45	~124	120	NA
2005	Dorsal 01	135	NA	91	130	132	>100
4998	Dorsal 04	124	290	103	122	117	~180
2006	Dorsal 05	118	~190	115	132	116	180
2007	Dorsal 06	~107	~160		~130	NA	NA
9120	Dorsal 07	112	>240	100	>91	120	222
9121	Dorsal 09	>95	300	>210	>120	>105	190
9090	Dorsal 10	~113	290	>130	>140	>140	240
2008	Dorsal 12	>105	NA	>120	>135	>130	235
4890	Dorsal 14	130	330	~150	~150	155	295

CAUDAL VERTEBRAE AND CHEVRONS

BYUVP Number	Element	Centrum Length	Max. TVP Total Width	Centrum Anterior Height	Centrum Proximal Width	Centrum Distal Width	Neural Arch Height
5086	Caudal 02 or 03	116	257	119	120	~115	184
5004	Caudal 04 or 05	127	NA	114	119	114	NA
4976a	Caudal 08	115	>280	93	>115	109	195
4976b	Caudal 09	118	>280	94	111	106	>140
4976c	Caudal 10	119	265	97	102	96	165
4976d	Caudal 11	116	~270	98	93	92	>140
4976e	Caudal 12	104	270	101	90	87	135
4976f	Caudal 12	109	280	86	91	94	>110
9013	Caudal 12~	>95	~160	99	87	>88	>158
4976g	Caudal 14	100	~260	84	90	~105	NA
4976h	Caudal 15	>80	~240	~80	<112	95	NA
4976i	Caudal 16	100	NA	~72	83	80	NA
9135	Caudal 22~	86	NA	72	73	NA	NA
4976a	Chevron of cdl 08	>230	80				
4976b	Chevron of cdl 09	>240	>31		72	~19	
4976c	Chevron of cdl 10	232	41		70	16	
4976d	Chevron of cdl 11	220	39		>60	14	
4976e	Chevron of cdl 12	190	46		62	15	
4976f	Chevron of cdl 13	185	37		58	14	
4976g	Chevron of cdl 14	~180	40		75	14	
4976h	Chevron of cdl 15	>150	NA		72	13	

LIMB ELEMENTS

BYUVP Number	Element	Side	Length	Minimum Circumference	Proximal Width	Distal Width	C/LX100
5029	Astragalus	R					
9621	Astragalus	R					
5020	Calcaneum	L					
9622	Calcaneum	R					
5129	Fibula	L	686	138	141	100	20
5136	Fibula	R	NA	135	~160	100	??
9620	Fibula	R	688	134	157	101	19
2002	Humerus (Holotype)	L	429	205	197	161	47
2002	Humerus	R	412	203	190	152	49
5276	Metatarsal II	R	288	186	120	92	64
5077	Metatarsal II	R	295	202	118	114	68
5147	Metatarsal II	L	303	185	~115	100	61
5281	Metatarsal II	L	307	200	138	100	65
5277	Metatarsal III	R	358	195	151	104	54
5009	Metatarsal III	R	348	181	137	102	52
5005	Metatarsal III	L	320	162	125	92	50
5280	Metatarsal III	L	365	200	155	108	54
5241	Metatarsal III	L	357	182	130	100	50
5278	Metatarsal IV	R	302	167	120	73	55
8966	Metatarsal IV	L	302	156	110	65	51
5279	Metatarsal IV	L	308	172	122	71	55
2002	Radius	R	187	118	71	68	63
2016	Tibia	R	725	327	250	233	45
2017	Tibia	R		343		244	??
2002	Ulna	L	229	133	76	59	58
2002	Ulna	R	225	130	84	61	57

CERATOSAURUS ?NASICORNIS ELEMENTS

NON-AXIAL

BYUVP Number	Element	Side	Length	Minimum Circumference	Proximal Width	Distal Width	C/LX100
5010	Metatarsal III	L					
5008	Metatarsal III	L		127	~105	67	47.

VERTEBRAE

BYUVP Number	Element	Length	Width	Height	Proximal Width	Distal Width	Neural Arch Height
4853	Caudal anterior						
8910	Caudal						
9161	Caudal	NA	NA	NA	NA	63	NA
9162	Caudal	NA	NA	60	53	NA	NA
9136	Caudal	NA	NA	~59	~56	56	NA
8982	Caudal	70	20	33	~28	33	49

VERTEBRAE (continued)

BYUVP Number	Element	Length	Width	Height	Proximal Width	Distal Width	Neural Arch Height
8938	Caudal	76	29	42	39	37	67
9152	Caudal	>80	22	~40	~40	39	>55
4838	Caudal	80	31	55	~54	~54	>35
9108	Caudal	83	34	48	50	47	NA
5254	Caudal	84	34	52	54	53	>30
9141	Caudal	90	NA	53	60	57	NA
8937	Caudal	92	NA	54	64	60	92
5092	Caudal	94	~52	53	~58	62	103
4908	Caudal	95	NA	70	65	61	NA
8974	Caudal posterior	91	~100	50	53	49	NA
9163	Caudal very post.	36	6	8	9	7.5	1
8907	Dorsal	88	NA	~80	76	~65	NA
9144	Dorsal mid. or post.	>70	NA	NA	NA	NA	NA
9142	Dorsal mid. or post.	83	NA	80	74	79	NA
9143	Dorsal mid. or post.	85	NA	75	64	63	NA
4951	Dorsal post.	<90	~170	<80	60	70	260
4952	Dorsal post.	96	206	85	75	~76	297

MISCELLANEOUS SMALL THEROPOD ELEMENTS

BYUVP Number	Genus	Element	Side	Length	Width	Height	Proximal Width	Distal Width	Neural Arch Height
5201	~Marshosaurus	Caudal		53	>40	28	>27	27	NA
4876	?Ornitholestes	Fibula	L	366			58	25	
5103	Stokesosaurus	Caudal		62	29	30	32	32	>15
8908	Stokesosaurus	Caudal Distal		66	NA	31	~35	35	NA
5073	Stokesosaurus	Caudal Distal		65	28	30	35	35	20
9012	Indeterminate	Caudal		50	7	22	23	19	20
4862	Indeterminate	Ischium	L	570			195	71	
4862	Indeterminate	Ischium	R	521			160	83	

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