ALLOSAURUS FRAGILIS: A REVISED OSTEOLOGY

by James H. Madsen, Jr.

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Frontispiece: Restoration of the skull and anterior presacral vertebrae of *Allosaurus fragilis.*

Preface to the Second Printing

My original revision of the osteology of *Allosaurus fragilis* was not intended as a morphological interpretation, but rather as a documentation of the *Allosaurus* skeleton based largely on the rich collection of fossils from the Cleveland-Lloyd Dinosaur Quarry. That work appears to have survived the test of time. The paper was out of print in less than a year of its publication and is now reprinted as an unchanged, second edition.

The essential descriptions have not changed with but two exceptions: 1) some of the elements originally interpreted as gastralia are now thought to be furculae by some workers and 2) the speculated placement of the proximal segment of metatarsal I of *Allosaurus* is now known to be metatarsal V based on the excellent skeleton of *Allosaurus* collected in northern Wyoming and presently under preparation and scrutiny at the Museum of the Rockies in Boseman, Montana.

The phenomenal, popular interest in dinosaurs has been a product of the explosive scientific interest and research in dinosaur paleontology in evidence over the past two decades. Hopefully, this second printing will be as well received and useful as the first.

Another publication by myself and Samuel P. Welles of the Museum of Paleontology at the University of California, Berkeley has been accepted for publication by the Utah Geological Survey. Its focus is a revised osteology for *Ceratosaurus*, modifying it to include two subfamilies. The methodology for the report is similar to that used in this publication.

I am very appreciative of the many, encouraging comments from friends and colleagues, too numerous to thoughtfully mention here. Any time is good, but right now is most certainly among the best times to be studying dinosaurs.

Jim Madsen - August 1993
Salt Lake City, Utah

Contents

ILLUSTRATIONS

in—internal naris

iptv—interpterygoid vacuity

isc—ischium, ischiac peduncle, or ischiac articulation

it—internal tuberosity or internal trochanter

ju—jugal or contact with jugal

juf—jugular foramen

jupr—jugal process

la—lachrymal or contact with lachrymal

lapr—lachrymal process

lav—lachrymal vacuity

li—scar for interspinous ligament

ls—laterosphenoid or contact with laterosphenoid

lt—lesser trochanter

ltf—lateral temporal fenestra

mc—Meckelian canal or metacarpal

meb—medial blade

mg—Meckelian groove

ms—medial symphysis or medial suture

mt—metatarsal

mvr—medial vertical ridge

mx—maxilla or contact with maxilla

mxf—maxillary fenestra

mxpr—maxillary process

mxr—maxillary ramus

mxs—maxillary septum

mxsi—maxillary sinus

na—nasal or contact with nasal

naf—nasal foramen

napr—nasal process

nar—nasal ramus

nc—neural canal

ne—facet for neurapophysis

ns—neural spine

o—olecranon process

oc—occipital condyle or facet for occipital condyle

od—odontoid

odc—concavity for odontoid

of—orbital fenestra

on—obturator notch

op—obturator process or opisthotic

or—orbit

os—orbitosphenoid

pa—parietal

pal—palatine or contact with palatine

papr—parietal process

pf—palatine fenestra

pitf—pituitary fossa

pl—pleurocoel

pm—premaxilla or contact with premaxilla

po—postorbital, contact with postorbital, or pos zygapophysis

pob—posterior blade

pof—postzygapophysial facet

popr—paroccipital process

pp—parapophysis

pr—prezygapophysis or prootic

pra—prearticular or contact with prearticular

prf—prefrontal or contact with prefrontal

ps—parasphenoid

pt—pterygoid

ptr—pterygoid ramus

pu—pubis, pubic peduncle, or pubic articulation

Abbreviations

aar—antarticular or contact with antarticular

ac—acromial process

act—acetabulum or acetabular border

amb—probable origin of ambiens muscle

an—angular or contact with angular

anb—anterior blade

aof—antorbital fenestra

ar—articular or contact with articular

ast—astragalus or contact with astragalus

at—facet for atlantal intercentrum

at in—atlantal intercentrum

ax—facet for axial centrum

axi—surface of contact with axial intercentrum

ax in—axial intercentrum

bi—biceps tubercle

bo—basioccipital

bpt—basipterygoid process, basal articulation of palate and braincase, or basipterygoid articulation

bs—basisphenoid

bt—basal tuberosity

c—coracoid or capitulum

ca—calcaneum or contact with calcaneum

ce—centrum

cf—coracoid foramen

ch—chevron

cn—cnemial crest

co—coronoid or contact with coronoid

de—dentary or contact with dentary

des—dentary symphysis, distal symphysis, or dorsum sellae

dp—diapophysis or deltopectoral crest

ecpt—ectopterygoid or contact with ectopterygoid

emf—external mandibular foramen

en—external naris or entepicondyle

eo—exoccipital

ep—epipophysis

ept—epipterygoid or contact with epipterygoid

F—femur

f—foramen

f'—posterior surangular foramen

f ''—midsurangular or external mandibular foramen

f '''—anterior surangular foramen

Fi—fibula

fib—fibular condyle or articular surface of fibula

fm—foramen magnum

fo—fenestra ovalis

fr—frontal or contact with frontal

frpr—frontal process

g—glenoid cavity

gl—jaw articulation (glenoid fossa)

gt—greater trochanter

H—humerus

h—head

hc—haemal canal

he—head of humerus

hu—attachment of the humeroradialis muscle

hy—hyposphene

i—intermedium

idp—interdental plates

il—iliac articulation

imf—internal mandibular foramen

qj—quadratojugal or contact with quadratojugal

qjpr—quadratojugal process

qu—quadrate or contact with quadrate

quc—quadrate cotylus

quf—quadrate foramen

R—radius

ra—radiale

repr—retroarticular process

rc—radial condyle

ru—distal articulation of radius and ulna

S—scapula

s—shaft

s_1, s_2, s_3, s_4, s_5—sacral vertebrae

sa—surangular or contact with surangular

saf—surangular foramen

sar—surangular ramus

sd—supradentary

snf—subnarial foramen

soc—supraoccipital

sp—splenial

sq—squamosal or contact with squamosal

sqpr—squamosal process

sr_1, sr_2, sr_3, sr_4, sr_5—attachment scars of sacral ribs

st—stapes

stf—subtemporal fenestra

T—tibia

t—tarsal

tf—temporal fenestra

tib—tibial condyle or articular surface for tibia

tr—transverse process

tr_1, tr_2, tr_3, tr_4, tr_5—transverse processes of sacral verte-brae or scars for attachment of sacral transverse processes

tr_4—fourth trochanter

tu—tuberculum

U—ulna

uc—ulnar condyle

un—ulnare

vo—vomer or contact with vomer

x—bone of uncertain nature

Acknowledgements

Many people have helped in various ways with the completion of this study. The manuscript was reviewed in its many stages by Edwin H. Colbert, Joseph T. Gregory, Robert A. Long, John H. Ostrom, William Lee Stokes, Samuel P. Welles, and Theodore E. White, to whom I offer my sincerest thanks for their contributions, encouragement, instruction, and patience.

Although I prepared many of the original bones, I received indispensible help from student assistants and preparators at the University of Utah over the past sixteen years. Among them are: Richard Allan, Patricia B. Bizuk, Donald M. Blue, Samuel Gary, Jr., Kermit F. Horn, Lori A. Kepner, Kristen Petersen, Russell E. Peterson, Robert L. Randolph, Dwayne D. Stone, Bryce T. Tripp, Glen J. Ungerman, and William W. White, III. Staff members of the Department of Geology who contributed their talents in preparation are Phyllis Wilcken and Golden York, retired Curator of Geology.

The illustrations were begun by Megan A. Friedland and completed by Ruth Ann Kocour and Sandie Kesler. Cover illustration by Greg F. McLaughlin. Photographic work was done by James R. Howell, III, and myself.

Requests for the loan of specimens were promptly answered by Nicholas Hotton, III, United States National Museum—holotype of *Antrodemus valens*; John H. Ostrom, Peabody Museum of Natural History—holotype of *Allosaurus fragilis*; Bryan Patterson, Museum of Comparative Zoology—undescribed specimen of *Allosaurus*; and Eugene Gaffney, American Museum of Natural History—type of *Epanterias amplexus*.

Special preparation to expose the palatal area of the fine skull (UUVP 6000) of *Allosaurus fragilis* was done by Tobe Wilkins under the supervision of Theodore E. White at Dinosaur National Monument.

Since the University of Utah Cooperative Dinosaur Project was originally conceived and designed to facilitate the collection of specimens for exhibit as well as for study, acknowledgement is due the institutions, aside from the University of Utah, that supported the project. The expense of conducting such an expedition was thought to be too much for a single institution and, therefore, the financial burden might be more practically shared by a maximum of five institutions per summer. Accordingly, each contributor would receive a mountable, composite specimen, as complete as possible, of *Allosaurus fragilis* or another dinosaur of its choice.[1] These supporting institutions are:

Brigham Young University, Provo, Utah (No. 30A/o, C/c)

Buffalo Museum of Science, Buffalo, New York (No. 25A/o)

Bureau of Culture Center, Kagoshima, Japan (No. 22A/o, C/o)

Bureau of Land Management, Cleveland-Lloyd Dinosaur Quarry, Emery County, Utah (No. 22A/o)

California Academy of Sciences, San Francisco, California (No. 33A/o)

City of Liverpool, England (No. 22A/c, C/c)

College of Eastern Utah, Price, Utah (No. 27A/o, C/c)

Emery County Museum of Natural History, Castle Dale, Utah (No. 22A/c)

Exhibit Museum, Ann Arbor, Michigan (No. 30A/o)

Fort Worth Museum of Science and History, Fort Worth, Texas (No. 22A/o, C/c)

Brazosport Museum of Natural History, Freeport, Texas (No. 33A/c)

Historical Museum and Institute of Western Colorado, Grand Junction, Colorado (No. 33A/c)

Hokkaido Centennial Office, Hokkaido, Japan (No. 33A/c)

Institute for Breeding Research, Tokyo University of Agriculture, Tokyo, Japan (No. 33A/c, C/c)

Joseph Moore Museum, Richmond, Indiana (No. 27A/o)

Los Angeles County Museum of Natural History, Los Angeles, California (No. 27A/o, C/o, S/o)

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[1] A key to the composition and identity of the specific skeletons is as follows: A = *Allosaurus* and its size; C = *Camptosaurus*; c = cast specimen; o = original specimen in part; and S = *Stegosaurus*.

ALLOSAURUS FRAGILIS: A REVISED OSTEOLOGY

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ABSTRACT

Forty-nine years have elapsed since the initial collection of dinosaur remains by professional paleontologists from the Cleveland-Lloyd Dinosaur Quarry, during which time little descriptive work has been published on this extraordinary site. A massive accumulation of dinosaur bones pertaining to at least eleven genera, and possibly more, lie within the Brushy Basin Member of the Late Jurassic Morrison Formation. *Allosaurus fragilis*, the most common taxon, is represented by bones from many individuals of different size. Bones from the Cleveland-Lloyd Dinosaur Quarry are extremely well preserved but from almost completely disarticulated skeletons. Sixty or more individuals are indicated by more than ten thousand elements. Practically every bone of the skeleton of *Allosaurus fragilis* from juvenile to adult has been recovered since the first organized excavation in 1927. Growth stages of this species represent individuals ranging from one to four and one-half meters in height and from three to twelve meters in length. The disassociation of skeletal material is an advantage in illustrating and describing contacts and sutures between those bones normally found together or coossified. The variety, preservation, and great number of bones may never be as well represented for any other theropod genus. Although descriptions and illustrations are often of composite bones, they are based on numerous elements. The material is also more than adequate for studies of growth, individual variation, and abnormality.

INTRODUCTION

Cleveland-Lloyd Dinosaur Quarry

The Cleveland-Lloyd site (figure 1) was worked as early as 1927, when a field party from the Department of Geology of the University of Utah under the direction of Chairman Ferdinand F. Hintze and his assistant, Curator of Geology, Golden York, visited the area. Over several weeks an estimated 800 bones, representing most taxa of the Cleveland-Lloyd fauna, were collected by the expedition.

No further institutional interest was shown in the locality until 1939, when a field party from Princeton University led by William Lee Stokes began work, which was to continue for three successive summers and which was to culminate in the collection of approximately 1,200 bones. A description by Stokes (1945) of the locality and its potential generated little interest in the discovery, and except for the depredations of amateur collectors, the Cleveland-Lloyd Dinosaur Quarry remained unprotected and unworked until 1960.

Based on the assumption that a single institution could no longer bear the entire financial burden of a systematic quarrying effort, Stokes and I organized the University of Utah Cooperative Dinosaur Project. At this writing nearly forty separate institutions and agencies have benefited from the quarrying activities during the summers of 1960 and 1965. The collections made by the University of Utah field parties and the bulk of the Princeton collection purchased by the project in 1964 totaled more than 10,000 bones. Even though over 50 composite skeletons, some entirely cast and others containing varying numbers of original bones, have been assembled and sent to contributing institutions over a period of 16 years, a comprehensive research collection has been assembled and maintained at the University of Utah. The collection has been available for study since the conclusion of the initial or collecting phase of the University of Utah Cooperative Dinosaur Project in 1965. The remaining collection, developed during the second or research phase, now consists of more than 5,000 elements, many of which are still not completely prepared.

The Cleveland-Lloyd Dinosaur Quarry, designated a Natural Landmark in 1967, is now under the jurisdiction of the Bureau of Land Management of the United States Department of the Interior. That agency has developed an interpretive center at the site and has plans for an *in situ* exhibit that will allow visitors to observe quarrying and preparation activities. As always, long-range plans of this kind are nebulous. However, as funds become available, Utah will add another important paleontological exhibit to its expanding list of natural history attractions.

General Discussion

Although some of the descriptions and illustrations prepared for this paper are repetitious of Gilmore's (1920) fine work, they are necessary to maintain continuity in presenting a complete description of the osteology of *Allosaurus fragilis*. No single, articulated skeleton is described from the Cleveland

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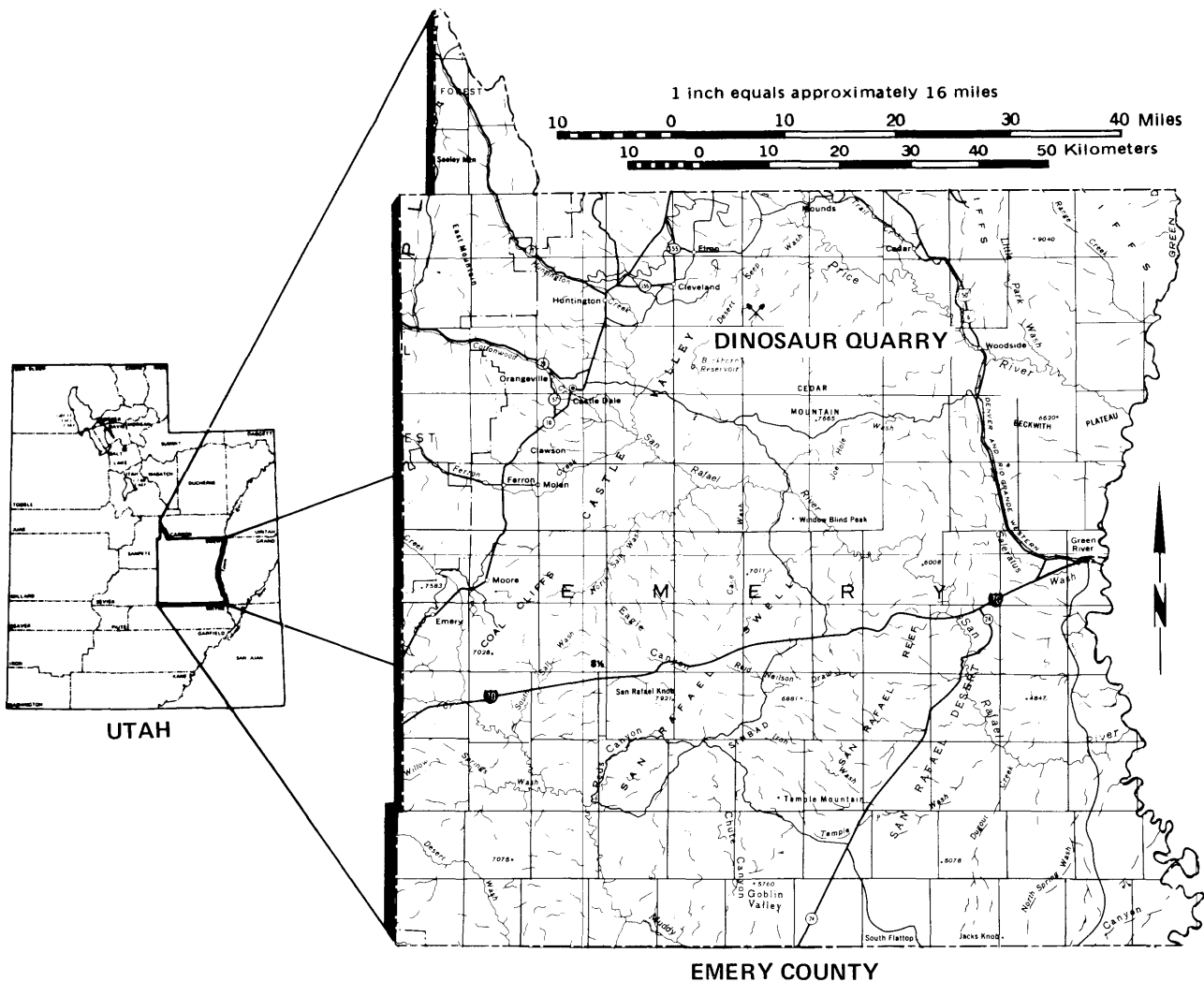
Figure 1. Location map, Cleveland-Lloyd Dinosaur Quarry.

Lloyd Dinosaur Quarry. There was near total maceration of carcasses prior to burial so that collecting complete, articulated skeletons is not possible. Therefore, the illustrations and descriptions are of composites represented by the best available elements in the University of Utah Vertebrate Paleontology Collection, which includes the excellent but incomplete articulated skeleton (UUVP 6000) collected from Dinosaur National Monument near Jensen, Utah. Rather than emphasize individual variation, an average *Allosaurus fragilis* is described and illustrated; specific exceptions are noted only where germane to a more complete understanding of the osteology.

The scattered condition of the bones in the Cleveland-Lloyd Dinosaur Quarry (figure 2) caused difficulties during the first year (1960) of the University of Utah Cooperative Dinosaur Project in

selecting mountable composite specimens for contributors. This problem was further complicated by the occurrence of *Allosaurus fragilis* in many growth stages (figure 3). My early attempts at separating the various sizes of *A. fragilis* were based on a proportional scale constructed from measurements of USNM 4734 (Gilmore, 1920) and my own measurements of UUVP 6000. By extrapolating in 2½-inch increments between the largest and smallest femora in the Cleveland-Lloyd Dinosaur Collection, an arbitrary size assignment was given to all *A. fragilis* material. The length of a femur was chosen as a basis for the size designations; for example, a femur with a maximum length of 30 inches belongs to a No. 30 *A. fragilis*. There were obvious pitfalls in using this method for assembling the composite skeletons of different sizes, the main problem being, of course, that it was necessary to assume all elements grow proportionately. This method allowed little room for a consideration of individual
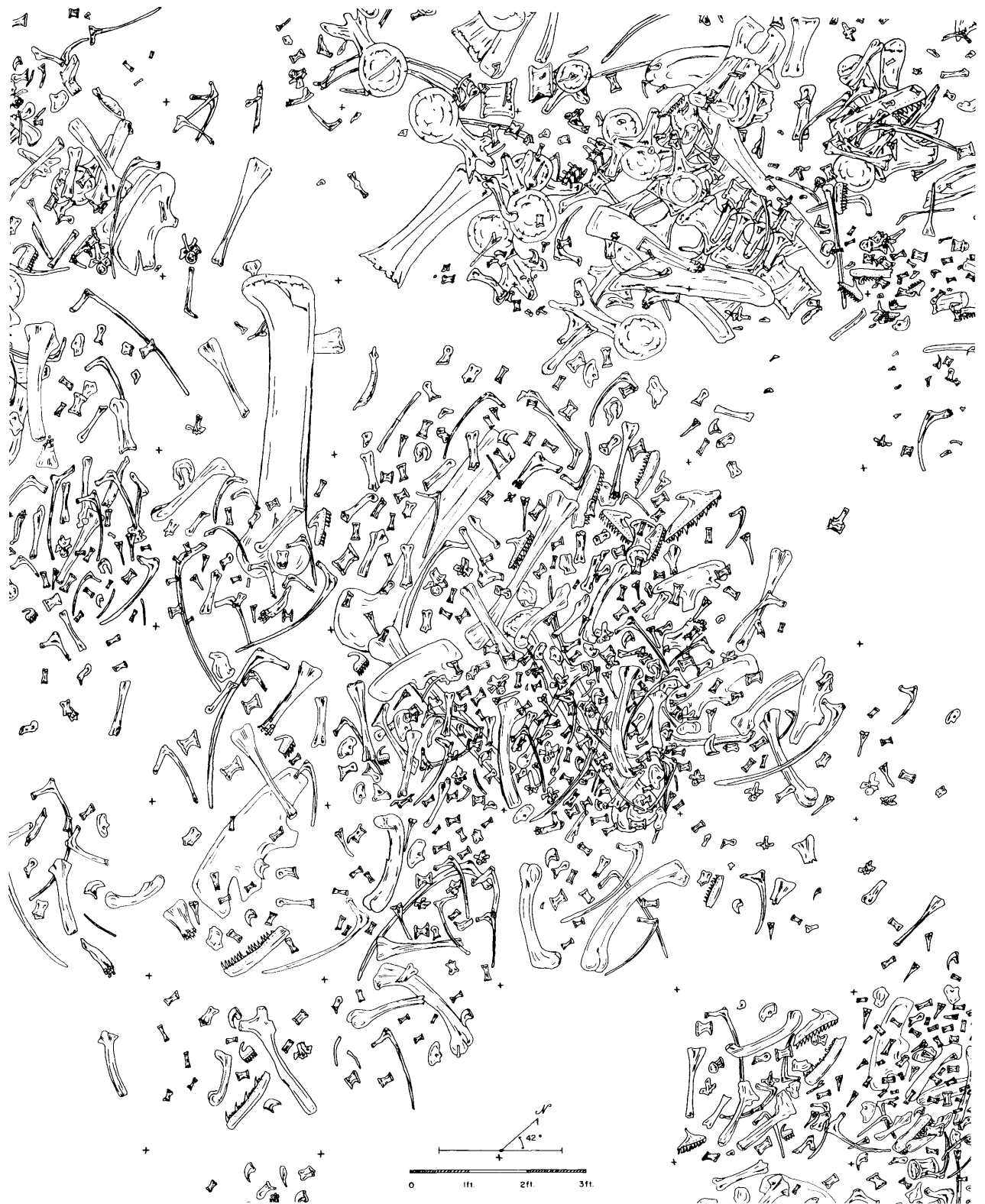
Figure 2. Section of composite map of the Cleveland-Lloyd Dinosaur Quarry, University of Utah Cooperative Dinosaur Project. Map compiled in August 1967 from quarry activity, 1960 through 1964.
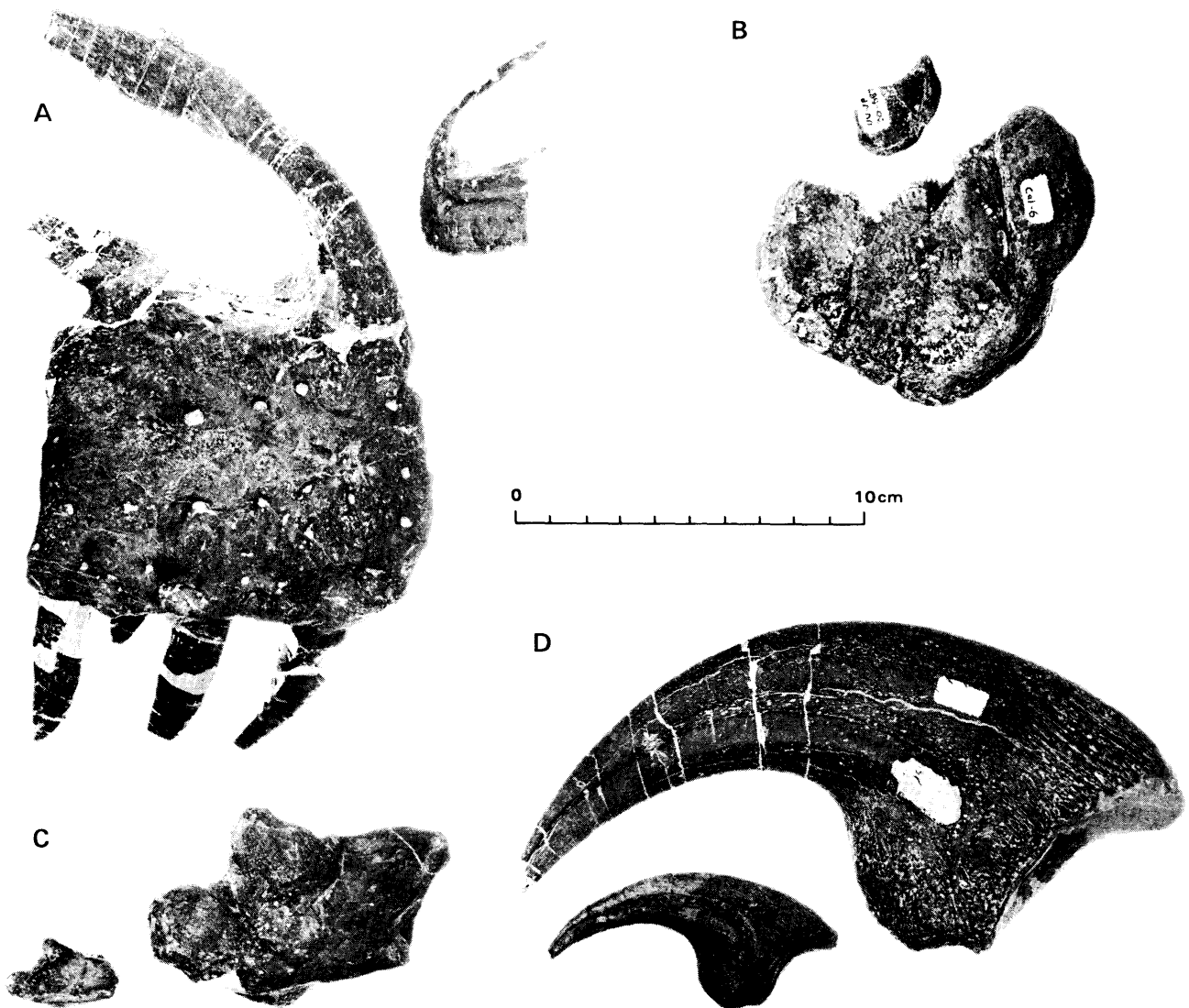
Figure 3. Examples of extremes in size of selected elements of *Allosaurus fragilis* from the Cleveland-Lloyd Dinosaur Quarry. Premaxillae
(A), calcanea (B), metacarpals (C), and unguals (D).

variation, pathology, sexual dimorphism, or allometric growth.

As a consequence, several of the first specimens delivered to contributors had to be returned to the University of Utah for resizing. In the years that followed, enough material was acquired to permit visual comparison of the various sizes of skeletons in addition to the proportional scale reference.

From the beginning, the project was organized so that at the conclusion of the first phase, after all commitments were met for original material, there would be ample research specimens available for later study. Therefore, great care was exercised over the years in retaining scientifically important elements in the collection to preclude possible recall of material at a later date. The policy then became one of preparing casts of original elements for which there were no original duplicates, which enabled me to send accurate plaster casts as substitutes for original elements used in exhibits. As the work of duplicating specimens with latex molds progressed, it was found practical to make complete sets of molds for the various sizes of *Allosaurus fragilis*. This ultimately resulted in numerous specimens cast entirely in plaster or plastic (Madsen,

1973). The large inventory of molds also enabled the project to supply missing casts as required in the preparation of exhibit specimens.

Acronyms for institutions that have specimens referred to in the text are as follows:

AMNH—American Museum of Natural History

MCZ—Museum of Comparative Zoology, Harvard

UUVP—University of Utah Vertebrate Paleontology Collection

USNM—United States National Museum

YPM—Peabody Museum of Natural History, Yale University

Fauna and Prehistory

At this writing the faunal elements recognized in the Cleveland-Lloyd Dinosaur Collection pertain to both orders of dinosaurs, Ornithischia and Saurischia. Ornithischians include *Camptosaurus, Stegosaurus,* and an unidentified quadruped with ankylosaurian affinities. Saurischians include the sauropods— *Camarasaurus,* and possibly *Apatosaurus, Barosaurus,* or *Diplodocus* and the theropods—*Allosaurus fragilis, Ceratosaurus sp., Stokesosaurus clevelandi* (Madsen, 1974), and *Marshosaurus bicentesimus* (Madsen, 1976).

Allosaurus fragilis, the most common member of the Cleveland-Lloyd fauna, constitutes almost three-quarters of the total dinosaur population. This estimate is based on the occurrence of 44 left femora of *A. fragilis.* In addition, there are diagnostic parts of five sauropods, five camptosaurs, three stegosaurs, one questionable ankylosaurid, one ceratosaur, and at least five small to moderate sized theropods assignable to two new genera.

The size range of allosaurs in the Cleveland-Lloyd Dinosaur Quarry, based on diagnostic material such as femora, indicates a maximum No. 40, and minimum No. 10. This material, loosely interpreted and assuming fully erect, bipedal posture, indicates an adult 12 meters in length, standing 4.5 meters tall, and a juvenile 3 meters in length, standing one meter tall. By applying these same proportions to the largest specimen of *Allosaurus fragilis* known to me (AMNH 5767, *Epanterias amplexus* Cope: see Osborn and Mook, 1921, p. 282), I find that *A. fragilis* would be 13 meters in length standing 5 meters tall. The largest *A. fragilis* would have rivaled *Tyrannosaurus* in size.

It is convenient to standardize references to theropod size, that is, make size comparisons, one

taxon with another, only when the maturity of the individuals are known or demonstrated. Otherwise, a comparison may imply that a given species occurs in one size only without deference to ontogenetic variation as evident in the Cleveland-Lloyd allosaurs. A convenient, however arbitrary, adjective scale for describing theropods in terms of overall length (snout to tip of tail) is as follows: very small, 0-1.5 meters; small, 1.5-3 meters; medium, 3-7 meters; large, 7-11 meters; very large, 11-15 meters; and extremely large, 15 meters and over. An application of these adjectives to theropods is as follows: *Allosaurus fragilis* (*Epanterias*), AMNH 5767, and *Tyrannosaurus,* USNM 973, are very large, whereas *Coelophysis* is small.

A general analysis of the conditions culminating in the rich accumulation of dinosaur remains in the Cleveland-Lloyd Quarry should include consideration of the following:

1. The ratio of carnivorous to herbivorous kinds (3:1) is out of balance when compared with typical or expected populations of large, terrestrial vertebrates.

2. As a rule, individual bones are usually intact, although some exhibit what appear to be green or willow breaks (figure 4) in contrast with the post-diagenetic distortion attributed to folding or faulting.

3. Scattering of disarticulated elements is evident. Bones belonging to an individual animal may be spread over an area six meters or more in diameter.

4. Many bones or parts thereof are free of the usual limy matrix. There is a preferred concentration of limestone matrix around many bones or areas on bones that have a rugose surface for the attachment of cartilage or ligamental tissue.

The fossiliferous sediments are poorly stratified, bentonitic, calcareous and siliceous shales that are overlain by a dense, hard, tuffaceous, freshwater limestone.

6. Invertebrates and plant fossils are rare in association with the dinosaur remains and consist of a few gastropods and charophytes. Some poorly preserved gastropods are sometimes uncovered during the preparation of bones but are almost unidentifiable below the genus level. They appear tentatively assignable to the genera *Amplovalvata, Amplovoluta, Valvata,* and *Viviparus*; however, they are diagnostic of little more than a freshwater environment of deposition (Norman F. Sohl and John H. Hanley, personal communications).

Gyrogonites found in washed samples from the quarry include *Aclistochara bransoni* Peck, *Latochara*
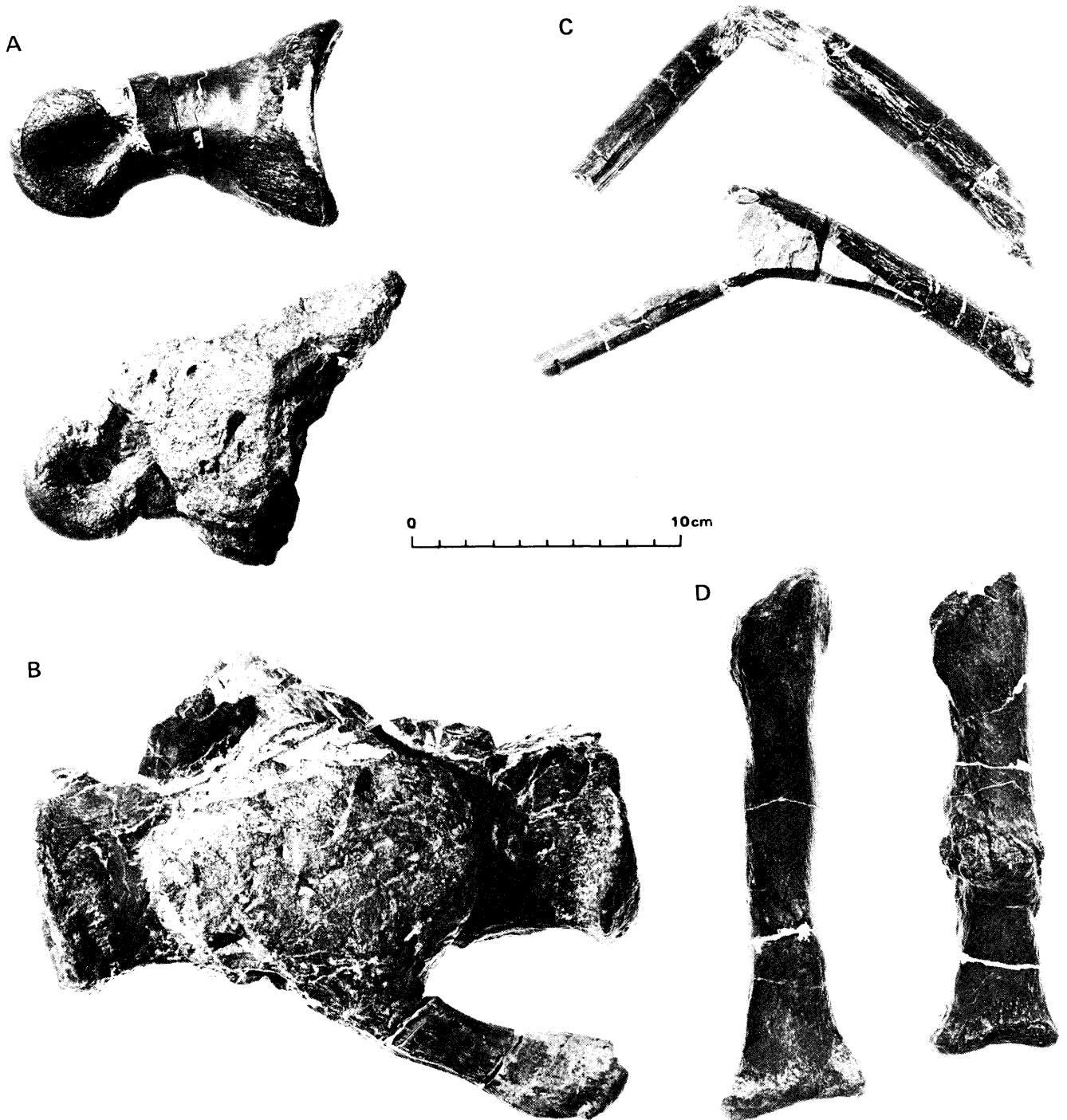
Figure 4. Bones of *Allosaurus fragilis* showing representative pathologies in the Cleveland-Lloyd Dinosaur Collection. Normal (UUVP 40-100) and abnormal (UUVP 1657) proximal phalanges, D-III, left pes (A); fused midcaudal vertebrae (UUVP 3771) and chevron (B); ribs with willow breaks (C); and normal (UUVP 86) and fractured (UUVP 687) right radii (D).

concinna Peck, *Latochara latitruncata* Peck, and *Stellatochara obovata* (Peck). Such fossils are indicative of shallow, quiet, or slowly moving bodies of fresh or brackish water, and these particular species are quite similar to charophytes from the Kimmeridgian of

Germany and bear some resemblance to those of the Purbeck (Raymond E. Peck, personal communication).

7. Although the scattering appears random, most elements with a significantly long dimension tend to be

A

B

C

0   10 cm
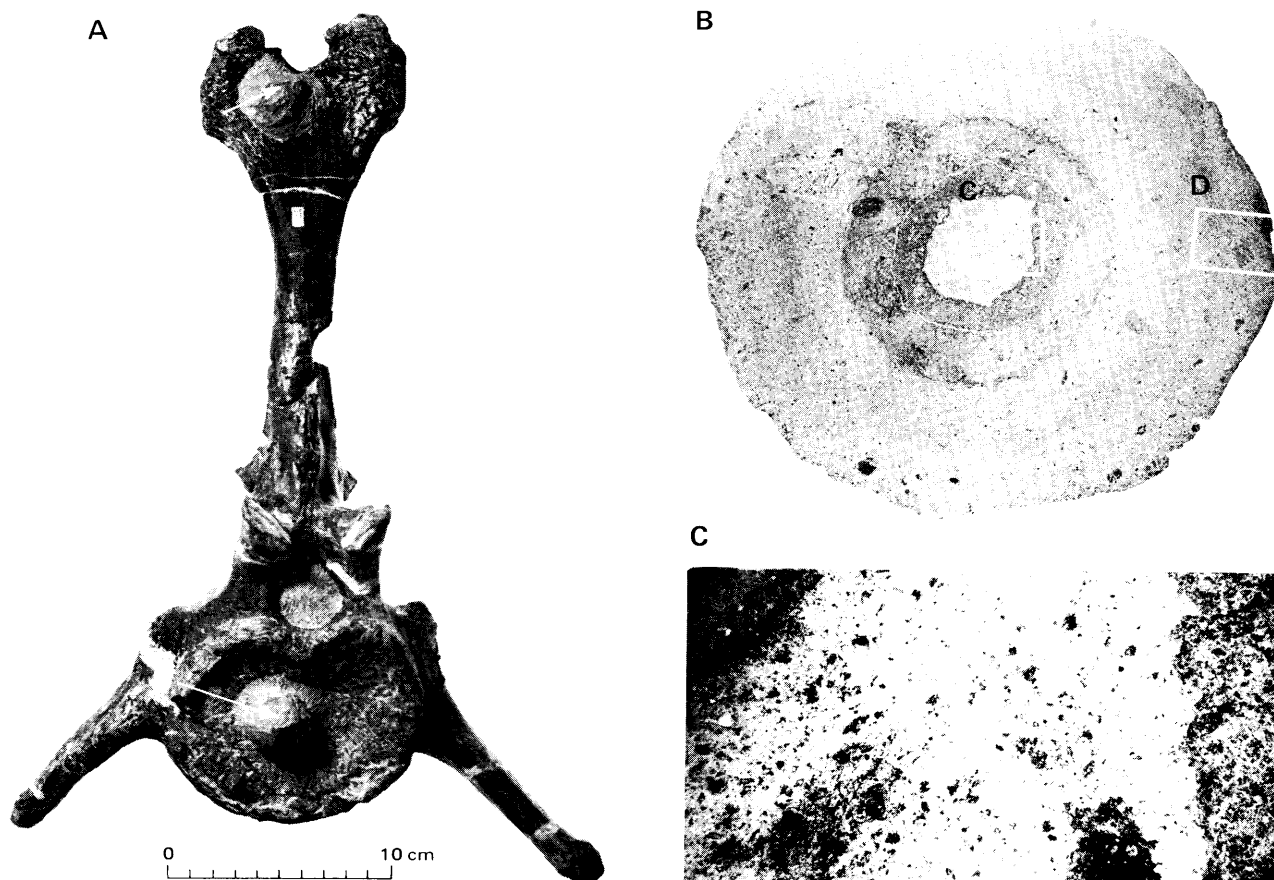
Figure 5. Proximal view of anterior caudal vertebra of *Stegosaurus sp.* (UUVP 10,049) showing two concretions (arrows) in place (A) and a cross section (x 2) through a concretion (B) with enlargements (x 14) of two areas (C, D).

D

oriented in a horizontal or nearly horizontal plane relative to the bedding, which indicates that perhaps disassociation of skeletons took place prior to their subsequent burial on a relatively flat substratum.

8. Growth stages of *Allosaurus fragilis* present at the Cleveland-Lloyd site indicate an apparent random sample of an average population and may be interpreted as evidence either for a gregarious habit of the species or for a catastrophic condition that worked to isolate only the more mobile types.

9. Small limestone concretions ranging from one to five centimeters in diameter are commonly found associated or, in some instances, attached to the bones (figure 5). They may also occur as part of the limestone matrix, which completely encases some elements.

10. An alternate grouping of the members of the Cleveland-Lloyd fauna, that is, bipeds versus quadrupeds, is even more dramatic than the imbalance between carnivores and herbivores. It suggests that

mobility may have been the most important factor in determining the members of the fauna.

11. Predator or scavenger activity is indicated by numerous elements which inconsistently lack fragile parts or exhibit fractures in weak areas that appear to have occurred in green bone. These conditions do not

appear to be related to depositional dynamics. A large number of bones, descriptively treated as partially digested or weathered, are loosely interpreted as material that may have been ingested by predators or scavengers during feeding activity. Few of these fragments are identifiable, and their wear suggests erosion or abrasion that removed perichondral bone from areas of high relief and left the underlying trabecular bone exposed.

12. Very small juveniles or hatchlings of *Allosaurus fragilis* are missing. Their absence might be attributed to predator or scavenger activity, restricted mobility, noninterest in the area, or even cannibalism.

13. An area two by six meters of the depositional interface between the limestone and the underlying fossiliferous beds was exposed. It revealed a gently undulating surface that suggests a definite change in deposition but not necessarily an erosional break or hiatus.

14. Isolated teeth of both carnivorous and herbivorous forms are commonly found in the quarry. The occurrence of the carnivorous types may be attributed to at least two causes: (a) fitting loosely in the alveoli they might easily be separated from the jaws by scavenger activity or by movement during burial; and (b) the teeth would be lost routinely during feeding, whether it be predation or scavenging.

15. The absence of other reptilian forms is unusual. The total amount of chelonian material (*Glyptops*) suggests only one or two individuals, and the presence of crocodilians such as *Goniopholis* has not been definitely established.

16. A current, but tentative, census of the Cleveland-Lloyd dinosaurs is as follows:

Theropods

(1) *Allosaurus fragilis* (figure 6)—at least 44 individuals based on a count of 83 femora (44 left and 39 right).

(2) *Ceratosaurus sp.*—disassociated elements, all of which seem assignable to a single individual.

(3) *Stokesosaurus clevelandi*—two individuals indicated by right and left ilia of significantly different size.

(4) *Marshosaurus bicentesimus*—two individuals of about the same size, based on two right ilia and tooth-bearing elements of the skull.

Sauropods

(1) *Camarasaurus* cf. *lentus*—two or three individuals.

(2) Unidentified—at least one and perhaps two noncamarasaurid genera indicated.

Nine coracoids indicate a minimum of five sauropods.

Ornithopods

(1) *Camptosaurus* cf. *browni* (figure 6)—at least five individuals, but the specific determination is questionable.

(2) Unidentified—diagnostic material is limited; it may be a juvenile camptosaur.

Stegosaurids

(1) *Stegosaurus* cf. *stenops*—at least two individuals.

(2) *Stegosaurus sp.*—related material unstudied; it may represent two or three individuals.

Ankylosaurid

(1) Unidentified—related material limited but diagnostic.

Theories on the demise of the Cleveland-Lloyd dinosaurs are but slightly fewer in number than visitors to the quarry. They range in scope from obvious association with the biblical flood to more scholarly interpretations of climatic change, regional uplift, disease, continental drift, and volcanic pollution, to name a few. Although the temptation is great to present a discussion of taphonomy at this point, it would be premature and somewhat beyond the scope of this study. Furthermore, a group of vertebrate paleontologists including Robert Bakker, Kay Behrensmeyer, Peter Dodson, and John McIntosh is preparing a detailed description of the paleoecology of the Morrison Formation, which is a better and more precise treatment than I am prepared to present at this time.

LOCATION AND STRATIGRAPHY

The Cleveland-Lloyd Dinosaur Quarry (figure 1) is approximately twenty miles south of Price, Carbon County, Utah, and eight miles east of Cleveland, Emery County, Utah (SE¼SE¼ sec. 21, T. 17 S., R. 11 E., S.L.B.M., lat. 39°19′00″N., long.
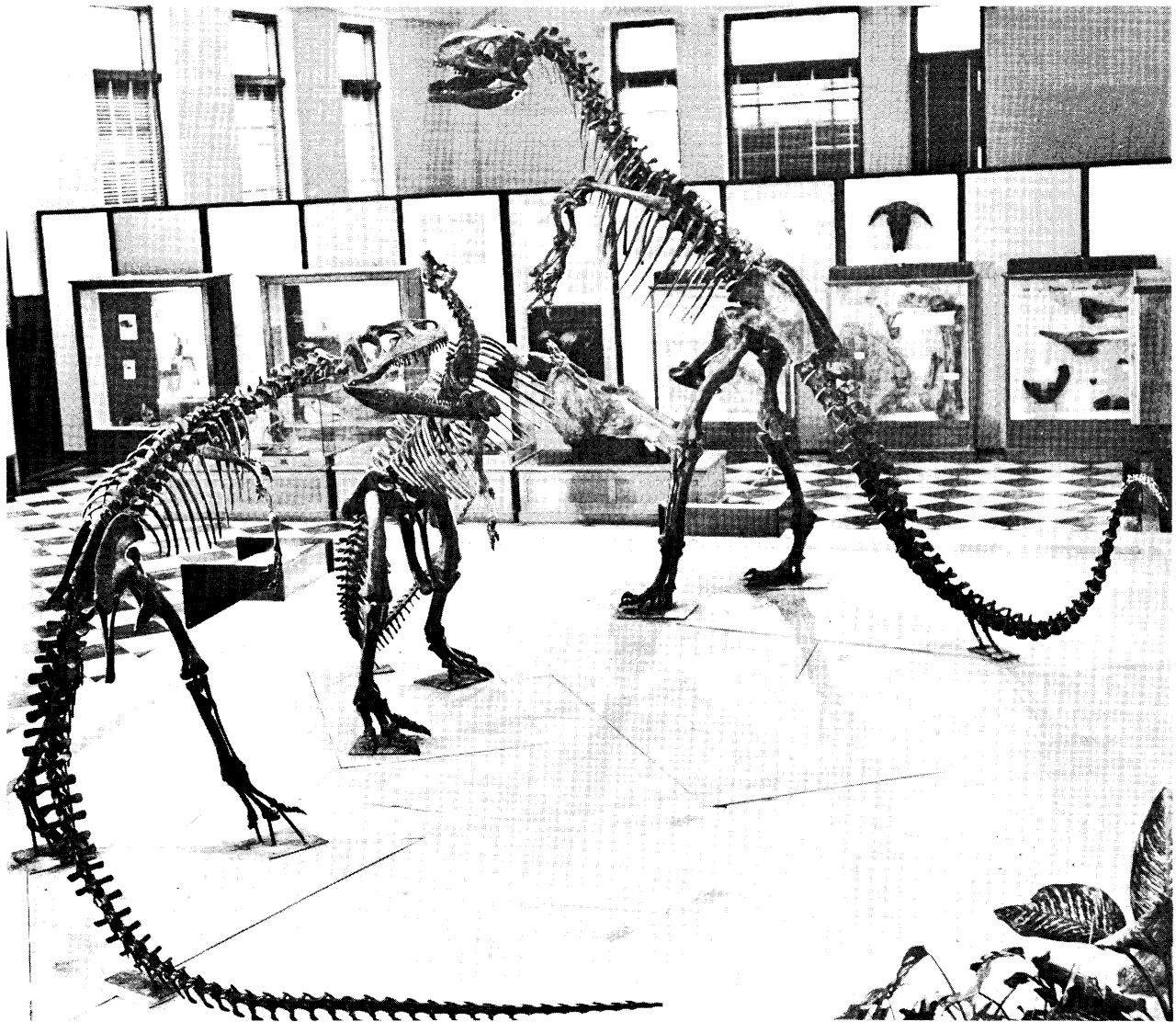
Figure 6. Dinosaur exhibit in the Utah Museum of Natural History on the University of Utah campus. Left side is *Allosaurus*, center is *Camptosaurus*, and right side is *Allosaurus*.

110°41'15"W.). Although fragmental and isolated dinosaur bones are commonly found along the extensive Morrison Formation outcrop around the north end of the San Rafael Swell, no concentration of bones similar to the Cleveland-Lloyd Dinosaur Quarry is known from contiguous areas.

The bone concentration at the quarry is overlain by an easily recognized dense, yellow-brown weathering, siliceous, freshwater limestone that forms low ledges in the vicinity of the quarry. The Morrison Formation is divisible into two members at the Cleveland-Lloyd Dinosaur Quarry, the Brushy Basin above and the Salt Wash below, and is underlain by the Summerville Formation (Stokes and Cohenour, 1956, p. 27). The upper limit of the Brushy Basin

Member is drawn at the top of the characteristic repetition of variegated shales and sandstones and at the base of the extensive basal conglomerate of the Lower Cretaceous Cedar Mountain Formation, which contact is approximately 150 feet above the fossiliferous bed.

SYSTEMATICS

Class REPTILIA
Order SAURISCHIA Seeley, 1888
Suborder THEROPODA Marsh, 1881
Family ALLOSAURIDAE Marsh, 1878

Definition. Medium- to very large-sized theropods, robust and completely bipedal. Skull large,

narrow, and elongate. Premaxilla with 5 teeth. Complex maxillary sinus, laterally, dorsally, and medially perforate. Interdental plates present and fused. Nine cervical, 14 dorsal, 5 sacral, and 48 to 51 caudal vertebrae. Manus and pes functionally tridactyl. Pubis with open obturator notch and large, distal expansion. Cervical and anterior dorsal vertebrae cavernous and opisthocoelus. Forelimb reduced, but strong.

Discussion. Marsh (1878, p. 242) based the Family Allosauridae upon the single genus *Allosaurus.* One year later (1879, p. 90) he added the genera *Creosaurus* and *Labrosaurus.* Ironically, the latter two genera were to become junior synonyms of the former, leaving the family monotypic, which is systematically how it should have remained. A review of all subsequent nomenclatural changes would be tedious and unnecessary. The fact remains that since Zittel (1890, p. 722) assigned the genus *Antrodemus* (=*Allosaurus*) to the Megalosauridae, it has remained there to the present (White, 1973, p. 120, 121) generally unchallenged in spite of common usage to the contrary (Colbert and Russell, 1969, p. 45).

An analysis of the polyphyletic genus *Megalosaurus* is far beyond the intent of this study, but consideration of the type material originally described by Buckland (1824) and later reviewed by Owen (1842, 1857) is relevant to this argument. Since the type of a genus is a species and the type of a family is that genus, then there should be many similarities between two genera in the same family, an obviously academic point. However, except for the recurved, serrate, sharply pointed teeth, the type of *Megalosaurus bucklandi,* a left dentary, differs from *Allosaurus fragilis* in virtually every respect:

Allosaurus fragilis	*Megalosaurus bucklandi*
anterior margin evenly rounded	anterior margin angularly rounded
symphysis flattened medially	symphysis rounded
interdental plates fused	interdental plates separate
lingual bar rounded	lingual bar flattened
ventral margin bowed	ventral margin straight
alveoli continuous to anterior margin	alveoli not continuous to margin
Meckelian groove uniformly narrow	Meckelian groove uneven
lateral surface evenly rounded	lateral surface flattened
replacement teeth hidden	replacement teeth exposed at base between interdental plates

The morphological disparity in these jaw elements alone precludes a close phylogenetic association of the two taxa and, accordingly, emphasizes the need to maintain the genera separate at the family level.

Walker (1964, p. 127) considers *Allosaurus* (his *Antrodemus*) to be typical of the Family Megalosauridae based on the lack of a surangular foramen. *Allosaurus* is definitely not a typical Megalosaur, and it does have a surangular foramen (f ', plate 9).

Distribution. Oxfordian to Portlandian; western interior of North America, East Africa, and England.

Allosaurus Marsh, 1877

Marsh, O. C., 1877. American Journal of Science, v. 3, no. 14, p. 514-516.

Type Species. Allosaurus fragilis.

Distribution. Kimmeridgian of northwest Colorado, southeast Wyoming, and eastern and east-central Utah.

Diagnosis. Same as for the species, given below.

Allosaurus fragilis Marsh, 1877

Marsh, O. C., 1877. American Journal of Science, v. 3, no. 14, p. 514-516.

Type. YPM 1930: a proximal phalanx of the third digit of a right pes, a centrum of a mid-dorsal vertebra, a centrum of the thirteenth or fourteenth dorsal vertebra, and a section from midshaft of a right humerus.

Paratype. USNM 4734 (Gilmore, 1920).

Neotype. UUVP 6000: a complete skull and a partial skeleton lacking all but the first caudal vertebra, chevrons, ribs, forearms, and some digital elements of the pes.

Horizon. Morrison Formation, uppermost unit.

Localities. YPM 1930 and USNM 4734 (Quarry No. 1, Gilmore, 1920, p. 7), Garden Park near Canon City, Fremont County, Colorado; and UUVP 6000, Dinosaur National Monument, five miles north of Jensen, Uintah County, Utah.

Diagnosis. A very large theropod with a large head. Skull and mandible elongate, robust, and subequal in

length to femora and ilia (within 5 percent). Tooth formula:

$$\frac{5+(15\pm1)}{16\pm1}$$

Maxilla with complex sinus (second antorbital fenestra of some authors) perforate laterally, dorsally, and medially. Vomers fused in an anteriorly elongated shaft divided posteriorly. Supraoccipital is unpaired and enters margin of foramen magnum. Quadrate inclined forward to nearly vertical. Mandible with three accessory bones including a true coronoid. Pubis strong with conspicuous, large, distal expansion may or may not be distally and medially fused. Distal end of ischium asymmetrically expanded. Nine cervical, 14 dorsal, 5 sacral, and 48 to 51 caudal vertebrae. Cervical and first two dorsal vertebrae strongly opisthocoelous. Third dorsal vertebra platycoelous. Posterior dorsals variably amphiplatyan. Sacral vertebrae locked by ridges and grooves on articular faces of centra. Anterior caudal vertebrae moderately amphicoelous, becoming increasingly so posteriorly. Except for the first caudal, the successive 40 or so vertebrae bear haemal arches. Caudal centra neither hollow nor cavernous. Forearm and manus long, strong with three digits in manus. Digital formula 2-3-4-0-0. Hind limbs robust, having four (five?) digits in pes with II, III, and IV evenly spaced or tridactyl anteriorly and I diminutive, posterolateral in approximate opposition to II, III, and IV; V may be represented by the proximal half only. Digital formula 2-3-4-5-0.

Discussion. The first scientific reference to fossil remains assignable to this theropod was published over one hundred years ago, so it seems appropriate to reexamine it now and attempt to eliminate some of the confusion that has accumulated over the years. Although numerous corrections to the work of others considering *Allosaurus fragilis* and related forms are to follow in this study, they are made in the interests of accuracy, and as such are not intended to demean earlier efforts. Stated another way: it is possible to restudy *A. fragilis* now, having the mass of original material from the Cleveland-Lloyd Dinosaur Quarry that was not available to previous authors.

The first reference to the taxon under discussion is in what appears to be the printed minutes of the weekly meetings of the Academy of Natural Sciences of Philadelphia, wherein Leidy (1870, p. 3) tentatively identified the posterior half of an anterior caudal centrum, submitted to him by Ferdinand Hayden, as belonging to the genus *Poicilopleuron*: "It is from Middle Park, Colorado, and Prof. Hayden thinks was derived from a Cretaceous formation." He concluded:

"The species represented by the fossil may be named *Poicilopleuron valens.* Should the division of the medullary cavity of the vertebral body into smaller recesses by the trabeculae be significant of other characters indicating the Colorado saurian to be distinct from *Poicilopleuron,* it might be named *Antrodemus.*"

Later, Leidy (1873, p. 276, plate 15) made a formal proposal of *Poicilopleuron valens* in a similar discussion but identified the specimen as *Antrodemus* in the plate explanation. He also indicated that Hayden received the specimen second hand.

In either account, the referred specimen (USNM 218), although definitely theropod, presents a problem for several reasons: (1) there are no finite stratigraphic data; (2) there is only a broad geographic reference; (3) Leidy received the specimen third hand; (4) the specimen is questionably diagnostic as to genus; and (5) the fragment is most certainly indeterminate as to species.

The third reference of importance to this discussion is by Marsh (1877, p. 515) in which he presents the name *Allosaurus fragilis.* The referred material in this case (YPM 1930), regardless of its fragmented condition and incompleteness, is diagnostic to the species level. Marsh describes the type as consisting of "a lumbar vertebra" [mid-dorsal], "an anterior caudal vertebra" [posterior caudal], and "feet bones" [proximal phalanx, D-III, right pes]; however, there is also an associated tooth of a right maxilla and a segment of the shaft of a right humerus, which has a diagnostic nutrient foramen and the distal half of the humeroradialis muscle scar. All of Marsh's material, however, is adequate for a specific determination, and the fragment of the humerus shaft (figure 7) may be most diagnostic of *A. fragilis.*

Two remaining points oppose retention of *Antrodemus,* based as it was on a specifically indeterminate type specimen: (1) preliminary investigation indicates a strong possibility of Jurassic speciation within the genus; (2) a growing number of theropods described from the Late Jurassic/Early Cretaceous formations make solid, specific determinations an absolute necessity.

It seems that Gilmore was not completely convinced that his choice of *Antrodemus* over *Allosaurus* was the only alternative, because he considered two others, one of which was to "regard the type of *Antrodemus* as an indeterminate specimen, and continue the use of *Allosaurus fragilis,* characterizing it on the splendidly preserved topotype No. 4734, U.S.N.M., to which Marsh has applied his name, a name that has become well established both in this
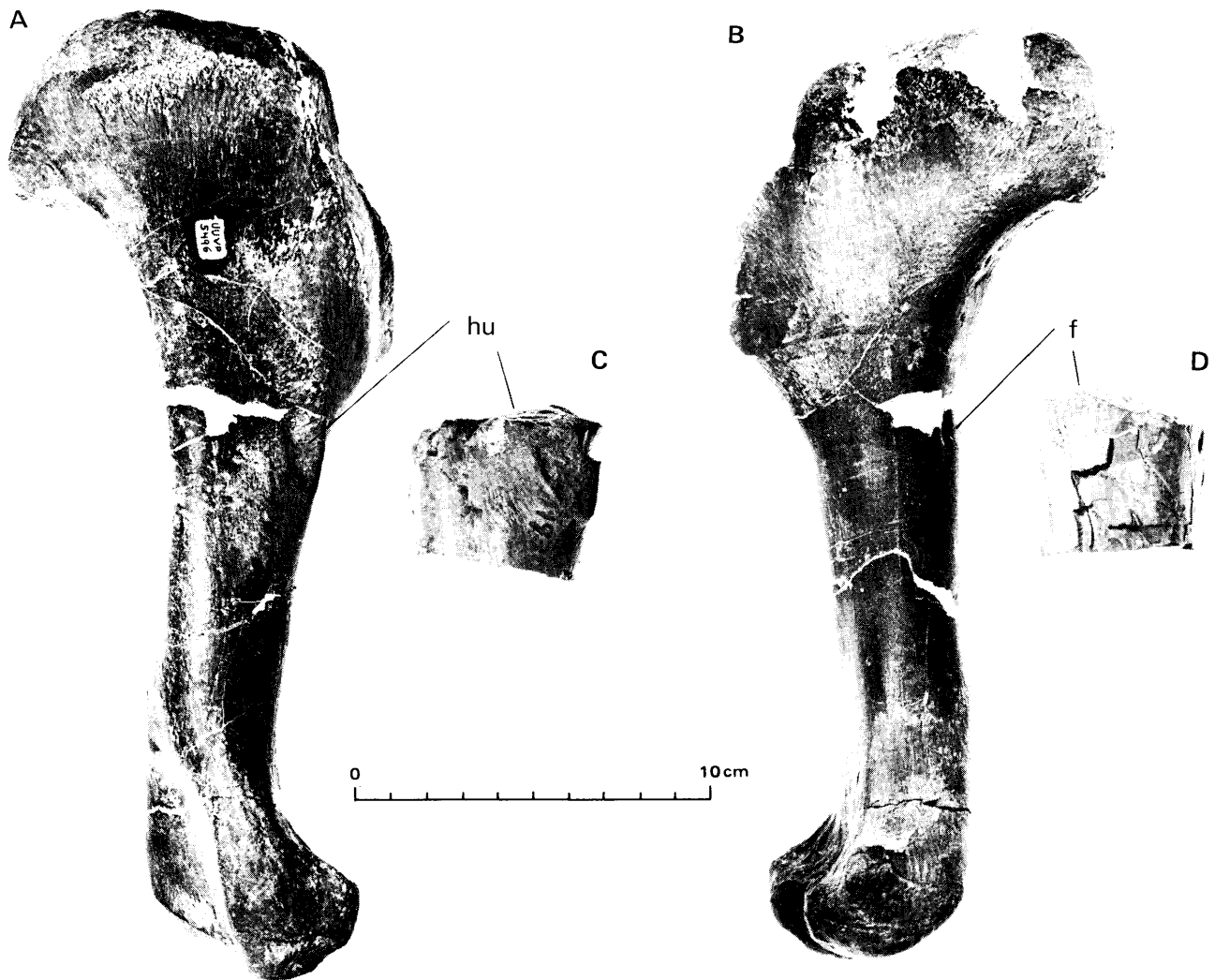
Figure 7. Right humerus (UUVP 5496) of *Allosaurus fragilis* in lateral (A) and medial (B) views and segment (C, D) right of humeral shaft (YPM 1930) showing principal nutrient foramen (f) and attachment scar of the humeroradialis (hu).

country and abroad" (Gilmore, 1920, p. 4). Had Gilmore seen all of the original material that belonged with the type of *Allosaurus*, rather than just the plaster copies supplied him by Lull (Gilmore, 1920, p. 4), which apparently did not include the humerus fragment, he might have chosen this alternative.

Gilmore's third alternative was to "regard both the types *Allosaurus fragilis* and *Antrodemus valens* as being indeterminate and create a new genus and species based on an adequate specimen." This last choice would certainly have created more confusion in the literature than either of the other two.

Preference for the genus, *Allosaurus*, is noted by Ostrom (1969a, p. 16), where he indicates a possible confusion with another Late Jurassic species, *Ceratosaurus*. However, detailed comparisons are now possible

that indicate few similarities in the anterior caudal vertebrae of *Allosaurus* and *Ceratosaurus* that would allow these bones to be confused. The caudal of *Allosaurus* is laterally compressed at midcentrum; that of *Ceratosaurus* is much more rounded. The internal structure of the *Allosaurus* centrum is divided by trabeculae, but that of *Ceratosaurus* is more complex. The top half of the *Ceratosaurus* centrum has many small trabeculae, and its bottom half is roughly divided vertically into two large chambers lined with trabeculae of moderate size. The ventral surface of the *Allosaurus* caudal vertebra has a slight longitudinal groove; whereas the centrum of *Ceratosaurus* has a deeper, symmetrically rounded groove (figure 8).

Having carefully examined the types of *Allosaurus* and *Antrodemus*, I favor retaining *Allosaurus*, since Leidy's type is indeterminate. *Allosaurus fragilis*

A


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0                                          5cm
L____I____I____I____I____J
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B
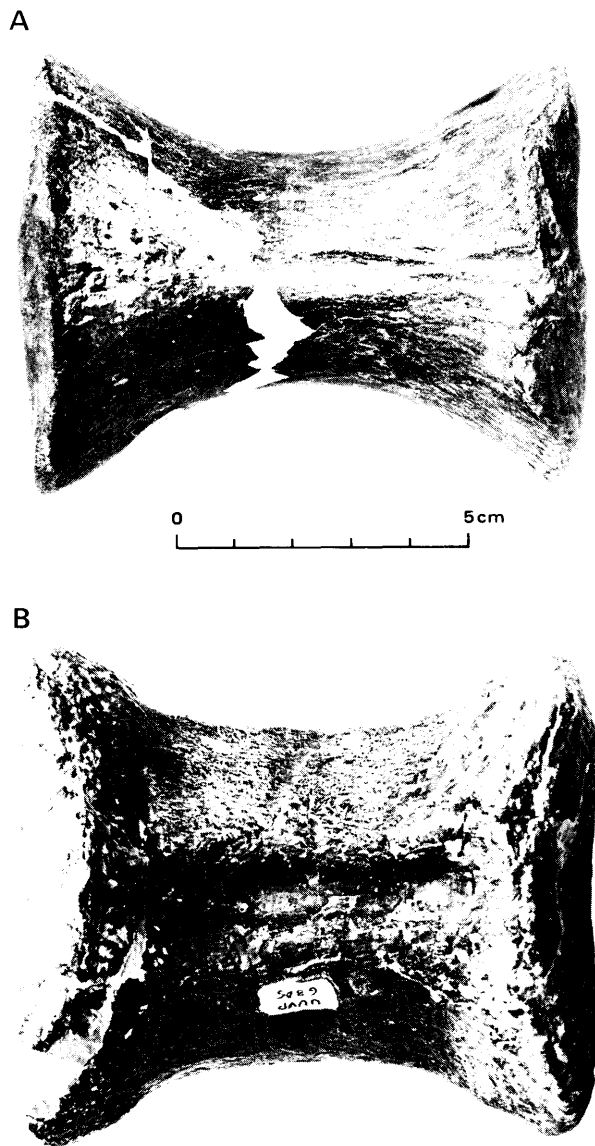
Figure 8. Caudal vertebrae of *Allosaurus fragilis* (A, UUVP 6625) and *Ceratosaurus sp.* (B, UUVP 6305).

is now based upon Marsh's original type (YPM 1930), the paratype (USNM 4734), and the neotype (UUVP 6000).

GENERAL DESCRIPTION

Morphologically, *Allosaurus* is a typical theropod that exhibits most of the general characters of the suborder (Romer, 1956, p. 609). The skull is disproportionately large as is true of the other carnosaurs. The axial skeleton consists of a series of elements each of which is distinct in character without exhibiting gross differences that might be attributed to a very specialized function. The pectoral girdle is well developed, and the forearms, although reduced, are strong in contrast to their relatively small counterparts in *Tyrannosaurus*. The strong hind limbs attest to a fully bipedal mode of locomotion and serve to identify *Allosaurus* as a very mobile dinosaur.

Skull and Mandible

Except for the hyoid bones, all elements of the skull of *Allosaurus fragilis* (plates 1-10), though commonly found disarticulated, have been recognized in the Cleveland-Lloyd Dinosaur Collection. Post-mortem maceration of carcasses prior to burial resulted in the nearly complete disarticulation of skulls and postcranial elements. Braincases are a common exception as they are often found intact except for the frontals. Lack of practical experience during the first years of collecting at the Cleveland-Lloyd Dinosaur Quarry resulted in the incomplete salvage of some of the more fragile skull bones; however, the large number of individual pieces recovered has allowed adequate restoration of most bones. Descriptions are based on composite elements, all of which have been adjusted to an average scale approximating the dimensions of the large allosaur skeleton, UUVP 6000, collected at the site of Dinosaur National Monument in 1924. The specimen, exhibited at the University of Utah for more than 40 years, was dissassembled in 1972 for study. Where gross morphological differences were detected between juvenile and adult forms, they are noted; however, the description of the skull and postcranial skeleton is that of a composite, which corresponds to a No. 33 in terms of the arbitrary size assignments (see *Fauna and Prehistory*) made to facilitate study of the Cleveland-Lloyd allosaurs (UUVP 6000 is a No. 33).

Terminology of preorbital fenestration in the theropod skull is varied and sometimes inconsistent; therefore, it is redefined below as used in this report.

1. Subnarial foramen, the dorsolateral opening in the premaxillary/maxillary suture. The third antorbital fenestra of Osborn (1912, p. 8).

2. Maxillary fenestra(e), the opening, which may be paired, that is confined to the superior or nasal ramus of the maxilla. It leads to an internal, maxillary sinus. The second antorbital fenestra of Osborn (1912, figure 1), which has been called the maxillary vacuity when closed (Hay, 1908, p. 362). Also referred to as the preantorbital fenestra.

3. Antorbital fenestra, the opening surrounded by the maxilla, the lachrymal, and sometimes the jugal. Also referred to as the preorbital fenestra. The first antorbital fenestra of Osborn (1912, figure 1).

Reference to other fenestration of the skull is consistent with common usage.

Dermal Roof Bones

Premaxilla. The body of the premaxilla (plate 6c), excluding processes, is quadrangular with subequal sides. Forty-nine premaxillae in the Cleveland-Lloyd Dinosaur Collection (table 1) show no variation in a tooth count of five. The teeth tend to be uniform in size and design with a D-shaped cross section. Fully erupted teeth often show abrasion of the tips and some occlusal wear (figure 9), which is most pronounced in the anterior teeth. The gently convex external surface of the premaxilla is perforated by numerous, randomly spaced foramina and one irregular row of foramina lying one centimeter above and parallel to the alveolar margin. The anterior margin of the external naris (en) is formed above by the ascending nasal process (napr) and below by a posteriorly directed maxillary process (mxpr). The margin of the external naris is enclosed behind by the anterior branches of the nasal and below by a short section of the maxilla. The nasal processes of the premaxillae meet anteriorly along a flattened symphysis but are separated posteriorly by the thin projections of the nasal, which meet at the midline. The posterior, elongate, sutural surface of the premaxilla, which contacts the maxilla, is rough and pitted, suggesting a firm but slightly flexible union. A thin vertical lip from the maxilla laps onto the lateral surface of the premaxilla, its contact represented by a low, obtuse, triangular area. Above this contact the maxillary process of the premaxilla laps over the maxilla, and together they contribute equally to the subnarial foramen (snf). Medial and anterior to the subnarial foramen a shelflike projection rises to meet the anteriomedial processes of the maxillae.

Gilmore (1920, p. 28) could find no evidence of a subnarial foramen on the skull (USNM 4734) of the *Allosaurus fragilis* he described. The apparent reason for the absence of the opening was the inaccurate plaster restoration of the left premaxilla and the right maxilla, which repair effectively foreshortened and thereby gave the specimen a significantly distorted lateral and dorsal configuration.

Maxilla. The maxilla (plate 6a, b) is the most massive and complex part of the dermal roof. The number of teeth in the maxilla of *Allosaurus fragilis* ranges from 14 to 16. Of 37 fairly complete maxillae that were closely examined (table 2): two had 14 alveoli; eight had 15 alveoli; twenty-five had 16 alveoli; and two had 17 alveoli. However, this variation does not appear to be related to age as one might suppose, since there is no apparent correlation between tooth number and maturity or size of the specimen.

The anterior teeth of the maxilla are slightly compressed, resembling somewhat the rear teeth of the premaxilla. Toward the posterior of the jaw, they become progressively more flattened and recurved. All of the teeth are serrate, and the anterior row of serrations on each tooth is shorter than the posterior one. Tooth size decreases noticeably through the posterior one-third of the tooth row.

Teeth from the maxillae, and other tooth-bearing elements as well, are commonly found disassociated throughout the quarry, many in contact with or in close proximity to bones clearly assignable to other genera. It seems that little postmortem disturbance was required to separate the teeth from their loose alveolar attachment. Furthermore, the apparently rapid replacement of teeth in *Allosaurus fragilis* would increase the possibility of teeth being lost during each feeding activity. The conclusion, therefore, is that disassociated theropod teeth are very risky evidence in a taxonomic determination involving bones not obviously associated with teeth. The large number of disassociated allosaur teeth in the Cleveland-Lloyd Dinosaur Quarry may also be evidence of scavenging activity.

The premaxillary contact is a vertically elongate groove that reflects the pitted and roughened surface of the premaxilla. This contact terminates above in the subnarial foramen, which is roofed by the maxillary process of the premaxilla. The broad tapering nasal process rises from the body of the maxilla to meet the nasal above, and, more posteriorly, the anterior process of the lachrymal. The nasal process is complexly excavated by a two-chambered sinus, which opens laterally as the maxillary fenestra. The sinus is enclosed medially by a very thin, curving, septumlike wall, rarely preserved intact, which is perforated posteriorly by a large oval foramen and anteriorly by a smaller, more elongate foramen, the borders of which are very thin.

The maxillary sinus is divided internally into a smaller, anterior chamber and into a larger, posterior chamber by a thin, narrow partition (figure 9), the maxillary septum (mxs), which extends from the floor to the roof. Each of the chambers has a separate medial and dorsal opening as well as being connected internally by vertically elongate openings on either side of the maxillary septum. This septum may be a homologue of the vertical partition separating the lateral fenestrae in other theropods, such as *Deinonychus* and *Marshosaurus*, that have two distinct openings. The chambering is variably developed in the maxillae of *Allosaurus fragilis*. In one instance, the vertical partition rises anteriorly from the floor of the chamber, sweeping upward and back to join the dorsolateral margin of the chamber. In another instance the

Table 1. Measurements and indices of some Cleveland-Lloyd and other theropod premaxillae.

	UUVP or other number	Side	Total alveoli	Depth[1] at 3rd alveolus (mm)	Length of tooth row (mm)	D:L x100	Identification
1	22999	right	4	64	29	220	*Stokesosaurus*
2	1945	left	5	29	30	97	*A. fragilis*
3	3266	right	4	34	42	81	*Marshosaurus*
4	40-601	left	5	43	44	98	*A. fragilis*
5	6737	right	5	48	50	96	*A. fragilis*
6	MCZ 3897	right	5	52	53	98	*A. sp.*
7	40-722	left	5	54	53	102	*A. fragilis*
8	5566	left	5	55	55	100	*A. fragilis*
9	1879	right	5	58	58	100	*A. fragilis*
10	139	right	5	59[2]	60[2]	98[2]	*A. fragilis*
11	5315	right	5	63	63	100	*A. fragilis*
12	30-723	right	5	63	63	100	*A. fragilis*
13	40-603	left	5	62	64	97	*A. fragilis*
14	3724	left	5[2]	65[2]	67[2]	97[2]	*A. fragilis*
15	1866	left	5	67	67	100	*A. fragilis*
16	1622	left	5	96	67	103	*A. fragilis*
17	30-293	left	5	66	68	97	*A. fragilis*
18	10,245	left	5	65[2]	68	95	*A. fragilis*
19	5490	left	5	64	69	93	*A. fragilis*
20	2843	left	5	69	70	99	*A. fragilis*
21	1869	right	5	68	72	94	*A. fragilis*
22	1927	right	5	70	72	97	*A. fragilis*
23	2545	left	5	74[2]	73[2]	101[2]	*A. fragilis*
24	1991	right	5	75[2]	73	102[2]	*A. fragilis*
25	1865	left	5	74	76	97	*A. fragilis*
26	1872	right	5	72	77	94	*A. fragilis*
27	740	left	5	72	77	94	*A. fragilis*
28	4596	right	5	79	79	100	*A. fragilis*
29	1878	right	5	85[2]	79[2]	107[2]	*A. fragilis*
30	1876	right	5	80	81	99	*A. fragilis*
31	6743	right	3	100	81	123	*Ceratosaurus*
32	6743	left	3	105	83	126	*Ceratosaurus*
33	3995	left	5	94	85	110	*A. fragilis*
34	2600	left	5	86	87	99	*A. fragilis*
35	3529	left	5	89	90	99	*A. fragilis*
36	3036	left	5	106	96	110	*A. fragilis*
37	6740	left	5	95[2]	100	95[2]	*A. fragilis*
38	5427	left	5	100	100	100	*A. fragilis*
39	685	left	5	103	100	103	*A. fragilis*
40	5427	right	5	100	102	98	*A. fragilis*
41	6000	right	5	104	102	101	*A. fragilis*
42	3670	right	5	108	109	99	*A. fragilis*
43	1863	left	5	110	109	101	*A. fragilis*
44	40-604	right	5	120	109	110	*A. fragilis*
45	1875	right	5	105	110	95	*A. fragilis*
46	6000	left	5	112	110	101	*A. fragilis*
47	1086	right	5	117	110	106	*A. fragilis*
48	856	left	5	125	110	114	*A. fragilis*
49	1873	right	5	122	118	103	*A. fragilis*

[1] From base of narial opening to lower margin of jaw.
[2] Estimated; incomplete, distorted, or pathological specimen.

Table 2. Measurements and indices of some Cleveland-Lloyd and other theropod maxillae.

	UUVP or other number	Side	Total alveoli	Depth[1] at 6th alveolus (mm)	Length of tooth row (mm)	D:L x 100	Identification
1	3279	left	16	31	180	17.1	*A. fragilis*
2	1891	right	16	44	184	23.9	*A. fragilis*
3	509	left	16	44	185	23.7	Unidentified
4	1890	right	16	48	190	25.2	*A. fragilis*
5	MCZ 3897	right	16	43	200	21.5	*A. sp.*
6	1881	left	16	51	200	25.5	*A. fragilis*
7	2186	right	16	51	206	24.7	*A. fragilis*
8	1892	right	16	40	210	21.0	*A. fragilis*
9	5386	left	15	61	211	28.9	*A. fragilis*
10	4695	right	16+	50	215	24.2	*Marshosaurus*
11	1894	right	16	52	220	23.6	*A. fragilis*
12	40-584	left	15+	52	220	23.6	Unidentified
13	40-586	left	15	54	228	23.6	*A. fragilis*
14	1883	left	16	50	230	21.7	*A. fragilis*
15	1846	right	16+	54	230+	23.4	*Marshosaurus*
16	1884	left	16	54	240	22.5	*A. fragilis*
17	1233	right	15	62	240	25.8	*A. fragilis*
18	4213	left	16	58	245	23.6	*A. fragilis*
19	1880	left	16	69	245	28.1	*A. fragilis*
20	4779	right	16	71	256	27.7	*A. fragilis*
21	1889	right	14	63	260	24.2	*A. fragilis*
22	1886	right	16	55	273	20.1	*A. fragilis*
23	4780	left	16	68	273	24.9	*A. fragilis*
24	2887	left	16	68	275	24.7	*A. fragilis*
25	4813	left	16	75	280	26.7	*A. fragilis*
26	1887	right	16	88	280	31.4	*A. fragilis*
27	3638	left	17	70	293	23.8	*A. fragilis*
28	1893	left	16[2]	76	295[2]	25.7[2]	*A. fragilis*
29	5427	left	15	98	306	32.0	*A. fragilis*
30	1517	right	16[2]	88	318[2]	27.6[2]	*A. fragilis*
31	1582	right	15	92	318	28.9	*A. fragilis*
32	10,237	left	14[2]	95	320[2]	29.7	*A. fragilis*
33	3836	left	15	92	328	28.0	*A. fragilis*
34	3587	left	16	93[2]	346[2]	26.8[2]	*A. fragilis*
35	1365	left	16	89	348	25.5	*A. fragilis*
36	5499	right	17	93	348	26.7	*A. fragilis*
37	5748	right	16[2]	90[2]	350[2]	25.7[2]	*A. fragilis*
38	6000	left	15	98	357	27.4	*A. fragilis*
39	6000	right	15	97	358	27.0	*A. fragilis*
40	40-587	left	16[2]	104	365[2]	28.4[2]	*A. fragilis*
41	5748	left	16[2]	92[2]	370[2]	24.8[2]	*A. fragilis*
42	674	left	12	124	391	31.7	*Ceratosaurus*

[1] From bottom of maxillary chamber to lower margin of jaw.
[2] Estimated; bone incomplete, distorted, or pathological.

septum joins the anterolateral margin medially so that it does not appear as a continuation of the superior margin of the chamber.

A similar chambering is noted in *Deinonychus* by Ostrom (1969a, p. 18) and in *Ceratosaurus* by Hay (1908, p. 362) who calls it the maxillary vacuity. A left maxilla of *Ceratosaurus* (UUVP 674) in the Cleveland-Lloyd Dinosaur Collection is free of distor-

tion or any evidence of pathology, and it is most interesting because the medial entrance to the maxillary sinus is restricted to a single, moderately small foramen. A new, recently described theropod in the Cleveland-Lloyd Dinosaur Collection, *Marshosaurus bicentesimus* (Madsen, 1976); also shows development of the maxillary sinus, but as in *Ceratosaurus* the medial fenestrae are very small in comparison with *Allosaurus fragilis*.
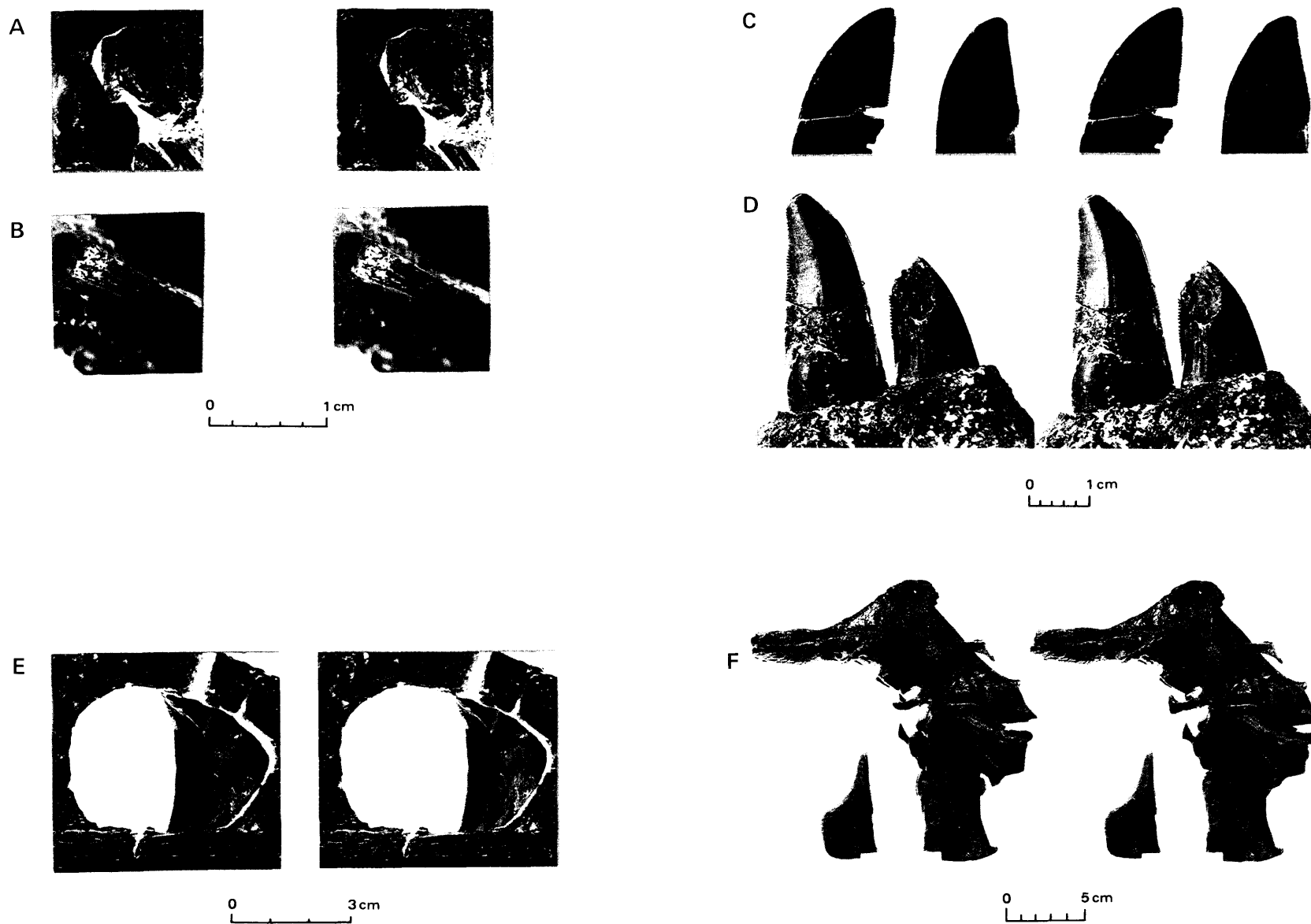
Figure 9. Stereo views of proximal (A) and distal (B) ends of *Allosaurus fragilis* stapes; teeth of *Allosaurus fragilis* (C) and *Ceratosaurus sp.* (D); maxillary sinus of *Allosaurus fragilis* (E) and endocranial cast of *Allosaurus fragilis* (F).

The position and complexity of the maxillary sinus is such that it may have served a function associated with olfaction. The relatively short narial chamber would limit the surface area for the development of the sensory epithelium, and it appears that the chambering of the maxilla might have served an auxiliary function for the development of such tissue. Although a more anteroventral position would be expected, perhaps the chamber housed an equivalent of Jacobson's organ. Further study is needed to determine the real significance of sinuses in the maxillae and their possible significance to organs of the facial region.

The maxilla tapers posteriorly, then expands vertically into an irregular, thin plate meeting the jugal and lachrymal in a strong, however flexible, complex. The lower part of the complex consists of interdigitating processes of the maxilla and jugal. Medially, the expanded ventral process of the lachrymal overlaps the thinning anterior plate of the jugal and encloses a short dorsal extension of the anterior plate. Laterally, the complex is partly covered by the irregular, thin plate arising posteriorly from the maxilla.

The maxilla is longitudinally grooved along the posterior one-third of its dorsomedial surface for reception of corresponding ridges of the ventrolateral process of the palatine. The antorbital fenestra is bounded by the maxilla anteriorly and by the lachrymal posteriorly. The thinning anterior plate of the jugal may also reach the margin of the antorbital fenestra.

Ahead of the internal exits of the maxillary sinus and overhanging the subnarial fenestra, there project the grooved anteromedial processes of the maxillae that meet at midline in an interdigitating suture. This interdigitation fits between the medial projections of the premaxillae; all of which form an arch over the anterior end of the vomer.

Nasal. Viewed laterally, the profile of the nasal (plate 1, na) is almost straight and just slightly convex, branching anteriorly to form the posterior margin of the external naris. The dorsal branch is vertically cleft to accept the ascending process of the premaxilla. The ventral branch follows the contour of the superior ramus of the maxilla, ending just short of contact with the premaxilla and almost excluding the maxilla from the margin of the external naris. Midway on the ventrolateral surface of the nasal is a large foramen (plate 1, naf) of variable size that leads internally to a series of intricate cavities. Posterior and lateral to this foramen, a spurlike projection rises to fit a corresponding slot in the anterior arm of the lachrymal. Medially, the nasal is flattened in a nearly horizontal plane, thinning posteriorly where the surface becomes longitudinally ridged on its ventral surface. The ridged

area overlaps the anterior, tapering edge of the frontal in squamous suture.

Rugose sculpturing and ornamentation is continuous from the lachrymal along the dorsolateral surface of the nasal. This is part of a continuous rugosity along the superior margins of the skull from postorbitals through nasals that may represent the surface for attachment of functional homologues of the paired crests which rise from approximately the same area on the skull of *Dilophosaurus.*

Frontal. The frontal of *Allosaurus fragilis* is a wedge-shaped block, about twice as long as it is wide, that has a smoothly flattened dorsal surface. The median contact (figure 10) is a plane surface but is intricately sculptured, making a firm suture that allows no movement between the frontals. The frontal thins anteriorly to underlap the nasal with an interdigitating ridge and furrow contact. Lateral to the nasal suture a small hooklike projection underlies the anteromedial process of the prefrontal. Posterior to this is a cavity, visible laterally, which receives the posterior apex of the prefrontal. Below this cavity a ridge converges posteromedially with its counterpart on the opposite side to form a constriction over the braincase opening of the olfactory tract. Anterior to this constriction on the underside of the frontal is the outline of a shallow concavity representing the area of contact for the olfactory bulbs. Strong suturing, below, on the posteroventral surface of the frontal identifies the area of articulation with the underlying laterosphenoid and, above, on the intricate parietal contact. The internal suturing of the frontal-parietal contact suggests a firm union; however, ridges and grooves are vertically oriented. In addition the frontal-laterosphenoid contact appears loose, and since frontals are not always recovered with the braincases found in the Cleveland-Lloyd Dinosaur Quarry, evidence seems to support a mesokinetic hinge between frontals and the firmly united laterosphenoids and parietals.

Parietal. The parietals (figure 11 and plate 2) meet dorsally in a low sagittal crest, deeply excavated on either side as the concave inner surfaces of the supratemporal fenestra. The parietal expands dorsally into a wide flange and tapers posterolaterally to a thin, pointed projection that fits between the paroccipital process and an anteromedial branch of the squamosal. The parietals surround the supraoccipital laterally and dorsally and merge above in the supraoccipital crest. They are not excluded from contact with the supraoccipital by an upward process from the exoccipitals as suggested by Gilmore (1920, p. 14). The dorsal process to which he refers (Gilmore, 1920, figure 4) is really part of the supraoccipital.
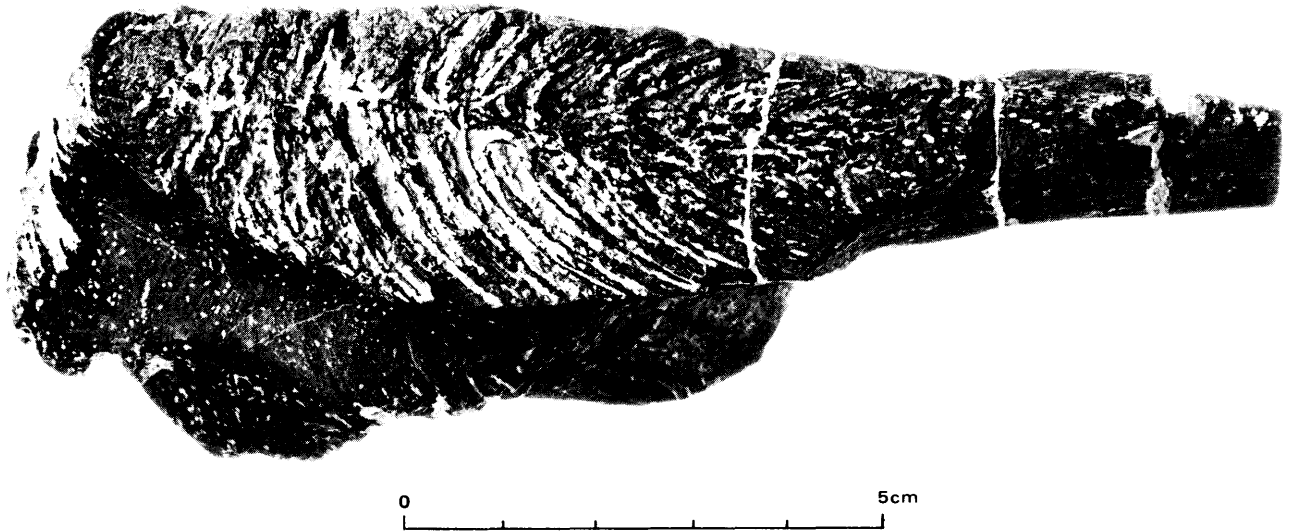
Figure 10. Midline suture of a left frontal (UUVP 1920) of *Allosaurus fragilis*.

There is no parietal foramen; however, the area beneath the parietal midline, at the intersection of the supraoccipital and parietals, is conspicuously excavated. This thinning of the skull roof suggests expansions at the apex of the endocranial cavity. Although the skull is noticeably thin in these areas, there is no external opening that might have been associated with a light-sensitive organ. Similar projections are noted by Osborn (1912, figure 17) in a description of an endocranial cast of *Tyrannosaurus*; they may have served a function related in some way to thermoregulation.

Prefrontal. The prefrontal (plate 4a, b) is shaped as a small arch with two tapering processes. The first extends dorsomedially between the lachrymal and the sutured frontal and posterior plate of the nasal. The second lies along the inner surface of the lachrymal. The lachrymal, prefrontal, frontal, and postorbital contribute subequally to the border of the deep supraorbital notch. The prefrontal and postorbital do not meet below the supraorbital notch as noted by Walker (1964, p. 120) in reference to the work of Gilmore.

The apex of the archlike prefrontal tapers irregularly to a point that fits tightly in a corresponding depression on the anterolateral side of the frontal. Similarly, a depression on the lateral surface of the prefrontal matches a blunted cone on the posteromedial surface of the lachrymal.

Postorbital. The postorbital (figure 12 and plate 1, po) is a heavy element, T-shaped in lateral outline. The ventral bar curves slightly forward and overlaps the ascending process of the jugal in a contact that appears to have allowed some movement. The tapering posterior bar of the postorbital lies in a deep groove in the squamosal; the two elements form a strong, but apparently flexible, supratemporal arch. Anteromedially, the postorbital meets the frontal in a tongue-and-groove suture above and forward of the deep cotylus for the laterosphenoid. There is no evidence of an anterior projection into the orbit from the postorbital of *Allosaurus* as in *Tyrannosaurus* (Osborn, 1912, p. 29), and without such a restriction the eye of *Allosaurus* may have been twice as large as that of a comparably sized *Tyrannosaurus*. The margins of the upper half of the orbit are ornamented with rugosae (figure 9), and, in this respect, *Allosaurus* resembles *Tyrannosaurus* and *Ornithosuchus* as suggested by Walker (1964, p. 111).

Jugal. The jugal (plate 4d, e) is a triradiate, laterally compressed bone. Its irregularly tapered ascending process joins by a lapping suture the ventral arm of the postorbital. The anterior extension of the jugal flares and joins in a complex, squamous contact with the ventral bar of the lachrymal and the posterior plate of the maxilla. Posteriorly, the jugal tapers and divides into an upper branch that lies in a dorsal groove in the quadratojugal and into a lower branch that underlaps the anterior arm of the quadratojugal. Although there are small nutrient foramina on the medial and lateral surfaces of the jugal, there is no evidence of a large lateral opening below the orbit as reported by Gilmore (1920, p. 84) for *Allosaurus fragilis* and *Tyrannosaurus*. Instead a foramen opens into an evenly curving groove on the anterior expanded end of the jugal at the lachrymal contact.

Lachrymal. The body of the lachrymal (plate 1) is ear shaped, having a conspicuous lateral fossa that leads into an extensive, thin-walled vacuity which
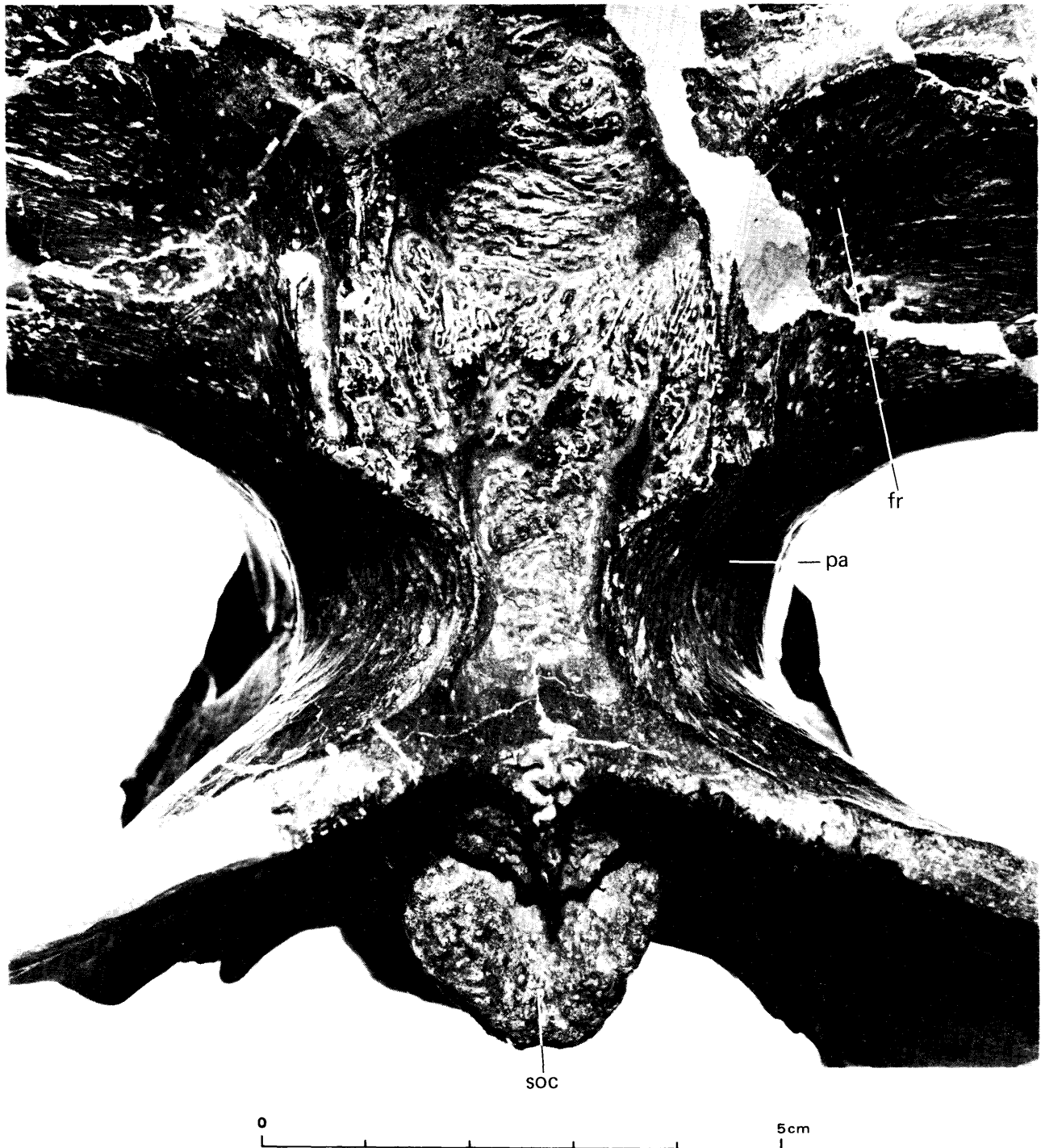
Figure 11. Dorsal view of parietal/frontal (UUVP 5961) suturing in *Allosaurus fragilis.* Abbreviations: fr—frontal, pa—parietal, soc—supraoccipital.

occupies most of the dorsal half of the element. Usually there is only one large, lateral entrance to the lachrymal vacuity; however, its dimensions and shape are variable. Gilmore (1920, p. 17) notes two openings in USNM 4734. The deeply excavated body of the lachrymal suggests a possible housing for a gland(s) that discharged posteriorly through the smaller of two foramina and dorsomedially through a foramen opening in the raised areas of the prefrontal contact. The larger, posterior foramen leads to a canal that

Figure 12. Right postorbital of *Allosaurus fragilis*. Note rugosity of supraorbital region.

appears continuous inside the antorbital margins and that opens on the medial surface of the anterior branch near its contact with the superior ramus of the maxilla. A third foramen immediately below the large lateral fossa of the lachrymal (plate 1, f) appears to connect with the main vacuity but ends in a small, blind chamber. Most of the nonsuturing surface of the lachrymal is noticeably rugose and grooved, which suggests complex and continuous muscular or ligamental attachment.

The tapered anterior arm of the lachrymal contacts the maxilla and nasal. Medially it lies against the forward branch of the prefrontal. The ventral limb of the lachrymal expands to join in squamous, sutural contact with the jugal and maxilla. The posteromedial surface of the lachrymal is deeply grooved to receive the ventral arm of the prefrontal.

Gilmore (1920, p. 17) concurred with Osborn (1903, p. 701) in postulating the lachrymal as a support for a low dermal horn. If such were true, since the highly ornamented surface strongly indicates an attachment of some complexity, the function would probably have been that of a brow or sunshade rather than just that of a buttress to protect the supraorbital

area from damage, because the superior walls of the lachrymal are so thin that the area would be very susceptible to injury, even from a very light blow. Perhaps this very thinness required horny protection.

Squamosal. The squamosal (plate 3a, b) has the appearance of a cupped hand, palm directed downward. A tapering anteromedial process lies against the paroccipital and continues forward between the paroccipital process and a small ventrolateral extension of the parietal. Above this contact the superior margin meets the lateral edge of the parietal. The squamosal is divided anterolaterally to form a groove for the posterior arm of the postorbital, the two bones together forming the supratemporal arch. Below the arch the deeply excavated quadrate cotylus of the squamosal encloses the top of the quadrate and forms a loose articulation that appears to allow considerable movement. Anterior to the cotylus a laterally compressed, anteroventrally directed plate meets the ascending bar of the quadratojugal in a loose, end-to-end contact that slightly restricts the lateral temporal fenestra. Though noticeable, this restriction is not nearly as severe and angular as in *Tyrannosaurus* (Osborn, 1912, plate 1) or as implied in the restoration of the skull of *Acrocanthosaurus* (Stovall and Langston, 1950, figure 2).

Quadratojugal. The quadratojugal (plate 1, qj) is L-shaped and laterally compressed. It has a flattened superior margin that abuts the squamosal above, in what was probably a flexible, ligamental contact. Posteriorly, it joins the quadrate in a right angle contact that widens ventrally into a complex of ridges and grooves that would allow minimal movement between these two bones. The anterior bar of the quadratojugal is tapered and deeply grooved above where it joins the posterior arm of the jugal at the lower margin of the lateral temporal fenestra.

Braincase

Basioccipital. The basioccipital (figure 13, bo) constitutes 60 percent of the occipital condyle. It lies in contact anterolaterally with the opisthotics and joins dorsolaterally with the exoccipitals to form the posterior floor of the cranium. Anteriorly, the inferior process of the basioccipital meets the posterior wings of the basisphenoid; together they surround the vertical, basicranial fontanelle. The fontanelle is bluntly terminated dorsally in the basisphenoid but is continuous posteriorly with an intricate chambering in the basioccipital condyle.

Basisphenoid. The basisphenoid (figure 14) is deeply excavated posteriorly and joins with the basioccipital to form a large chamber. A thick median
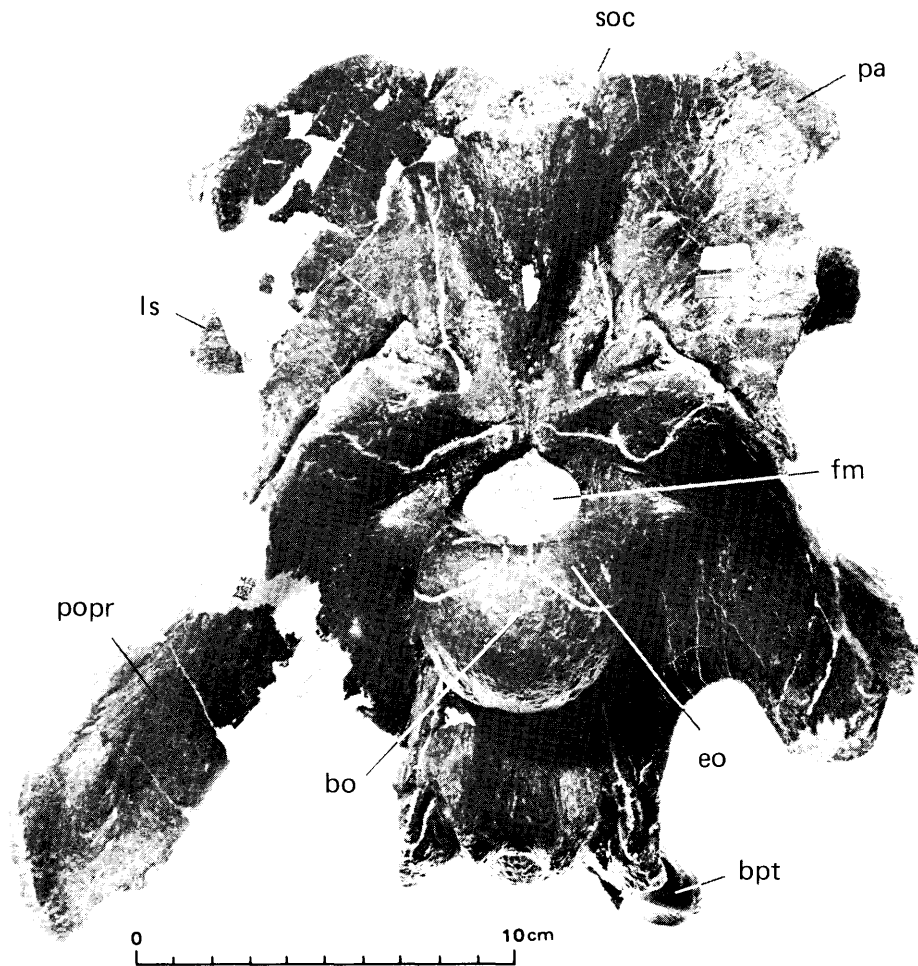
Figure 13. Posterior view of braincase (UUVP 5583) of *Allosaurus fragilis*. Abbreviations: bo–basioccipital, bpt–basipterygoid process, eo–exoccipital, fm–foramen magnum, ls–laterosphenoid, pa–parietal, popr–paroccipital process, soc–supraoccipital.

septum separates the larger posterior sinus from the smaller, conical excavation that lies between the basipterygoid processes and terminates dorsally in a blunted point.

The basipterygoid processes project slightly forward and downward to terminate in rounded, dorso-ventrally elongate, articular surfaces. From the basipterygoid processes, convergent laminae rise upward, separated by a deep, narrow groove. They finally merge near the tip of the parasphenoid. The basisphenoid and parasphenoid are completely fused, and there is no visible suture. Dorsally, the basis-phenoid forms a very small part of the anterior floor of the cranial cavity surrounded anteriorly by latero-sphenoids, laterally by the prootics and opisthotics, and posteriorly by the basioccipital. On the antero-dorsal surface between the lower margin of the optic foramen and the base of the parasphenoid lies the well-defined sella turcica or pituitary fossa. The large

opening of the carotid canals are conspicuous posterior to the angle between the parasphenoid and the basipterygoid process.

The parasphenoid (plate 1, ps) rises anteriorly from the basisphenoid, from which it is suturally indistinct. The parasphenoid is a thin, vertical plate that makes contact above with the orbitosphenoids and the anteromedial processes of the laterosphenoids near their dorsal extremity. The parasphenoid lies beneath but probably does not contact the frontals at their midline, although it is high enough to serve as a divider or a support of the olfactory nerves. Possibly, the presphenoids of Gilmore (1920) and Osborn (1912) are remnants of the parasphenoid, which remained attached to the dorsal parts of the orbitosphenoids and adjoining projections from the laterosphenoids. The entire plate, which appears as an interorbital septum, is termed parasphenoid in this study.
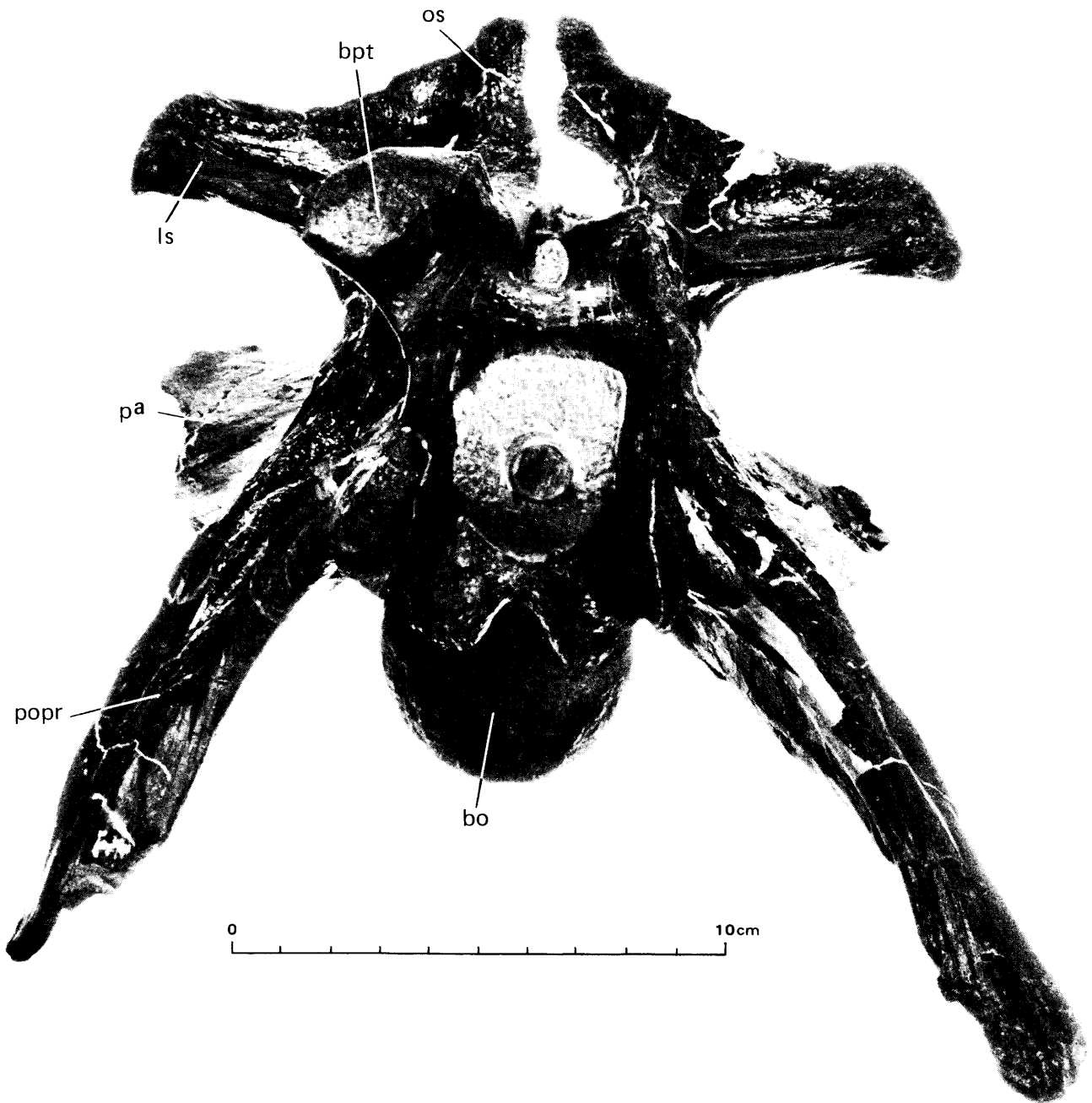
Figure 14. Ventral view of braincase (UUVP 5583) of *Allosaurus fragilis*. Abbreviations: bo—basioccipital, bpt—basipterygoid process, ls—laterosphenoid, os—orbitosphenoid, pa—parietal, popr—paroccipital process.

Exoccipital-opisthotic. The exoccipitals (figure 15) and the winglike, laterally projecting opisthotics (paroccipital processes) must fuse at a very early stage of development, since there is no evidence of suturing even in juvenile specimens. The paroccipital process of the opisthotic projects obliquely from the skull at an angle of approximately 45 degrees from the horizontal, saggital, and occipital planes. It is finely grooved on the ventrolateral surface where it joins with the prootic

in an inflexible suture; together they form the posterior segment of the stapedial canal leading to the fenestra ovalis. The exoccipitals are a conspicuous part of the occipital complex in posterior view, where they constitute approximately 40 percent of the circumference of the occipital condyle. They are separated medially by a longitudinal furrow in the dorsal surface of the basioccipital. The exoccipitals do not meet at midline above the foramen magnum as believed by

Figure 15. Lateral view of braincase (UUVP 5583) of *Allosaurus fragilis.* Abbreviations: bo—basioccipital, bpt—basipterygoid process, ls—laterosphenoid, op—opisthotic, pa—parietal, popr—paroccipital process, pr—prootic, soc—supraoccipital.

Gilmore (1920, p. 11) but are separated by the arched, ventral surface of the supraoccipital, which comprises approximately 12 percent of the circumference of the foramen magnum. Above the foramen magnum the exoccipital-opisthotic meets the ventrolateral margin of the supraoccipital. Ventrally, the lateral suture between the exoccipital and basioccipital is horizontal and straight, continuing forward to the vertical suture with the great ventral buttress of the opisthotic. Laterally, the opisthotic part of the exoccipital-opisthotic is over-

lapped by the prootic; the meandering prootic-opisthotic suture continues anteriorly through the foramen ovale and then ventrally along the postero-lateral margin of the basisphenoid.

Prootic. The prootic rests upon the basisphenoid. Laterally, the prootic (figure 12) overlies the opisthotic; together they form the roof of the stapedial canal and the fenestra ovalis. Their suture becomes complex laterally and is represented externally as a meandering line that continues to a common inter-section with the laterosphenoid and parietal. The prootic is bounded anteriorly by the laterosphenoid, posteriorly by the opisthotic, and dorsally by the parietal, although there is no actual contact with the parietal.

Orbitosphenoid. The orbitosphenoids (figure 16) are small, thin, subcrescentic, platelike elements lying within the large vacuity in the anterior floor of the cranial cavity. They are joined dorsally and ventrally at midline to form a ring around the optic foramen. They suture above with fragile delicate projections from the laterosphenoids to serve as a basal support of the olfactory nerve. The lower part of the orbitosphenoid and laterosphenoid suture appears to contact the para-sphenoid dorsally at its posterior angle.

The occurrence of the ethmoid in *Allosaurus fragilis* is questionable even though Gilmore (1920, p. 14) suggests that there is sutural evidence between the orbitosphenoids and the alisphenoids (laterosphenoids of this paper). The sutural contacts appear to be that point at which the ascending process of the para-sphenoid meets those two elements. In USNM 4737 the ascending process of the parasphenoid is missing and the absence of this part of the basisphenoid complex is understandable because of its very thin and fragile nature. Of the numerous cranial complexes of varying sizes in the Cleveland-Lloyd Dinosaur Collec-tion, only two show the complete or nearly complete parasphenoid intact (figure 17).

Osborn (1912) notes the presence of an ethmoid in *Tyrannosaurus,* as similarly reported by Stovall and Langston (1950, p. 704) in *Acrocanthosaurus.* The element called orbitosphenoid by Osborn (1912) is the laterosphenoid of this paper.

Laterosphenoid. The laterosphenoid of this paper (figure 17)—the orbitosphenoid of Osborn (1912) and alisphenoid of Gilmore (1920)—is quadriradiate, surrounded above by the frontal and the anterolateral extension of the parietal and below by the prootic and basisphenoid. The laterosphenoids meet ventrally at midline suture to form the upper part of the dorsum sellae, that part of the floor of the braincase between
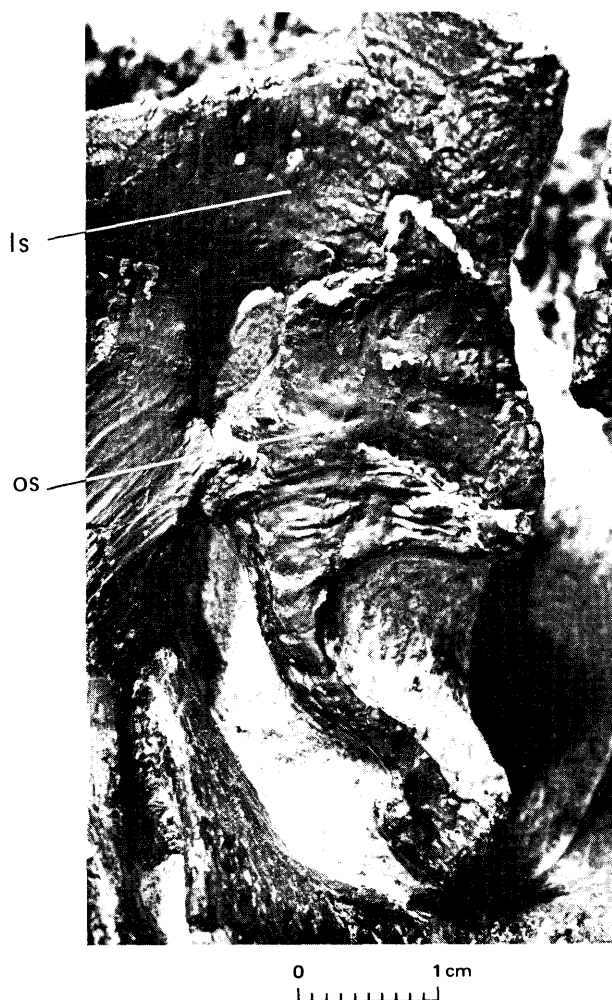
Figure 16. Anterior view of right orbitosphenoid (UUVP 5583) of *Allosaurus fragilis.* Abbreviations: ls—laterosphenoid, os—orbitosphenoid.

the basisphenoid and the optic foramen. An antero-medial extension of the laterosphenoid meets with the orbitosphenoids at the superior angle of the para-sphenoid to form a trough under the olfactory nerve at its exit from the braincase. Laterally, a barlike extension terminating in a rounded knob, the distal cotylus, articulates with the postorbital. There is a deep groove on the anterior surface of the ventral segment of the laterosphenoid. Below this, the latero-sphenoid contacts the thin, bladelike, ventral arm of the prootic. Above this groove and lateral to the contact between the laterosphenoid and the orbito-sphenoid is the opening of the fourth cranial nerve, which is entirely surrounded by laterosphenoid.

Supraoccipital. The dorsally prominent element of the occipital ring, the supraoccipital (plates 1 and 2, figures 13 and 15), has wedge-shaped lateral processes, which project from its base separating the exoccipital-
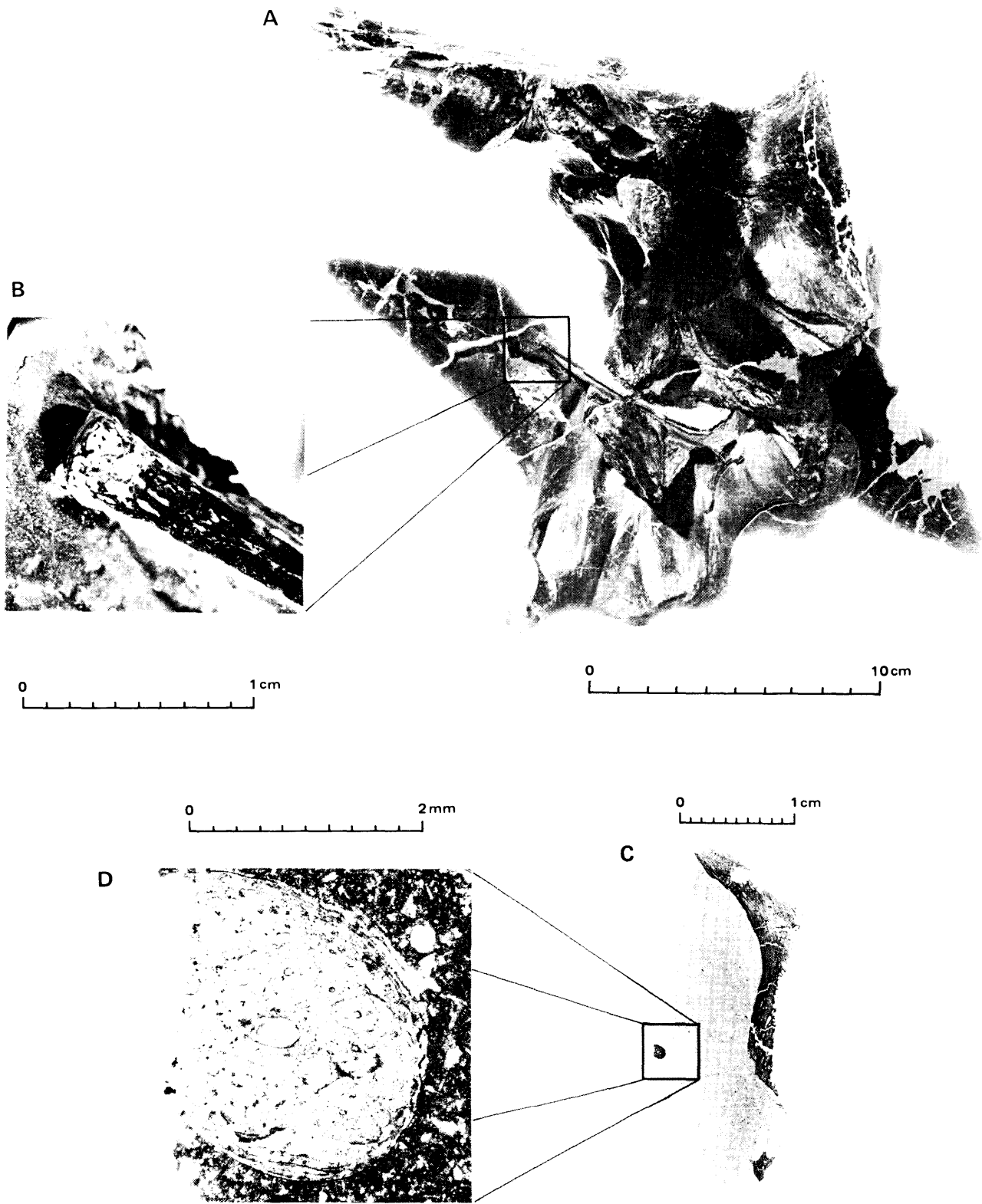
Figure 17. Braincase (A, UUVP 5961) of *Allosaurus fragilis* and stapes in distal (B) and cross sectional (C, D) views. Note that parasphenoid (ps) is rotated downward approximately 12 degrees.

opisthotics and parietals. The supraoccipital lies dorso-medially between the parietals, expanding upward into a conspicuous ledge that terminates below the transverse supraoccipital crest and projects back from the parietals.

Stapes. The stapes (figure 17) is a thin, delicate, elongate rod with proximal and distal ends noticeably expanded. There is no evidence of an ossified extra-columella. Excellent preservation of an articulated braincase (UUVP 5961) of *Allosaurus fragilis* and careful preparation permit the first description of an intact specimen of this interesting element for this genus. Fortunately, prior to deposition of the enclosing sediments, the soft tissues surrounding the stapes were pressed anteriorly against the prootic and the superior extension of the parasphenoid so that, although in an obviously unnatural position, the bone was preserved intact. Preparation of a second specimen (UUVP 5748) revealed the internal position and shape of the proximal end of the stapes as it lies beneath the endo-lymphatic complex (figure 9a).

The distal part of the stapes is slightly flared, flattened, and squared at its termination. The shaft is a long, slender rod (figure 17), an estimated 100 mm in length and 1 mm in diameter at midlength. The proximal end is more complicated than the distal. It is flared but oblique to the shaft and terminates in a nearly square, flat-bottomed foot plate. In general, the stapes of *Allosaurus fragilis* fits the descriptions by Colbert and Ostrom (1958) and Colbert and Russell (1969) for *Dromaeosaurus*. It differs mainly in its greater length, since in a restored position it appears to extend enough beyond the edge of the quadrate to eliminate the need of an extracolumella of any size.

Palatal Complex

The palate of *Allosaurus fragilis* is vaulted; the paired pterygoids, ectopterygoids, and palatines rise and meet medially at an approximate right angle to each other. These elements are separated posteriorly by a moderately narrow interpterygoid vacuity. The elongate internal nares are separated anteriorly by the vomer, which abuts the premaxillary symphysis and joins posteriorly with the palatines at their dorsomedial contact. The moderately large palatine fenestra is almost completely enclosed posteriorly by the ecto-pterygoid and anteriorly by the palatine. The sub-temporal fossae are by far the largest openings of the palate, down through which project conspicuous bars formed by the combined posteroventral processes of the ectopterygoids and pterygoids. These bars extend well below the margin of the jaw and are in plain view seen laterally. The bars appear to have served as guides for large bolts of food as they were swallowed and to maintain alignment of the lower mandible as it closed.

Vomer. A vomer (plate 10e, f) is recognized for the first time in *Allosaurus fragilis*. An intact specimen has yet to be retrieved from the Cleveland-Lloyd Dinosaur Collection; however, a complete element was exposed (figure 18) in the fine skull from Dinosaur National Monument (UUVP 6000). It is a single, fragile, elongate bone consisting of two posterior, sub-rectangular, vertical plates that are separated by a deep, narrow cleft. The plates merge into a shaft, triangular in cross section, that terminates anteriorly in a blunted point. Posteriorly, the vertical plates attach inside the anterodorsal arch of the palatines, not with the pterygoids as in *Tyrannosaurus* (Osborn, 1912, p. 6). Anteriorly, the point of the vomer fits a notch at the medial symphysis of the premaxillae just above the base of the interdental plates. The vomer also lies very close to and may contact the anteromedial process of the maxillae. Evidently the vomers are not paired in *Allosaurus fragilis*, but, if they are, fusion must occur embryonically, because even the smallest, apparently juvenile, examples show no separation. The anterior half of the vomer is slightly expanded laterally but much less so than in the tyrannosaurs.

Palatine. The palatine (plate 10a, b) contacts the maxilla laterally along its posterior one-third. From the maxillary contacts, anteromedial plates rise and meet dorsally at midline. Posteriorly, the palatine joins in squamous suture with the thin, underlying palatal ramus of the pterygoid.

Ectopterygoid. The ectopterygoid (plate 10c, d) is hook shaped, having a curved posterolateral arm contacting the slightly concave, ventromedial surface of the jugal. The ectopterygoid is widely expanded medially, sharing an extensive contact with the palatal and ventral rami of the pterygoid. The body of the ectopterygoid is deeply hollowed and thin walled, a condition considered a "carnosaurian" characteristic by Ostrom (1969a, p. 27).

The ventral projections of the posteromedial arm of the ectopterygoid and ventral bar of the pterygoid from the roof of the mouth served to maintain the alignment of the lower mandible and possibly aided in guiding bolts of food as they were swallowed.

Pterygoid. The pterygoid (plate 10i) is tripartite, consisting of a near vertical quadrate ramus, an anterior palatal ramus, and a ventral extension that joins with the ectopterygoid to project down as a bar from the roof of the mouth.

The quadrate ramus, a subrectangular, thin plate rising above the socket for the basipterygoid process, lies alongside but apparently not in contact with the lateral elements of the braincase. Its anterior edge is vari-
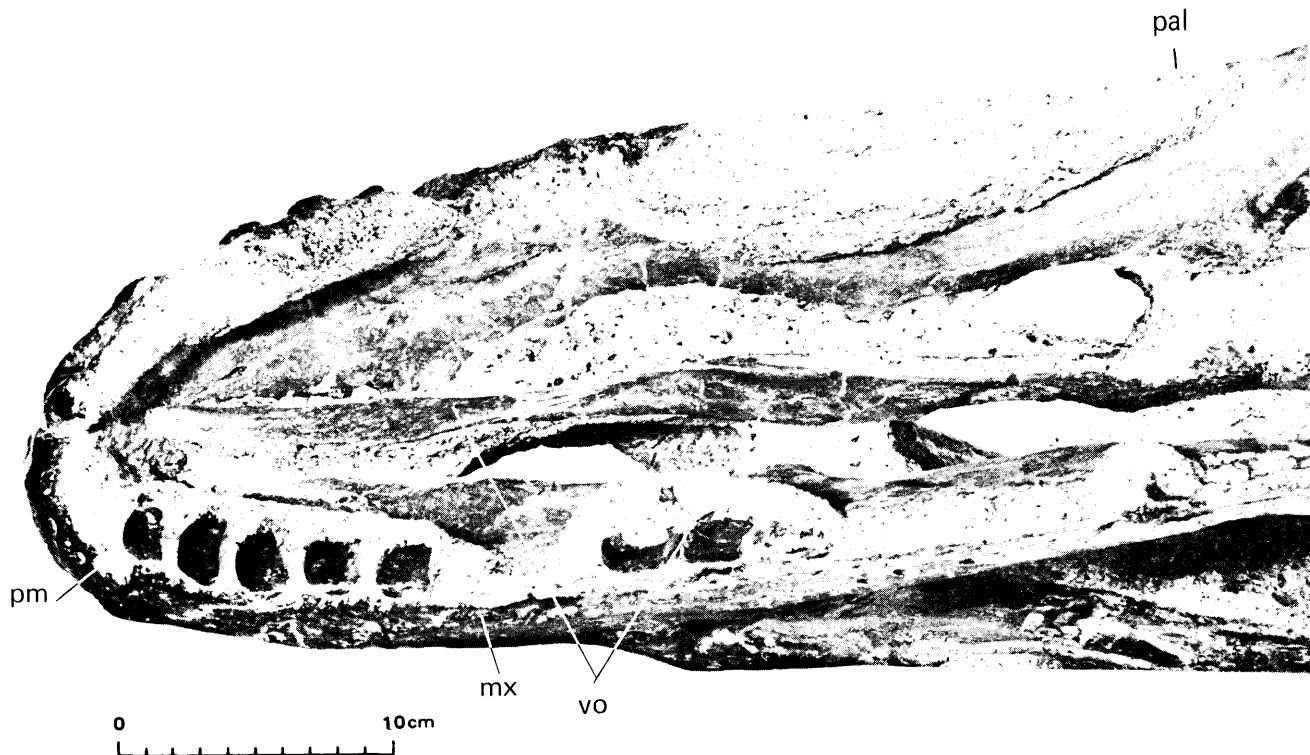
Figure 18. Palatal view of skull (UUVP 6000) of *Allosaurus fragilis* showing anterior palatal elements in place. Abbreviations: mx—maxilla, pal—palatine, pm—premaxilla, vo—vomer.

ably indented with a groove that continues for a short distance along the lateral surface. This groove indicates the line of epipterygoid attachment. Posteriorly, the pterygoid joins the quadrate, which laps over pterygoid's lateral edge and continues down and around part of the ventral margin. The basipterygoid cotylus loosely encloses the basipterygoid process and suggests an extensive cartilaginous cover and a fairly kinetic joint.

The entire anterior margin of the ventral arm of the pterygoid is enclosed by the ectopterygoid, forming a contact which continues forward over half of the lateral surface of the palatal ramus. The ventral blade is thin enough that it probably allows some lateral flexion with the overlying ectopterygoid.

The thin palatal ramus continues forward and projects well beneath the palatines, which it joins in squamous suture. The anterior blades of the pterygoids appear to have been very close, almost meeting at midline. Although they extend well under the palatines, they fall far short of contact with the vomer.

Epipterygoid. An epipterygoid (plate 10g, h, i) has not been found in close association with any of the pterygoids in the Cleveland-Lloyd Dinosaur Collection. The morphology and articulation of the few isolated examples are confirmed, however, by the

complete skull of UUVP 6000, which has both epipterygoids in place.

The bone is so thin in the adult that its ossification in younger individuals is improbable. It is almost symmetrical in lateral aspects, thinning and flaring ventrally to its squamous, lateral attachment on the anterodorsal surface of the pterygoid. The epipterygoid lies close to, if not in contact with, the laterosphenoid immediately beneath the postorbital arch. Both contacts appear highly kinetic, which is consistent with the supposed flexibility of the palate.

Quadrate. The shaft or body of the quadrate has a slight anterior bow in *Allosaurus*, and the entire element is slanted noticeably forward. The head of the shaft is rounded but not significantly expanded. The shaft is widely expanded below into two large, oval condyles—the outer one of which is somewhat larger than the other. The condyles are separated by a moderately deep, oblique groove. The total width of the condyles is approximately one-half the overall height of the quadrate in mature specimens.

At about midheight along the quadrate-quadratojugal suture, the shaft is pierced by the quadrate foramen, which is almost entirely closed within the quadrate. Immediately below the quadrate foramen on the lateral surface a suboval concavity with

radiating ridges and grooves provides a strong, immovable, sutural attachment for the quadratojugal. Limited anteroposterior movement would be allowed at the head of the quadrate, but there appears to have been considerable lateral flexion.

Osborn (1912, p. 27) cited fifteen characteristics of the *Allosaurus fragilis* skull that he considered primitive. His analysis is not questioned; neither does the following analysis imply that *A. fragilis* was or was not ancestral to *Tyrannosaurus*; however, some of his observations require clarification: "(6) supraorbital rugosity not developed"—the supraorbital area formed by the lachrymal and postorbital is decidedly rugose (figure 8); "(7) nasal rugosity not pronounced"—nasal rugosity is pronounced; "(9) supraoccipitals narrow, rectangular, bearing large keel for *ligamentum nuchae*"—supraoccipitals are noticeably expanded ventrally, subtriangular; "(10) above the occipitals a pair of pits lodging rounded prominences possibly represent a portion of the periotic mass"—the pits and rounded prominences are on the occipital surface of the supraoccipital, which is excluded from the periotic mass; and "(13) exoccipitals closing in over foramen magnum, suturally separate from supraoccipitals"—exoccipitals are separated dorsally by the supraoccipital, which enters the margins of the foramen magnum.

Mandible

There are nine paired elements in the mandible of *Allosaurus fragilis* : articular, dentary, splenial, angular, surangular, prearticular, coronoid, intercoronoid (supradentary), and antarticular (a neomorph).

Articular. The articular (plate 7b, c) is complexly rugose and irregularly excavated. The dorsal surface has a moderately deep, oval concavity, which receives the inner condyle of the quadrate; this cavity is separated by the hooklike retroarticular process from a deeper, narrower fossa. Dorsolaterally, the articular and surangular contribute equally to form the outer fossa. The articular is firmly joined to the surangular along an intricately grooved and firm sutural contact. The anterodorsal surface of the articular, the internal process of the surangular, and the posterior end of the prearticular meet medially to form a socket for a small, rounded bone that lies anterior to the quadrate cotylus. The apparent neomorph seems to function as a stop that would limit posterior disarticulation of the mandible.

Dentary. The most massive element of the mandible is the dentary (plates 1 and 9d and table 3),

a long, narrow, robust bone covered on its lingual surface by the coronoid(s), the splenial, and the prearticular. The dentary forms the anterior one-half of the lower jaw. It joins posteriorly with the surangular, prearticular, and angular in a lapping, kinetic contact. The posterior third of the dentary is thin and vertically expanded, tapering to a uniform depth at midlength that continues to the symphysis. Medially, the interdental plates are underlain by a uniformly rounded, lingual bar, which begins at the symphysis and continues back posterior to the tooth row. Under the lingual bar, between the thirteenth and fourteenth alveoli, are two foramina leading into the body of the dentary. The lower of the two foramina continues internally along the bases of the alveolar crypts to emerge anteriorly near the pitted end of the groove below the lingual bar. Above the lingual bar the inside margin of the dentary, as in the premaxilla and maxilla, is formed by a battery of low, fused interdental plates. The external surface of the dentary is marked by numerous foramina, at least one series of which is arranged in a line approximately parallel to the tooth row. The numerous other foramina entering the external surface are randomly distributed.

The mandibular symphysis, though weak, is usually a fairly well-defined, slightly flattened surface that indicates a ligamentous, kinetic attachment. The average number of teeth in the dentary of *Allosaurus fragilis* is sixteen. Of forty-four dentaries examined : one had 14 alveoli; two had 15 alveoli; twenty-seven had 16 alveoli; and fourteen had 17 alveoli.

Splenial. The splenial (plate 9a, b) is a thin, subtriangular plate that covers much of the posterior, lingual surface of the dentary. The apex of the triangle lies closely against the dentary, barely reaching the superior margin of the mandible. The splenial is gradually tapered anteriorly, but just beyond a ventral foramen it tapers abruptly to a sharp point that terminates near midlength of the tooth row. Although of moderate size, the splenial foramen is significantly smaller in *Allosaurus fragilis* than in the *Tyrannosaurus rex* mandible (AMNH 5027) described by Osborn (1912, p. 20). This foramen, apparently not completely closed in *Tyrannosaurus* and variably so in *Allosaurus,* is bordered by a solid margin in *Ceratosaurus*. Posteriorly, the splenial thins and tapers beneath without contacting the anterior end of the prearticular and is underlapped by the dentary. The dentary and the splenial form a slot for insertion of the anterior, tapering end of the angular. The splenial of *Allosaurus* is an interesting contrast with those of *Ceratosaurus* and *Deinonychus,* which are thickened, stout, and slightly curved upward as if to serve as a point of rotation for the anterior half of the mandible.

Table 3. Measurements and indices of some Cleveland-Lloyd theropod dentaries.

	UUVP or other number	Side	Total alveoli	Depth[1] at 6th alveolus (mm)	Length of tooth row (mm)	D:L x 100	Identification
1	1910	right	15	41	153	27	*A. fragilis*
2	870	right	16	36	156	23	*A. fragilis*
3	142	left	16	40	167[2]	24[2]	*A. fragilis*
4	2456	right	17	36	170	21	*A. fragilis*
5	1895	left	16	44	173	25	*A. fragilis*
6	1974	left	16[2]	44	173[2]	25[2]	Unidentified
7	1900	left	16	44	173[2]	25[2]	*A. fragilis*
8	1904	right	16[2]	47	173[2]	27[2]	*A. fragilis*
9	699	left	16	42	177	24	*A. fragilis*
10	3389	right	16	45	177	25	*A. fragilis*
11	1909	right	16[2]	44	182[2]	24[2]	*A. fragilis*
12	1906	right	14	48	184	26	*A. fragilis*
13	1901	left	16	45	190	24	*A. fragilis*
14	40-555	left	19[2]	34	193[2]	18[2]	Unidentified
15	5289	right	17	48	194	25	*A. fragilis*
16	3454	left	20	34	196	17	Unidentified
17	1908	right	16[2]	48	200[2]	24[2]	*A. fragilis*
18	702	left	17	50	200	25	*A. fragilis*
19	3502	right	22	33	203[2]	16[2]	Unidentified
20	40-331	right	16	58	208	28	*A. fragilis*
21	4233	right	15	49	210	23	*A. fragilis*
22	1897	left	16[2]	51	210[2]	24[2]	*A. fragilis*
23	1907	right	17	51	211	24	*A. fragilis*
24	2903	right	17	57	211	27	*A. fragilis*
25	1046	left	16[2]	58	212	27	*A. fragilis*
26	1905	right	17	57	215	27	*A. fragilis*
27	1896	left	16	60	217	28	*A. fragilis*
28	1898	left	16	57	222	26	*A. fragilis*
29	1903	right	17	58	231	25	*A. fragilis*
30	6742	right	16[2]	65	235[2]	28[2]	*A. fragilis*
31	4778	right	17	60	240	25	*A. fragilis*
32	5079	left	16	63	240	26	*A. fragilis*
33	Cast[3]	right	16	60	251	24	*A. fragilis*
34	Cast[3]	left	17	60	269	22	*A. fragilis*
35	10,093	right	17	69	269	25	*A. fragilis*
36	30-296	left	16[2]	63	281[2]	22[2]	*A. fragilis*
37	2001	left	16	71	281	25	*A. fragilis*
38	5427	right	16	74	284	26	*A. fragilis*
39	4029	left	17	71	295	24	*A. fragilis*
40	3810	right	16	74	295[2]	25[2]	*A. fragilis*
41	5748	left	16	79	298	27	*A. fragilis*
42	6000	right	17	76	303	25	*A. fragilis*
43	10,250	left	17	74	303	24	*A. fragilis*
44	40-553	left	16	75	317	24	*A. fragilis*
45	158	left	15[2]	75	321	23	*Ceratosaurus*
46	871	left	16	89	325	27	*A. fragilis*
47	155	right	15[2]	83	326[2]	25[2]	*Ceratosaurus*
48	6000	left	16	75	330	23	*A. fragilis*

[1] Distance between upper and lower margins of dentary.
[2] Estimated; bone incomplete, distorted, or pathological.
[3] Original quarry number unknown.

Angular. The angular (plate 7d, e) is relatively long, slightly bowed, and platelike. Lying below the surangular it is continuous with the ventral surface of the surangular but extends beyond and inside of the posteroventral margin of the dentary. The postero-lateral surface of the surangular is subtly scarred and indented at its contact with the angular. Together with the prearticular, the angular extends almost one-half of the length of the mandible and forms the floor of the adductor fossa.

Surangular. The surangular (plate 8) is the largest element of the posterior half of the mandible. Anterior and lateral to the articular contact, a browlike longi-tudinal ridge overhangs a relatively small foramen that pierces the wall of the surangular, although Gilmore (1920, p. 26) only recognized such an opening medially. This foramen, though seemingly homologous to a large opening noted by Lambe (1904, p. 15) for *Dryptosaurus (Albertosaurus)* and by Osborn (1912, p. 24) for *Tyrannosaurus*, represents a sharp contrast in size. Although smaller, it is closer in size to the posterior surangular foramen of *Deinonychus* (Ostrom, 1969a, p. 33) and *Dromaeosaurus* (Colbert and Russell, 1969, p. 29). Russell (1970, p. 20) reports a small surangular foramen in *Tarbosaurus* (Maleev, 1955).

The ventral margin of the surangular is deeply notched at midlength, but only part of the opening is exposed laterally above the angular, appearing as the external mandibular foramen. A third nutrient foramen opens anteriorly on the lateral surface of the surangular. The superior surface of the surangular is flat to slightly concave, where it lies in opposition to the jugal in the articulated skull. Internally, the surangular is deeply excavated which provides an extensive area for insertion and attachment of the adductor mandibularis muscle. The surangular does not overlap the posterior end of the dentary as reported by Gilmore (1920, p. 26); rather the dentary overlaps the surangular.

Coronoid and accessory elements. The coronoid and accessory elements are three in number and occur anteriorly, at midlength, and posteriorly near the dorsal surface of the mandible. The first is long, narrow, and splintlike, covering the interdental plates over their entire length; the intercoronoid or supra-dentary (plate 10d), a term proposed by Osborn (1912, p. 5) and adopted by Gilmore (1920, p. 89) in his description of *Ceratosaurus*, apparently served as a cover plate protecting the vascular system and interdental plates along the lingual base of the tooth row. The intercoronoid shares a contact with the splenial below the posterior one-third of the tooth row, and there is no question as to the separate identity of the two bones. Brown and Schlaikjer
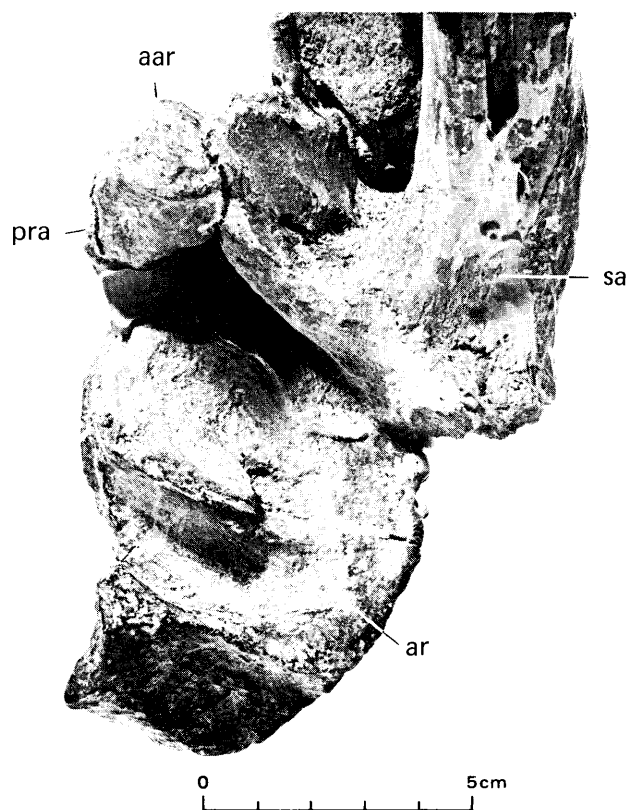
Figure 19. A neomorph of *Allosaurus fragilis*, the antarticular, in the articular surface of the mandible (UUVP 6000). Abbreviations: aar—antarticular, ar—articular, pra-prearticular, sa—surangular.

(1940) recognized the intercoronoid in several ceratopsians, in *Plateosaurus*, and in *Tyrannosaurus*, where it was called supradentary by Osborn.

A second bone, the coronoid (plate 7a), is a very thin, subtriangular element lying at midlength of the mandible between the surangular and the prearticular. It completes the anterior margin of the adductor fossa. It fits into the grooved anteromedial surface of the surangular and meets near a common point with the splenial and anterior end of the prearticular. It overlaps the anterior end of the prearticular. The thin and fragile nature of this element suggests that it was of limited functional value to the lower mandible and may explain its rare occurrence and infrequent recovery.

A third element, a neomorph, which appears unique to *Allosaurus fragilis*, is set in a socket formed by a medial process of the surangular, the postero-dorsal extremity of the prearticular, and the medial surface of the articular at their contact (figures 19 and 20). The bone, which I have termed the antarticular (aar), is rounded and subrectangular in form, and

therefore reminiscent of the mammalian sesamoids; however, no real or functional homology is inferred. Neither does identification with the existing coronoid seem appropriate inasmuch as it is significantly removed from the superior margin of the mandible. Functionally, the antarticular increases the surficial area of the glenoid fossa, acting as a buttress to restrict posterior disarticulation of the mandible.

Prearticular. The prearticular (plate 7f, g) is bowlike, thickened at midshaft, and flared at either end. Anteriorly, it contacts the superior surface of the surangular, the posteromedial surface of the dentary, and the ventral margin of the coronoid. Antero-ventrally, a small spurlike projection borders an internal mandibular foramen (infra-Meckelian fenestra of Romer, 1956, p. 210). The prearticular rests in contact with the angular below and rises to overlap lingually the articular and antarticular behind. A thin backward process of the prearticular underlies the posteroventral surface of the articular.

Axial Skeleton

Cervical Vertebrae

There are nine vertebrae (plates 11-15) in the neck of *Allosaurus fragilis*, which, except for the atlas, are strongly opisthocoelous and bear paired ribs. The opisthocoelous type of centrum persists through the thirteenth presacral (fourth dorsal) vertebra. In a resting pose the articulated cervical vertebrae describe an elongate "S" or sinusoidal curve (frontispiece), and their articulation is such that it would have been difficult for *A. fragilis* to fully straighten its neck.

In the anterior part of the cervical series, zygapophyses are spaced so that the distance from the prezygapophyses to the postzygapophyses is greater than the width. The distances are subequal in the mid-cervical region and reverse in the posterior part of the series. From juvenile to adult there is a recognizable, disproportionate increase in the height and mass of the neural spines, which is consistent with the fact that as the animal grows there is a disproportionate increase in skull weight. In response to an increase in size, longer spines must develop to accomodate the additional musculature required for support. Although distinct, the ninth cervical vertebra may be referred to as a cervico-dorsal (Osborn, 1906, p. 288), since it does exhibit characteristics common to the posterior cervicals and the anterior dorsals. The parapophysis lies forward and low on the centra of the anterior cervicals and assumes a higher position posteriorly so that by the eighth cervical vertebra it is bisected by the suture between centrum and neural arch. The diapophyses of the anterior cervical vertebrae are diminuitive and

directed downward, but they increase in size posteriorly, rising to assume an angle of 90 degrees to the axial plane of the neural arch.

Wieland (1942), Russell (1965), Bakker (1971 and 1972), and Ostrom (1969b) have discussed the possibility of endothermy and an avian relationship of the dinosaurs, although the popular or broadly accepted notion through the years has been that the group as a whole were poikilotherms. If some dinosaurs were endothermic, particularly the theropods, it might be consistent with the occurrence of the pneumatic or cavernous condition of cervical and anterior dorsal vertebrae in *Allosaurus fragilis*, which parallels the internal structure of the homologous bones in birds.

Atlas-axis. As is true for all theropods, the atlas-axis is a combination of bones consisting of paired neurapophyses, atlantal intercentrum, axial inter-centrum, odontoid, centrum, and neural arch of the axis (plate 11). The neurapophyses are flattened, triangular elements that articulate anteriorly with the axial intercentrum and form an arch over the spinal cord. They articulate posteriorly with the pre-zygapophysis of the axis. There is no cervical rib on the atlas.

The neural arch of the axis is large, having a massive, posteriorly directed neural spine that is expanded dorsally. The posterior zygapophyses of the axis are similar to those on the other anterior cervical vertebrae in that they support a dorsal process, the epipophysis of Ostrom (1969a, p. 46) which projects posterolaterally above and over the articular facets. The diapophyses are weakly developed; but each supports a thin, tapering cervical rib. A lateral cavity (pleurocoel) behind the capitular facet, typical of the first thirteen presacral vertebrae, is well developed on the centrum of the axis.

Postaxial cervicals. The cervical vertebrae following the axis are strongly opisthocoelous. A slight median keel is developed on the ventral surfaces of the third and fourth cervical centra. Neural spines are stout and long anteroposteriorly through the seventh cervical vertebra. They become squared in cross section on the eighth and ninth cervicals. The diapophyses are small on the anterior cervicals and directed posteroventrally. They tend to increase in size and become more elevated in the posterior elements of the series. A gradual transition occurs in the posterior cervicals where the diapophyses are well developed and positioned at right angles to the neural arch.

The epipophyses of the postzygapophyses, long in the anterior part of the series, decrease in size
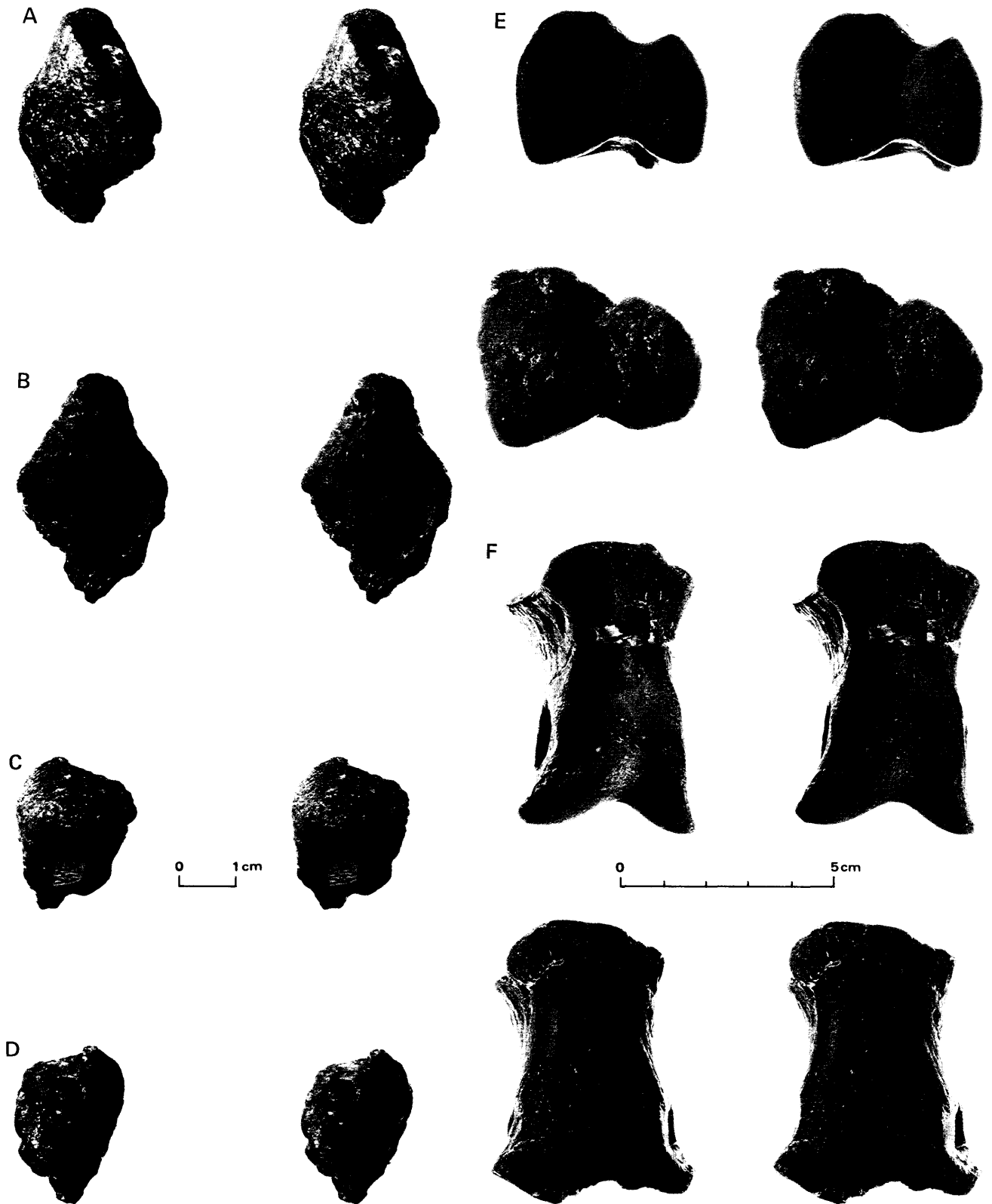
Figure 20. Stereo views of antarticular of *Allosaurus fragilis* in labial (A), lingual (B), dorsal (C), and ventral (D) views, and pathological and normal D-IV, proximal phalanges of *Allosaurus fragilis* (E, F).

through the sixth cervical vertebra, where they barely project beyond the margin of the articular facets. The decrease in size of the epipophyses continues posteriorly through the series, and the ninth cervical retains only a small ridge.

Dorsal Vertebrae

Anterior dorsals. The first dorsal vertebrae (plates 15-23) show a gradual transition posteriorly from a cervical to a dorsal design, a change that is completed by the fifth dorsal vertebra. Posterior to the fifth, the dorsal vertebrae are fairly uniform in shape.

The marked opisthocoelian development of the two anterior dorsal centra is in contrast with that of the third dorsal vertebra, which has a rather flat anterior end but is typically concave posteriorly. Similarly this condition may be repeated in the fourth dorsal centrum, but posteriorly the centra are amphiplatyan and only slightly concave. A hyposphene-hypantrum articulation is first apparent on the fifth or sixth dorsal vertebra, a condition that increases posteriorly to its maximum development on the fourteenth dorsal vertebra. The transverse processes or diapophyses of the dorsal neural arches are strong and well developed, characteristically directed slightly upward and backward. They are proportionate in size to the dorsal ribs that they support.

The capitular facets, which assume a high position in the anterior cervical vertebrae, gradually shift downward so that by the last or ninth cervical and first dorsal centra they are quite low. Their position begins to shift upward off the centra in the anterior dorsal vertebrae and continues to do so through the fifth dorsal after which they are completely confined to the neural arch.

The anterior dorsal vertebrae have ventral keels on the centra that are most prominently developed on the second dorsal where there is in addition a small anteroventral spurlike projection. The keel is still evident through the fourth dorsal and, though poorly defined, may be recognized on some centra of the fifth dorsal vertebra.

The maximum development of pleurocoels occurs on the first dorsal centrum, behind which they gradually decrease in diameter through the fourth dorsal centrum and may be lost entirely or occur only on one side of the fifth dorsal centrum. Above the pleurocoel a secondary foramen sometimes occurs in the neural arch; the best development of which is noted on the third dorsal vertebra, where it connects with the neural canal. This might represent a branch of the pectoral ganglion or brachial plexus. There is an

enlargement of the neural canal at the ninth cervical vertebra that continues through the third or fourth dorsal vertebra. The enlargement no doubt is associated with the innervation of the forelimb.

In contrast to the anteroposterior development of neural spines in the anterior cervicals, the neural spines of the anterior dorsal series tend to expand laterally. This condition continues through the fourth dorsal vertebra, posterior to which the neural spines are nearly square in cross section. Behind the fourth vertebra the anteroposterior dimension exceeds the transverse width; neural spines posterior to the sixth dorsal vertebra are fairly uniform in shape, although a slight but progressive increase in height occurs posteriorly.

The prezygapophyses are as widely separated in the anterior dorsals as they are in the posterior cervicals; that is, their lateral separation is half again as much as the distance between the prezygapophyses and postzygapophyses. The zygapophyses become closer posteriorly, and by the fifth dorsal they are at the approximate position assumed through the remaining dorsals.

Posterior dorsals. Whereas the transverse processes of the anterior dorsal vertebrae are directed at right angles to the neural spines, throughout the posterior half of the dorsal series they are oriented approximately 30 degrees above the horizontal and 60 degrees posterior to the transverse axis. Beginning with the twelfth dorsal vertebra, the transverse processes deviate from a posterodorsal angle; there they project at right angles from the neural spine and gradually change in position on the thirteenth and the fourteenth dorsals, where the transverse process becomes nearly horizontal, shortened, and directed forward at an angle of approximately 25 degrees. The transverse processes of the fourteenth dorsal vertebra lie within and in line with the anterior margin of the ilium. The fourteenth dorsal vertebra bears diminuitive ribs, which lie just inside the anterior blades of the ilia.

Sacral Vertebrae and Ribs

Many of the five vertebrae of the sacral series (plates 24-28) are found articulated, although it is not uncommon in the Cleveland-Lloyd Dinosaur Collection to find the smaller elements that represent juvenile stages articulated and the large, massive elements attributed to fully adult specimens disarticulated. This inconsistent sacral articulation will receive further consideration later in the paper, since it may represent a characteristic also attributable to sexual dimorphism, rather than solely to age as is commonly thought.

The basic number of sacral vertebrae in the saurischian sacrum is three according to Romer (1956, p. 266); and as indicated by Gilmore (1920, p. 43) it is probable that the second and third sacrals of *Allosaurus fragilis* are the primary elements. However, the center three may be considered the stem sacrals as described by Russell (1972, p. 377), since they are the only ones with true sacral ribs and transverse processes. The iliac connections of the first and fifth sacral vertebrae arise solely from the neural arches. Judging by the transitional appearance of the sacral vertebrae, the sequence of incorporation appears to be fourth, fifth, and first. Though other elements of a sacrum might be found disarticulated, the neural spines of the first and second vertebrae are often found fused. Some of the first sacral vertebrae bear nondescript remnants of ribs on the underside of the foreshortened diapophyses, but such ribs are not always evident. The other sacral ribs attach intervertebrally between the sacral vertebrae, only the first four of which have diapophyses. There is no distinction between diapophysis and rib on the fifth sacral vertebra. Instead, a single projection is shaped as the diapophysis of the first caudal vertebra. These processes of the fifth sacral are morphologically similar to those described as "clearly caudal ribs in hadrosaurs" by Langston (1960, p. 335).

Stated another way, the primitive sequence of inclusion of vertebral elements recorded in the sacral arcade of *Allosaurus fragilis* seems to be : (1) sacral two from a dorsal vertebra and three from a caudal vertebra; (2) sacral four from a caudal vertebra; (3) sacral five from a caudal vertebra; and (4) sacral one from a dorsal vertebra. The order and stage of incorporation of the sacral vertebrae may be phylogenetically significant.

Generally the sacral complex is a strongly developed unit: the transverse processes articulate dorsolaterally and the sacral ribs articulate ventrolaterally with the ilia. Even in juvenile specimens the neural spines of the sacral series may be fused into a rectangular, median blade.

Movement between centra in the sacral series is extremely limited, and practically all movement is eliminated when the neural spines are fused. Well-developed grooves and ridges on the articular facets of the centra radiate ventrally from the base of the neural canal, except for the surfaces of presacral and postsacral articulation. The anterior face of the first sacral centrum is smooth and slightly concave, but its posterior face has ridges and grooves. Articulating surfaces of the second, third, and fourth sacral vertebrae plus the anterior face of the fifth sacral centrum also have ridges and grooves. The posterior face of the fifth sacral centrum is slightly concave and circular in outline. The sacral centra are spool shaped with an elongate concavity or coel developed under the sutural margin of the neural arch. The coel is not continuous with any internal chambering of the centrum as seen in some of the anterior presacral vertebrae.

Caudal Vertebrae

Approximately fifty vertebrae are in the tail of *Allosaurus fragilis*, and the total number is variable. Each element of the caudal series (plates 29-36) differs from the next; however, some of the differences are so slight that they are most easily recognized over a series of three or more vertebrae. The transverse processes of anterior members are large, laterally expanded, and slightly inclined to the rear. Though bladelike in the anterior caudals, they become increasingly small posteriorly and are retained as small ridges in the midcaudal region, where they are finally lost—the "transition point" of Russell (1972, p. 378). Similarly the stout neural spines in the anterior caudal series tend to become smaller and directed slightly backward in the anterior fourth of the series, finally becoming so small that they do not rise above the postzygopophysis in the midcaudal section (at approximately the twenty-eighth caudal). The caudal centra are generally amphicoelous, although the anterior elements of the series exhibit a posterior face which is slightly convex to flat. The anterior twelve centra of the caudal series are slightly compressed laterally and taper ventrally to a shallow, longitudinal groove that is approximately three-quarters of the length of the centra and that persists throughout the caudal series. A similar ventral groove is noted in the caudal vertebrae of *Ceratosaurus* but is significantly deeper, longer, and more rounded (figure 8). Centra become proportionately more elongate posteriorly, and by the thirtieth caudal the length is twice the width. This trend continues through the most distal caudals where the length is three times the width. A terminal caudal vertebra, as such, has not been recognized in any of the Cleveland-Lloyd materials, so it is presumed that it may have been cartilaginous. Except for the first caudal vertebra, successive centra in the series have an anterior and posterior chevron facet, a condition that persists well into the distal part of the tail and is lost in the vicinity of the forty-fifth caudal.

The first caudal vertebra is the largest of the series having a stout, nearly vertical neural spine that terminates dorsally in an expanded posterior surface and a thinning anterior edge. Throughout the anterior half of the caudal series the neural spines are slightly inclined backward and in the midcaudal region begin to divide dorsally into a smaller, pointed, anterior segment and a higher, rodlike, posterior extension. The

neural spines become diminuitive in the posterior one-fourth of the caudal series, being entirely lost posterior to the thirty-eighth caudal. Not uncommonly in the Cleveland-Lloyd Dinosaur Collection, the neural arches of the caudal vertebra are found disarticulated from the centra through the twentieth caudal, posterior to which, even in juvenile specimens, the neural arch is so firmly coossified with the centrum that the suture is lost. The prezygapophyses increase in length in the distal half of the tail, and toward the end of the series they project more than halfway over the preceding vertebra. The angle of the zygapophysial facets increases from about 45 degrees through the proximal one-half of the series to a near vertical position in the distal one-half. Posterior to the twentieth caudal vertebra the prezygapophyses extend beyond the anterior face of the centra, reaching anteriorly three-quarters of the length of the next centrum. The post-zygapophyses are directed downward slightly above the horizontal, becoming laterally compressed posteriorly in the series.

Chevrons

Except for the first caudal vertebra a haemal arch or chevron (plate 37) is borne through the caudal series as far back as the forty-fifth caudal. Beyond this point a cartilaginous element may have been present since the more distal caudals retain facets. Anteriorly the chevrons are long and uniformly bladelike, having a slight curve to the rear. Posteriorly the chevrons shorten and become more curved in the midcaudal region, posterior to which the shaft is more laterally compressed and increasingly hooklike. Anterior processes, which project from either side above the haemal canal, are evident on all chevrons. Viewed anteriorly the chevrons are Y-shaped and the haemal canal is always enclosed.

A cross section through the anterior part of the tail appears as a vertical ellipse due to the strong development of the neural spine and ventrally projecting chevrons, but much less so than in *Cerato-saurus* (figure 21). The dorsoventral dimension decreases through the midcaudal area so that distally the restored tail would be nearly round in cross section.

Ribs

Cervical ribs. The axis is the first presacral vertebra with ribs (plate 38). A well-developed capitulum articulates closely with the parapophysis of the axial centrum. The tubercular articulation is comparatively weak and limited to a digitate projection on the proximal end of the rib that meets the small diapophysis of the neural arch. The shaft of the rib is
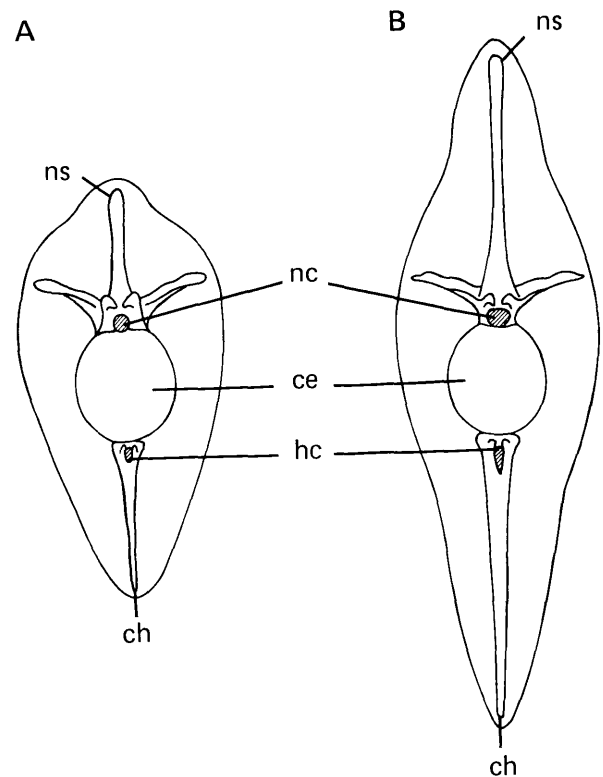

Figure 21. Anterior view of outlines at the base of the tails of *Allosaurus* (A) and *Ceratosaurus* (B). Abbreviations: ce–centrum, ch–chevron, hc–haemal canal, nc–neural canal, ns–neural spine.

directed ventrally and posteriorly with a slight downward curve. The shaft extends to the fifth cervical vertebra. The same pattern is reflected in successive ribs of the cervical series, but by the eighth cervical vertebra a transition begins toward the dorsal rib form. Cervical ribs are bicipital with long tapering shafts directed downward and backward from the diapophysis. Anterior and posterior cervical ribs are subequal in length, but a noticeable shortening occurs in the midcervical region. The ribs overlap at least one-half of the following centrum. No cervical ribs have been found attached to allosaur vertebrae in the Cleveland-Lloyd Dinosaur Collection, nor are they evident on UUVP 6000 from Dinosaur National Monument or the smaller MCZ 3897.

Dorsal ribs. The dorsal ribs (plates 39 and 40) are shaped as the number seven, the shaft curving ventromedially and reflecting the contour of the body cavity, which is narrow anteriorly and rounded posteriorly. Dorsal ribs four, five, and six are distinctly squared at the distal end of the shaft, which indicates articulation end to end or continuation in cartilage with the sternal elements. Curiously, the distal ends of dorsal ribs are frequently missing in the Cleveland-Lloyd Dinosaur Collection, a loss due either to

predator activity or to careless collecting in the field that is further complicated by difficulty of preparation in the laboratory.

Ventral ribs. Some of the chevron-shaped elements, identified by Gilmore as "abdominal ribs" or incorrectly termed "gastralia," have been found in the Cleveland-Lloyd Dinosaur Quarry; however, their infrequent occurrence is such as to substantiate the premise that scavengers may have ingested them while feeding on the carcasses. An alternate explanation might be that these elements were primarily cartilage with only one or two medial, ossified elements.

I have seen only ten of these curious bones in the Cleveland-Lloyd Dinosaur Collection. Their typical shape is that of a broad V or chevron (figure 22). Although other elements presumably of the abdominal basket have been recovered, material has been inadequate to allow a reasonable reconstruction on the order of that proposed by Gilmore (1920, p. 55).

A generic determination of abdominal ribs in the Cleveland-Lloyd Dinosaur Collection is a perplexing problem. There is no conclusive evidence that they belong to *Allosaurus fragilis* and, in fact, they may all be assignable to *Ceratosaurus*.

I have used frequency of occurrence and a process of elimination to isolate nonallosaur, theropod material in the Cleveland-Lloyd Dinosaur Collection. My reasoning is that since there are at least forty-four allosaurs of various sizes from the quarry and representative elements were collected in proportion, then bones for which there are few examples, even though morphologically similar to *Allosaurus fragilis*, are probably of another genus. Application of this reasoning to the infrequent occurrence of abdominal ribs is most interesting. Simply stated, there are not enough abdominal ribs of varying sizes in the collection to justify their assignment to *Allosaurus fragilis*. This is especially so if the cuirass as reported by Gilmore (1920, p. 53; plate 15) contains as many separate elements as he proposes.

The problem then becomes one of explaining the existence in the Cleveland-Lloyd Dinosaur Collection of a limited number of elements identical to those figured by Gilmore (1920, p. 53; plate 15) and speculatively similar to the ones mentioned by Osborn (1906, p. 283) for *Allosaurus fragilis*. There is no specimen reference by Osborn, but Gilmore's description is of USNM 4734 and 8367. The abdominal ribs associated with USNM 8367 are relatively fragmental; however, those of USNM 4734 are well preserved. Also well preserved are the excellent skeletons, USNM 4734 of *A. fragilis* and USNM 4735 of *Ceratosaurus*

nasicornis from "Quarry No. 1" near Canon City, Fremont County, Colorado, which were collected by M. P. Felch in 1883-1884 (Gilmore, 1920, p. 7, 77). Therefore, I believe there is a strong likelihood that it is *Ceratosaurus* and not *A. fragilis* that has the ventral rib complex. Furthermore, most of the similar elements in the Cleveland-Lloyd Dinosaur Collection were collected from a limited area near the west corner of the quarry, which yielded most of the bones assignable to *Ceratosaurus*. A small allosaurid, MCZ 3897, with the rib cage fairly intact shows no evidence whatsoever of ventral elements as shown in figure 22.

Sacral ribs. True sacral ribs (plates 24-27) are recognized only on the second, third, and fourth sacral vertebrae, each in contact with the centrum and neural arch as well as with the ilium to form a strong sacral complex.

The attachment of the last sacral vertebra (plate 28) to the ilium might be termed either a sacral rib or a modified transverse process, since it resembles a transverse process of the anterior caudals but ossifies separately and is sutured strongly to the neural arch.

The caudal vertebrae of *Allosaurus fragilis* do not bear ribs, nor is there any evidence in the Cleveland-Lloyd Dinosaur Collection of the ossified tendons associated with forms such as *Deinonychus* and *Velociraptor* (Kielan-Jaworowska and Barsbold, 1972). Distally there is an obvious trend toward the progressive elongation of prezygapophyses in the caudal vertebrae, which is an interesting tendency in comparison with the extreme development of these processes as reported by Ostrom (1969a, p. 60). There is not, however, a similar tendency toward elongation of processes on the chevrons.

Appendicular Skeleton

Pectoral Girdle

Scapula. The scapula (plate 41c, d, e, f) widens proximally, but narrows abruptly, then gradually widens again distally into an elongated, flattened blade. The scapula of *Allosaurus fragilis* differs significantly from *Ceratosaurus* (figure 23), which has a proportionately heavier, wider, and more uniformly flattened blade. The anteromedial edge is deeply grooved for the coracoid nerve.

The proximal end is laterally compressed above, rising to the rounded deltoid border. The scapula joins the coracoid in a firm, interdigitating suture (plate 42b, f). Below the coracoid foramen it widens into the deep glenoid fossa to which it contributes equally with the coracoid.
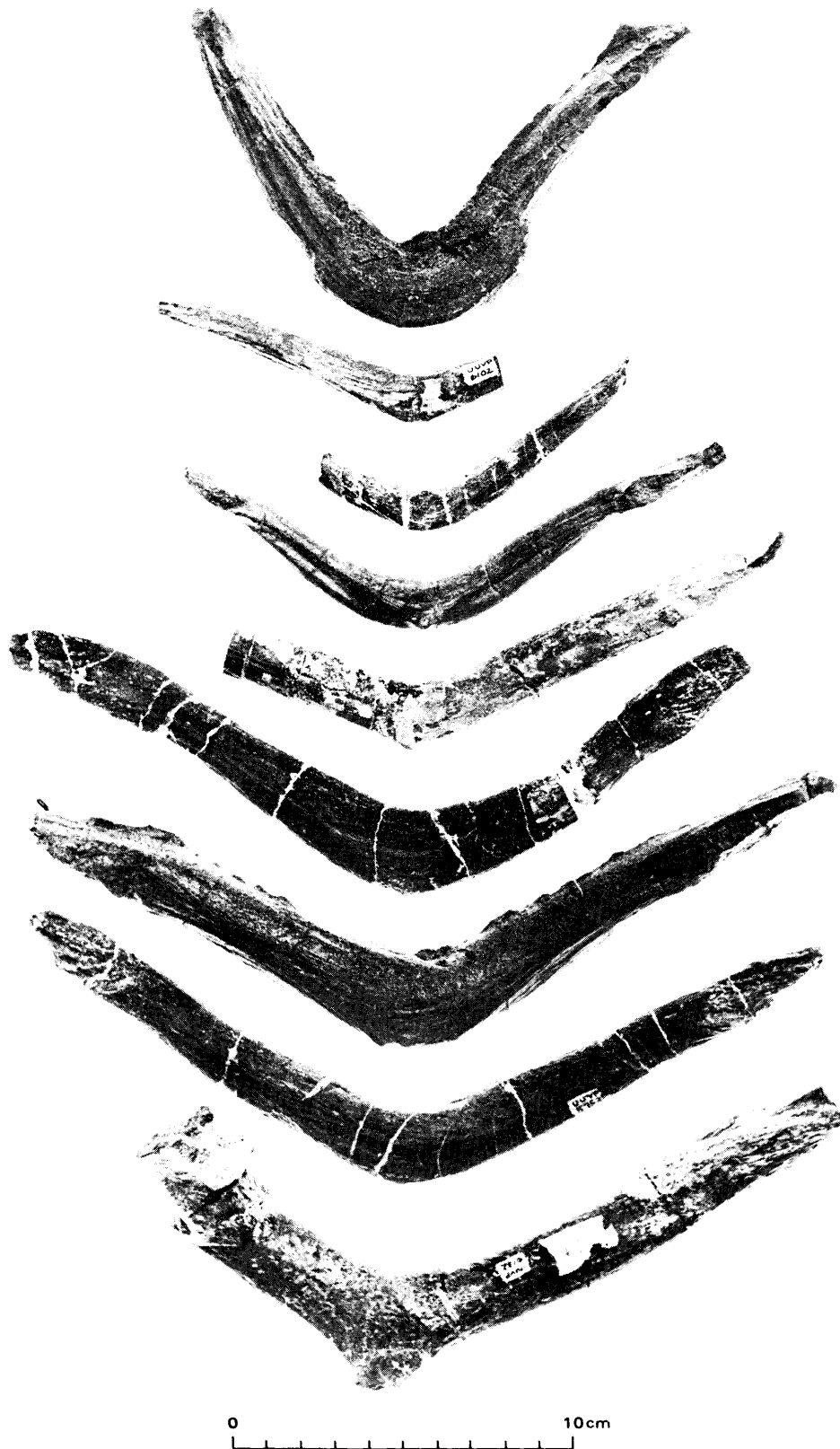
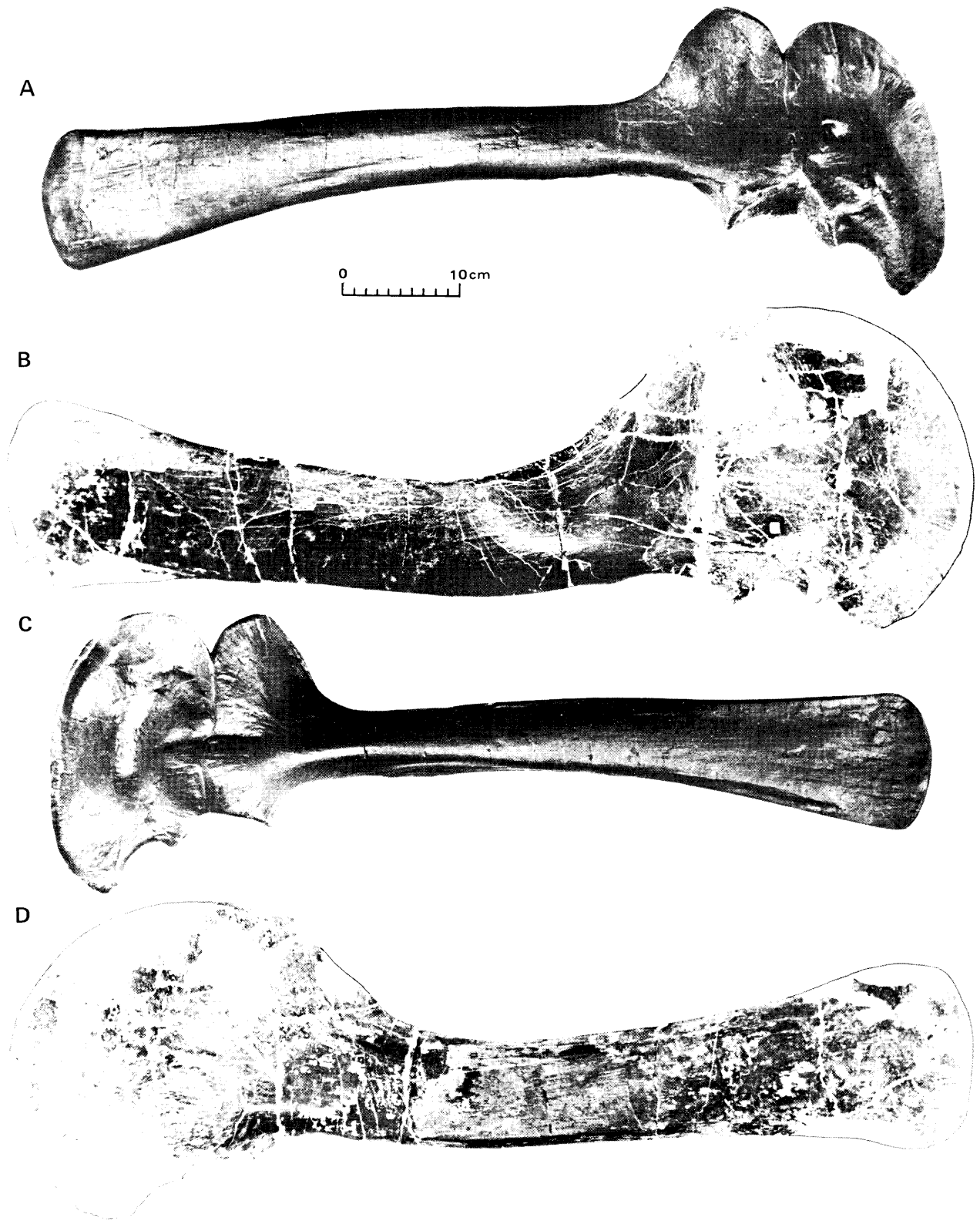Figure 22. Ventral ribs of unidentified species.

Figure 23. Articulated right scapulae and coracoids (A, C, cast) of *Allosaurus fragilis* and *Ceratosaurus sp.* (B, D, UUVP 317) in lateral (A, B) and medial (C, D) views. Abbreviation: bi–biceps tubercle.

Coracoid. The coracoid (plate 41a, b, d, g) is moderately convex outward and suboval in outline, having an anteroposterior width approximately 60 percent of the dorsoventral dimension. The dorsal margin is uniformly rounded to the scapular articulation. Ventrally the coracoid tapers to an asymmetrical, blunt point. Anterior to the glenoid fossa is the large coracoid foramen that angles posteromedially toward its opening on the grooved internal surface near the scapular contact. Below the coracoid foramen and midway between it and the ventral margin of the coracoid is a conical projection of variable size; this raised area is the biceps tubercle (bi) of Walker (1972, p. 6) and Ostrom (1974, p. 3) and the coracoid tuber of Osmolska and others (1972, p. 125). The biceps tubercle is high and well developed on some specimens and almost nonexistent on others, a characteristic apparently unrelated to maturity. The coracoid forms the anterior half of the deep glenoid fossa.

Forelimb and Manus

Humerus. The humerus (plate 42a, b and table 4) is robust, having a moderately curved shaft with the distal end rotated outward. The deltopectoral crest rises at an angle of 90 degrees to the plane of the distal end. Below and lateral to the deltopectoral crest is the vertically elongate scar for attachment of the humeroradialis muscle (figure 7). The characteristic, principal nutrient foramen (plate 43a, f) is almost directly opposite this scar. The breadth of the articular surface of the ulnar condyle is half again that of the outer or radial condyle from which it is separated by a shallow groove, but the two condyles are subequal in length.

Principal nutrient foramina are readily apparent on the long bones of *Allosaurus fragilis* but are also noted on most material in the Cleveland-Lloyd Dinosaur Collection. They may prove to be of generic significance, since their specific location is remarkably consistent within a single taxon but variable from one to another on homologous elements. These foramina lead to extensive, elongate, marrow cavities in most of the major elements of the appendicular skeleton: humeri, radii, ulnae, femora, tibiae, and metatarsals. Though proportionately smaller in diameter, marrow cavities are also present and distinct in the fibulae and in the phalanges of the manus and pes.

An alternate but plausible explanation of the well-defined principal foramina of the long bones of *Allosaurus fragilis* would have them be pneumatopores as discussed by Seeley (1967 [1901], p. 209) and more recently by Bakker (1971, p. 650). Such an interpretation would be consistent with the arguments of Ostrom (1973, p. 136) and Bakker (1971, p. 650)

wherein strong points are made for a close phylogenetic relationship between birds and theropod dinosaurs.

Ulna. The ulna (plate 42d, f) is slightly bowed laterally. It terminates proximally in the heavy olecranon process, which is deeply and symmetrically grooved for the ulnar condyle of the humerus. The proximal end of the ulna is indented laterally and scarred where it contacts the radius. The lower edge of this indentation rises to a conspicuous, blunted point. The ulna is asymmetrically expanded distally and rounded, rising to a flattened pedestallike radial contact. A principal nutrient foramen pierces the superior surface of the shaft near midlength.

Radius. The radius (plate 42c, e) is nearly straight. The proximal end flares slightly and the articular surface is somewhat dished for the radial condyle of the humerus. The distal end of the radius is expanded and rounded with its articular surface at an angle of about 30 degrees to the shaft. The inferior edge of the distal articular surface is rugose and flattened and is variable in shape at the ulnar contact.

Carpus. The exact construction of the theropod carpus is an enigma and especially puzzling in *Allosaurus fragilis*. Gilmore (1915, p. 508; 1920, p. 60) indicated that five and possibly six elements are in the carpus of *A. fragilis*, but he illustrates three and discusses only four. The Cleveland-Lloyd Dinosaur Collection has yielded four—two of which cannot be positioned with certainty because of their consistent disassociation. One associated complex, however, consists of MC-I, MC-II, radiale and carpale(?). Since these elements have been recovered from the same, relatively small, block of matrix, it is presumed that they pertain to the same individual. Although the carpal elements fit closely against the metacarpals, they articulate loosely with the radius and ulna, which indicates that the region of greatest flexion was epicarpal.

The wrist as described by Gilmore (1920, p. 60) includes an intermedium, carpale 2, radiale, and an element "regarded doubtfully as representing carpale 3." Identical elements occur in the Cleveland-Lloyd Dinosaur Collection, but an alternate arrangement is possible that would require different names: Gilmore's intermedium, the large, single element between MC-I and the radius, becomes carpale 1, and the small carpale 2 remains the same. This tiny element in fourteen out of eighteeen specimens examined is fused to carpale 1 without regard to the maturity of the specimen. Gilmore's radiale also remains the same but will fit in an alternate position between MC-II and the ulna, which, if correct, would make it the ulnare. The nondescript element that Gilmore tentatively describes

Table 4. Measurements and indices of some Cleveland-Lloyd theropod humeri.

	UUVP number	Side	Circumference at midshaft (mm)	Length[1] (mm)	C:L x 100	Identification
1	4220	right	49	150	33	*A. fragilis*
2	1980	right	49	156	31	*A. fragilis*
3	1981	right	55	162	34	*A. fragilis*
4	3312	right	62	183	34	*A. fragilis*
5	566	right	72	199	36	*A. fragilis*
6	30-77	left	72	202	36	*A. fragilis*
7	5423	left	76	205	37	*A. fragilis*
8	40-729	left	90	240	38	*A. fragilis*
9	Cast[2]	right	95	240	40	*A. fragilis*
10	2327	right	84	244	34	*A. fragilis*
11	Cast[2]	left	90	250	36	*A. fragilis*
12	2765	left	90	251	36	*A. fragilis*
13	40-227	right	93	252	37	*A. fragilis*
14	4387	left	102	254	40	*A. fragilis*
15	3342	left	105	255	41	*A. fragilis*
16	4792	left	109	264	41	*A. fragilis*
17	5496	right	119	276	43	*A. fragilis*
18	4909	left	90	277	33	Unidentified
19	2998	right	91	280	33	Unidentified
20	30-778	right	127	280	45	*A. fragilis*
21	4908	left	118	280	42	*A. fragilis*
22	10,161	left	130	280[3]	47	*A. fragilis*
23	273	right	123	290	42	*A. fragilis*
24	5501	right	115	295	39	*A. fragilis*
25	549	left	132	330	40	*Ceratosaurus*
26	5982	right	135	330	40	*Ceratosaurus*
27	5577	left	151	333	45	*A. fragilis*
28	1334	right	144	334	43	*A. fragilis*
29	10,154	right	141	340	42	*A. fragilis*
30	3435	right	180	343	52	*A. fragilis*
31	5472	right	155	351	44	*A. fragilis*
32	1169	left	187	379	49	*A. fragilis*
33	3607	right	173	386	45	*A. fragilis*

[1] From high point on head of humerus to extremity of ulnar condyle.
[2] Original quarry number unknown.
[3] Estimated; bone incomplete, distorted, or pathological.

as carpal 3, however, can be placed as in this paper lateral to carpale 2, thus identifying it as the ulnare (plates 43 and 45).

Manus. The manus of *Allosaurus fragilis* (plates 43, 44, and 45) has three digits, each of which terminates in a strongly curved and sharply pointed ungual. They are digits I, II, and III; the fourth and fifth have been lost, and the presence of either is not suggested by any material studied from the Cleveland-Lloyd Dinosaur Quarry. The phalangeal formula is 2-3-4.

Metacarpal I is the shortest of the three, blocky in form, and subequal in length and width, a distinctive characteristic in theropods. The distal end of metacarpal I has a deep groove for articulation of the proximal phalanx. Metacarpal II is approximately 1½ times the length of metacarpal I, and similarly it has a deep, anterior groove separating the distal condyles, thereby providing a strong articular surface for the proximal phalanx. Metacarpal III is rodlike and loosely joined to the other wrist elements. Digits I and II are much stouter than III.

The distal attachments of the collateral ligaments are represented by shallow to deep pits on the metacarpals and phalanges. These areas are best developed on the second and third metacarpals and phalanges supporting the unguals.

Function of the forelimb. The deep articulation of the humerus in the glenoid cavity is additional evidence of the functional role of the forearm in

Allosaurus fragilis. The elements of the forearm comprise a useful and powerful appendage that certainly was very effective in predations, insofar as holding and grasping are concerned. However, the forelimbs were not strong enough to allow any significant pectoral support for quadrupedal locomotion. The forelimbs of *A. fragilis* are in sharp contrast with their diminuitive homologues in *Tyrannosaurus rex*.

Pelvic Girdle

Ilium. The ilium (plates 46 and 47) is a massive, subrectangular plate, dished inward, which forms the dorsal half of a deep, subspherical, perforate acetabulum. The anterior end is expanded, projecting very slightly beyond the pubic peduncle above which it terminates in a blunted point. A hoodlike ridge extends from the pubic to the ischiac peduncle, overhanging a deep, open acetabulum. In most specimens the articular surface of the pubic peduncle is rugose, which denotes a firm union with the pubis. The ischiac peduncle is rounded to fit into a corresponding socket on the ischium, an articulation that allows significant lateral flexion of the ischium. The external surface of the ilium is finely sculptured with scars for the origin of the various pelvic muscles. The medial surface is complexly ornamented with the sutural attachments of the sacral ribs and transverse processes. The posterior margin of the ilium is squared with rounded corners. The medial blade arises as an elongate shelf extending obliquely from the ischiac peduncle to the upper corner of the posterior blade. Its upper surface is finely grooved and sculpted for attachment of the fifth sacral rib. As expected, a comparison between juvenile and adult ilia reveals a more intense sculpturing for bone and muscle attachments on mature specimens.

Pubis. The pubes (plates 48 and 49) form a strong, inverted yoke that attests to a structural adaptation on the order of the "sit down bones" described by Marsh (1896) as well as for muscle attachment. The pubis of *Allosaurus fragilis* does not have an enclosed obturator foramen but instead a deep notch anterior to the ischial articulation. The downcurved ischiac process meets the ischium in a flexible symphysis. Medially at the base of the pelvic opening, the pubes meet along a symphysis, which continues downward to terminate above the elongate opening over the conspicuous footlike expansion of the distal end.

The development of the foot of the pubis appears consistent from juvenile to adult; however, the pubes are found distally ankylosed in approximately half of the specimens at hand. The anomalous percentage of pubes found in articulation generates speculation as to sexual dimorphism.

The hormone, relaxin, produced in the ovaries of some reproductively active higher vertebrates (Steinetz and others, 1959) serves to soften ligamentous tissues in the pelvic region, specifically at the pubic symphyses prior to the passage of an egg or fetus through the pelvic opening. Steinetz and others (1959, p. 420) also report the occurrence of relaxinlike substances in groups as diverse as elasmobranchs and birds. Therefore, if a similar condition is theorized for some reptiles, such as the dinosaurs, then it might be concluded that other sutural contacts, involving cartilagenous tissues, may also be affected. The implication is that many other elements found in disassociation, such as neural arches and centra, may relate to a reproductive female rather than to a juvenile as commonly thought. There is no apparent consistency in the occurrence of disarticulated sacral elements of *Allosaurus fragilis* in the Cleveland-Lloyd Dinosaur Collection to indicate an expected progressive ankylosis of increasingly large sacral complexes solely as a function of age.

Ischium. The ischium (plates 48 and 49) tapers abruptly from the prominent pubic and iliac articulations into a long, slender shaft with an asymmetrically expanded distal end. The distal end is flattened medially where it joins with the opposite ischium in a loose ligamental contact. Although pubes are found coossified in the Cleveland-Lloyd Dinosaur Collection, in no instance have ischia been found ankylosed. A medial, ligamental contact of the ischia appears to have been continuous from the floor of the pubic opening to the distal expansion.

Hindlimb and Pes

Femur. The femur (plate 50 and table 5), the longest element of the hindlimb, is a sturdy, uniformly curved bone nearly circular in cross section (figure 24). Well-defined greater and fourth trochanters project from an otherwise smooth shaft.

The head projects from the shaft of the femur at an approximate right angle. Its rounded, elongate, articular surface inserts deeply into the moderately perforated acetabular socket, a position which indicates a near vertical placement of the legs well under the body mass.

The lesser trochanter rises proximally as a stout plate separated from the head of the femur by a deep slot. It terminates below the proximal surface of the head in a blunted, thinning margin. The principal nutrient foramen enters just below the lesser trochanter on the anterior (dorsal) surface of the shaft.

The distal end of the fourth trochanter rises at midshaft in an elongate, posteriorly directed ridge that

Table 5. Measurements and indices of some Cleveland-Lloyd and other theropod femora.

	UUVP or other number	Side	Circumference at midshaft (mm)	Length[1] (mm)	C:L x 100	Identification
1	6023	right	74	245	30	*A. fragilis*
2	3872	right	104	350	30	Unidentified
3	40-264	right	116	385	30	Unidentified
4	2559	left	138	435	32	*A. fragilis*
5	MCZ 3897	left	161	437	37	*Allosaurus*
6	847	left	142	450	32	*A. fragilis*
7	30-35	left	147	465	32	*A. fragilis*
8	30-752	right	155[2]	465	33[2]	*A. fragilis*
9	3164	right	147[2]	475	30[2]	*A. fragilis*
10	492	left	162	480	34	*A. fragilis*
11	2280	right	168	505	33	*A. fragilis*
12	30-724	right	165	525	31	*A. fragilis*
13	30-16	left	179	535	34	*A. fragilis*
14	30-743	left	175	535	33	*A. fragilis*
15	718	left	179	535	34	*A. fragilis*
16	40-268	right	174	535	33	*A. fragilis*
17	3192	left	194[2]	545	35[2]	*A. fragilis*
18	5991	right	184	555	33	*A. fragilis*
19	1364	left	210[2]	575	37[2]	*A. fragilis*
20	30-17	right	206	605	34	*A. fragilis*
21	3980	right	210[2]	630[2]	33[2]	*A. fragilis*
22	3385	left	217[2]	660	33[2]	*A. fragilis*
23	5302	left	252	695	36	*A. fragilis*
24	Cast[3]	left	255	700	36	*A. fragilis*
25	Cast[3]	right	276	730	38	*A. fragilis*
26	56	left	267[2]	765	35[2]	*Ceratosaurus*
27	5993	left	290	800	36	*A. fragilis*
28	6000	left	337	850	40	*A. fragilis*
29	1165	right	295	865	33	*A. fragilis*
30	6000	right	313	880	36	*A. fragilis*
31	DNM No. C[4]	right	326	880	37	*A. fragilis*
32	3694	left	307	905	34	*A. fragilis*
33	DNM No. D[4]	left	348	905	39	*A. fragilis*
34	DNM[4]	left	335	910	37	*A. fragilis*

[1] Measured along outer (superior) curve.
[2] Estimated; bone incomplete, distorted, or pathological.
[3] Original quarry number unknown.
[4] From Dinosaur National Monument, original quarry number unknown.

continues half the distance to the proximal end of the femur. Its medial surface is a broad, shallow concavity lying in a plane parallel to the axis of rotation of the shaft. The posterior surface falls away from the irregular crest of the ridge to merge with the ventral surface of the shaft.

The distal end of the femur terminates in two near-circular condyles separated by a squared rotular groove. The inner condyle is larger; the outer condyle grades posteriorly into a blocky protuberance.

Tibia. The tibia (plates 51 and 52 and table 6) of *Allosaurus fragilis* is 87 percent of the femur length. It has a very slight posterior curve to the shaft. The proximal articular surface is flattened, vaguely resembling a footprint; the prominent cnemial crest represents the heel. The cnemial crest is large and pronounced in *A. fragilis* but noticeably less elongate than in *Ceratosaurus.* The medial surface is curved outward, and the lateral and posterior borders are grooved to form a buttress for proximal attachment of the fibula.

Distally the tibia widens abruptly to accomodate the calcaneum and astragalus. The anterior face of the expansion is unevenly inset for the ascending process of the astragalus. The distal surface of the tibia is also excavated for the posterior brow of the astragalus.

Fibula. The shaft of the fibula (plate 52) is relatively straight. It is evenly expanded at its upper

Table 6. Measurements and indices of some Cleveland-Lloyd and other theropod tibiae.

	UUVP or other number	Side	Circumference[1] at midshaft (mm)	Length (mm)	C:L x 100	Identification
1	30-55	right	97	343	28	*A. fragilis*
2	2584	right	73	358	21	Unidentified
3	MCZ 3899	right	135	375	36	*Allosaurus*
4	40-299	left	106	379	28	Unidentified
5	30-727	left	100	374[2]	27	Unidentified
6	154	right	147[2]	410[2]	37[2]	*A. fragilis*
7	2977	right	122	433	28	Unidentified
8	3233	left	122	444	28	Unidentified
9	Cast[3]	right	147	468	31	*A. fragilis*
10	40-768	right	152	475[2]	31	*A. fragilis*
11	Cast[3]	left	149	480	31	*A. fragilis*
12	30-714	left	170[2]	500	34[2]	*A. fragilis*
13	40-306	left	180	525	34	*A. fragilis*
14	40-298	left	182	525	35	*A. fragilis*
15	3835	right	197	540	37	*A. fragilis*
16	40-308	right	205	540	38	*A. fragilis*
17	249	left	197	542	36	*A. fragilis*
18	3249	right	194	543	36	*A. fragilis*
19	5990	right	191	546	35	*A. fragilis*
20	1599	left	169	550[2]	31[2]	Unidentified
21	40-301	right	181	552	33	*A. fragilis*
22	40-304	right	183	552	33	*A. fragilis*
23	3833	left	195	553	35	*A. fragilis*
24	Cast[3]	right	226	560	40	*A. fragilis*
25	5301	right	177	567	31	*A. fragilis*
26	5988	left	195	577	34	*A. fragilis*
27	5361	left	202	596	34	*A. fragilis*
28	40-297	right	231	612	38	*A. fragilis*
29	5300	left	219	622	35	*A. fragilis*
30	1473	right	230[2]	637	36[2]	*A. fragilis*
31	5681	left	240[2]	640[2]	38[2]	*Ceratosaurus*
32	5682	right	241	650[2]	37[2]	*Ceratosaurus*
33	10,248	right	267	695	38	*A. fragilis*
34	Cast[3]	left	275	702	39	*A. fragilis*
35	Cast[3]	left	241	705	34	*A. fragilis*
36	Cast[3]	right	262[2]	711	37[2]	*A. fragilis*
37	6000	right	278	730[2]	38[2]	*A. fragilis*
38	6000	left	290	745[2]	39[2]	*A. fragilis*

[1] Least circumference.

[2] Estimated; bone incomplete, distorted, or pathological.

[3] Original quarry number unknown.

end and subcrescentic in proximal view. Cross sections of the lower part of the shaft, except the distal end, are crescentic in outline (figure 24).

The medial surface of the proximal end is deeply excavated between the tibial contacts. The fibula terminates distally in an expanded and rounded knob that fits snugly in the smooth, proximal concavity formed by the calcaneum and an anterolateral tuberosity of the astragalus.

Tarsus. Of the four tarsal bones present in *Allosaurus fragilis*, the astragalus is the largest and most complex. It is a massive, moderately elongate, grooved block with an anterior ascending process and two lateral tuberosities. The anterior and posterior faces are divided by a superior groove for reception of the tibia. A fairly deep, rounded pit lies near the base of the tibial surface of the ascending process. The uniform development of this pit appears to be a useful diagnostic characteristic since it is easily recognized in more than two dozen specimens in the Cleveland-Lloyd Dinosaur Collection. The height/breadth index (H:B) of the astragalus as applied by Welles and Long (1974) ranges from a value of 100 in juvenile specimens to 85 in old individuals. The index tends to drop below 90
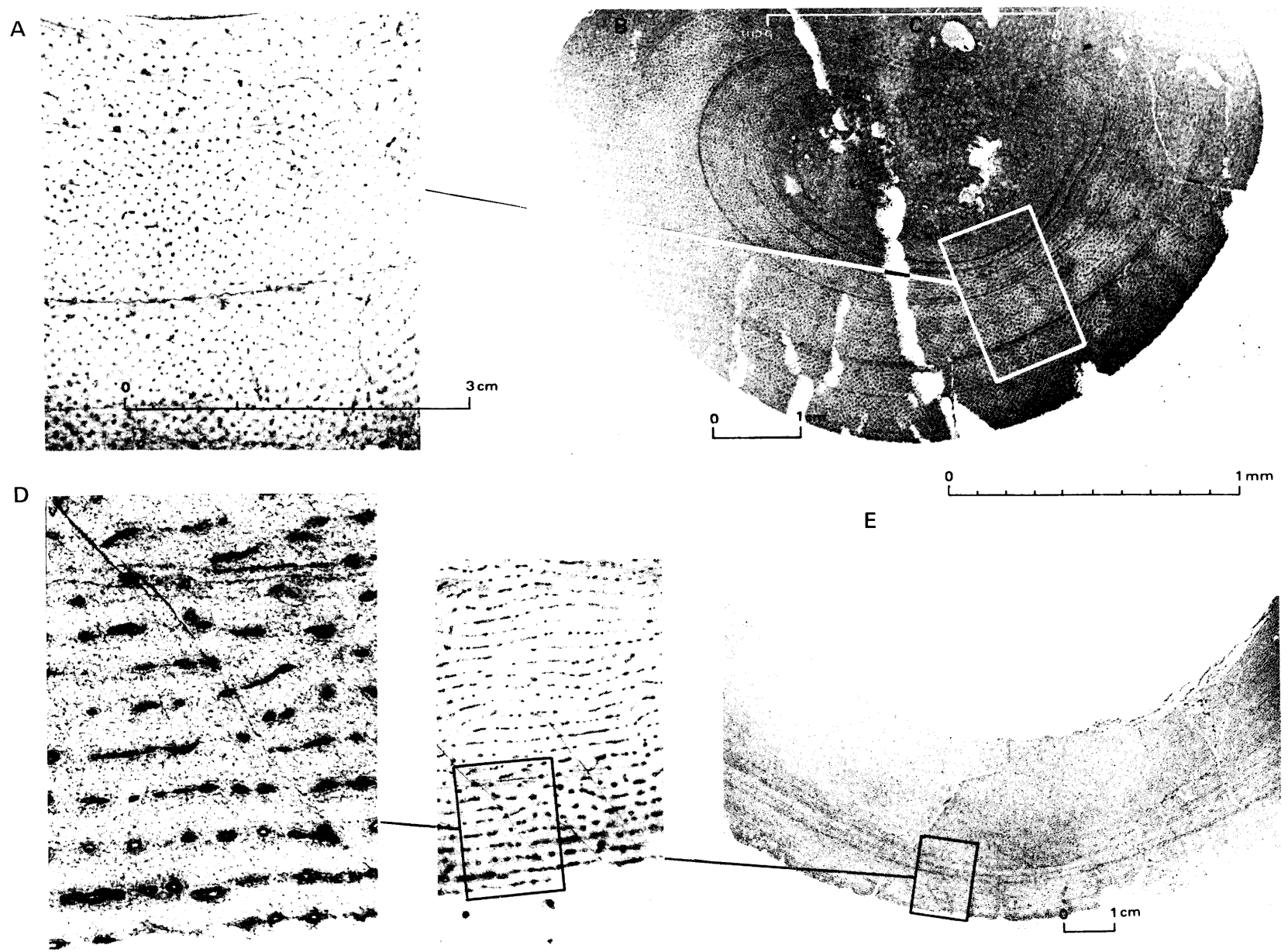
Figure 24. Cross sections and enlargements of a femur (A, B, C) and fibula (D, E) of *Allosaurus fragilis* showing laminar development of chondral bone.

Table 7. Measurements and indices of some Cleveland-Lloyd theropod astragali.

	UUVP number	Side	Height[1] (mm)	Breadth (mm)	H:B x 100	Identification
1	6062	left	65[2]	70	93[2]	*A. fragilis*
2	5998	right	74	75	99	*A. fragilis*
3	454	right	80	80	100	*A. fragilis*
4	2909	right	80[2]	84	95[2]	Unidentified
5	6063	left	90[2]	90	100[2]	*A. fragilis*
6	5420	right	85	90	94	*A. fragilis*
7	Cast[3]	right	96[2]	96	100[2]	*A. fragilis*
8	2549	left	99	99	100	*A. fragilis*
9	6103	left	99[2]	100	99[2]	*A. fragilis*
10	40-25	right	102	112	91	*A. fragilis*
11	3733	left	110[2]	112	98[2]	*A. fragilis*
12	5682	right	85	115	74	*Ceratosaurus*
13	5681	left	87	123	71	*Ceratosaurus*
14	3753	left	115[2]	122	94[2]	*A. fragilis*
15	5141	right	113[2]	123	93[2]	*A. fragilis*
16	40-308	right	117	123	95	*A. fragilis*
17	40-21	left	115	126	91	*A. fragilis*
18	6061	right	120[2]	130	92[2]	*A. fragilis*
19	6738	left	120[2]	133	90[2]	*A. fragilis*
20	5358	left	118	134	88	*A. fragilis*
21	Cast[3]	right	120[2]	136	88[2]	*A. fragilis*
22	Cast[3]	left	121[2]	138	88[2]	*A. fragilis*
23	5436	left	127[2]	140	91[2]	*A. fragilis*
24	40-22	left	130[2]	142	92[2]	*A. fragilis*
25	4127	left	132	146	90[2]	*A. fragilis*
26	2567	right	135[2]	152[2]	89[2]	*A. fragilis*
27	10,249	right	152[2]	154	99	*A. fragilis*
28	4493	right	138	158	87	*A. fragilis*
29	10,149	left	152[2]	159	95	*A. fragilis*
30	6000	right	155	180	86	*A. fragilis*
31	Cast[3]	left	155	180	86	*A. fragilis*
32	Cast[3]	right	163	183	89	*A. fragilis*

[1] From top of ascending process to line between lowest points of distal surface.
[2] Estimated; bone incomplete, distorted, or pathological.
[3] Original quarry number unknown.

as the breadth of the astragalus exceeds 135 mm (table 7) but not below 85 in *A. fragilis*.

The crescent-shaped calcaneum, which is cupped proximally for insertion of the rounded distal end of the fibula, articulates laterally with the astragalus. Two elongate pits on the medial surface of the calcaneum receive the lateral tuberosities of the astragalus to form a relatively strong joint.

Tarsals III (table 8) and IV are the remaining elements of the ankle of *Allosaurus fragilis* (figure 25). Tarsal III is subrhomboid and flattened, having a smoothly rounded, proximal articulation with the posterior half of the proximal surface of metatarsal III. The distal surface is somewhat angular with two well-defined cavities, one near the outer lateral margin and

the other in the middle of the opposite side. The latter pit is poorly defined in young specimens.

Tarsal IV has a broadly concave proximal surface. Its distal surface is less so, lying in close articulation with metatarsal IV, covering most of the proximal surface, and lapping slightly over the posterior margin. Tarsal IV is flattened, as is tarsal III, but is more blocky and robust. Typically there are three irregular pits on the edges of tarsal IV, two on the lateral side and one on the medial.

There is no tendency toward fusion of the tarsal bones to each other or to the metatarsals. There are only a few instances when two or more have been collected in articulation or even close proximity.

Table 8. Measurements and indices of some Cleveland-Lloyd theropod metatarsal III.

	UUVP or other number	Side	Circumference at midshaft (mm)	Length (mm)	C:L x 100	Identification
1	2775	left	39	145	27	Unidentified
2	3630	left	53	191	27	A. fragilis
3	1989	right	70	228	31	A. fragilis
4	40-222	left	92	243	38	A. fragilis
5	40-221	left	81	247	33	A. fragilis
6	2308	left	67	251	27	Unidentified
7	5579	right	84[1]	252	33	A. fragilis
8	5379	left	92	257	36	A. fragilis
9	1987	right	79	265	30	Unidentified
10	40-219	left	99	269	37	A. fragilis
11	Cast[2]	right	114	273	42	A. fragilis
12	5983	left	99	276	36	A. fragilis
13	4877	left	106	280	38	A. fragilis
14	1075	right	96	284	34	A. fragilis
15	2923	right	103	284	36	A. fragilis
16	40-217	right	101	285	35	A. fragilis
17	5415	right	103	285	36	A. fragilis
18	Cast[2]	left	110	285	39	A. fragilis
19	5237	left	118	291	41	A. fragilis
20	4445	right	120	292	41	A. fragilis
21	40-216	left	133	296	45	A. fragilis
22	4958	right	106	298	36	A. fragilis
23	40-739	right	111	298	37	A. fragilis
24	30-90	right	110	300	37	A. fragilis
25	5445	right	126	310	41	A. fragilis
26	1743	right	162	313[1]	52	A. fragilis
27	30-782	left	158	318	50	A. fragilis
28	40-214	left	137	333	41	A. fragilis
29	4785	left	144	336	43	A. fragilis
30	4385	right	144	338	43	A. fragilis
31	40-738	left	168	343	49	A. fragilis
32	4223	left	157	345	46	A. fragilis
33	5985	right	175	350[1]	50	A. fragilis
34	10,169	right	147	365	41	A. fragilis
35	1551	left	150	367	41	A. fragilis
36	6000	left	167	372	45	A. fragilis
37	6000	right	165	375	44	A. fragilis

[1] Estimated; bone incomplete, distorted, or pathological.
[2] Original quarry number unknown.

Pes. Of the four digits in the pes of *Allosaurus fragilis* (plates 53, 54, and 55), only three (II, III, and IV) function as weight bearing elements. The first digit, or hallux, initially described by Osborn (1899), is attached to the posterior medial surface of metatarsal II as a dew claw. Although the first digit has no apparent support function in a large adult, it may have had some purpose in juveniles as a semiopposable, grasping appendage.

The first metatarsal, if interpreted correctly as such, is in two sections, which were probably never in physical contact. The upper segment, which might also be MT-V, tapers from a triangular proximal end downward, curving slightly forward, to terminate in a blunt point. The inner surface is flattened, whereas the outer side has a longitudinal ridge on the proximal half and a shallow concavity on the distal half. I have some reservations about the identity (right or left) and the placement of the proximal segment, but I would need an articulated pes of *Allosaurus fragilis* to settle the question. The distal segment of metatarsal I is abbreviated. It consists of a condyle and a short, triangular shaft that tapers upward to a point. The anterior part of the condyle is evenly rounded, but the posterior part is grooved, dividing the condyle
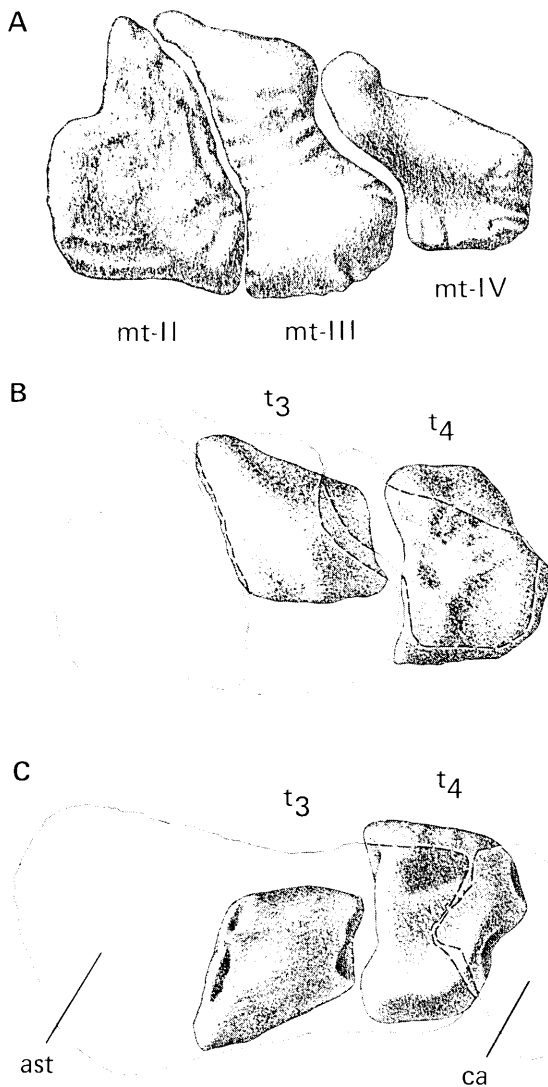
Figure 25. Left metatarsals (A) and tarsals (B, C) of *Allosaurus fragilis* in proximal (A, B) and distal (C) views, at approximately one-half of natural size. Abbreviations: ast—astragalus, ca—calcaneum, mt—metatarsal, t—tarsal.

inferiorly. The outer, collateral ligament fossa is a shallow concavity that contrasts with the inner one which is much deeper.

Metatarsals II, III, and IV are all robust bones. Metatarsal III is the longest, but II and IV, although shorter, are nearly equal in length. Metatarsals II and IV fit closely together against III at their proximal end but curve outward distally so that the attached digits are about evenly spaced. The hind foot would have made a fairly symmetrical track but the short first digit would probably not have been evident. Externally the collateral ligament fossae are shallow on metatarsal II and virtually absent on IV. The fossae are subequal in depth on metatarsal III. The development of the

fossae as noted on the metatarsals is reflected in the phalanges of each digit.

The digits of the pes have a phalangeal formula of 2-3-4-5-0. The first digit is of such design and position as to be relatively useless as a weight bearing element in the adult, even though it is equipped with a curving, pointed ungual that appears to have been quite capable of movement.

COMPARISONS

Following White (1973) as a guide to valid, megalosaurid genotypes of the Late Jurassic and Early Cretaceous, with the exception of his usage of the genus *Antrodemus* (see discussion under *Systematics*), several medium to large-sized dinosaurs might be compared with *Allosaurus fragilis*.

Lower Cretaceous
Acrocanthosaurus Stovall and Langston, 1950
Carcharodontosaurus Stromer, 1931
Erectopus Huene, 1923

Upper Jurassic
Aggiosaurus Ambayrac, 1913
Ceratosaurus Marsh, 1884
Metriacanthosaurus Walker, 1964

The only other carnivorous saurischian known from the Morrison Formation at this time to attain the large size of *Allosaurus fragilis* (see *Fauna and Prehistory*) is *Ceratosaurus*. Gilmore (1920, p. 76) supported separation of these genera at the family level (Ceratosauridae, Marsh, 1884), and Huene a short time later (1923, p. 457) restated his preference to regard *Ceratosaurus* as a coelurosaur. These systematic determinations emphasize the dissimilarities between the genera and make detailed comparisons unneccessary; however, an interesting difference, which may be of infraordinal importance, is the persistent development of a medullary cavity in the caudal centra of *Ceratosaurus* in contrast with the trabecular internal structure of *A. fragilis* caudals (figure 26). Colbert and Russell (1969, p. 36) regard *Ceratosaurus* as an aberrant megalosaur. A comparison with *Megalosaurus* (*sensu stricto*) is impractical at this writing, and some megalosaurs will be dealt with in a paper now in preparation.

Only two non-Morrison genera, regarded allosaurids by Colbert and Russell (1969, p. 36), appear phyletically close to *Allosaurus fragilis*. They are *Acrocanthosaurus* (Stovall and Langston, 1950) and *Chilantaisaurus* (Hu, 1964).

Some of the comparisons drawn between *Acrocanthosaurus* and *Allosaurus fragilis* were based on
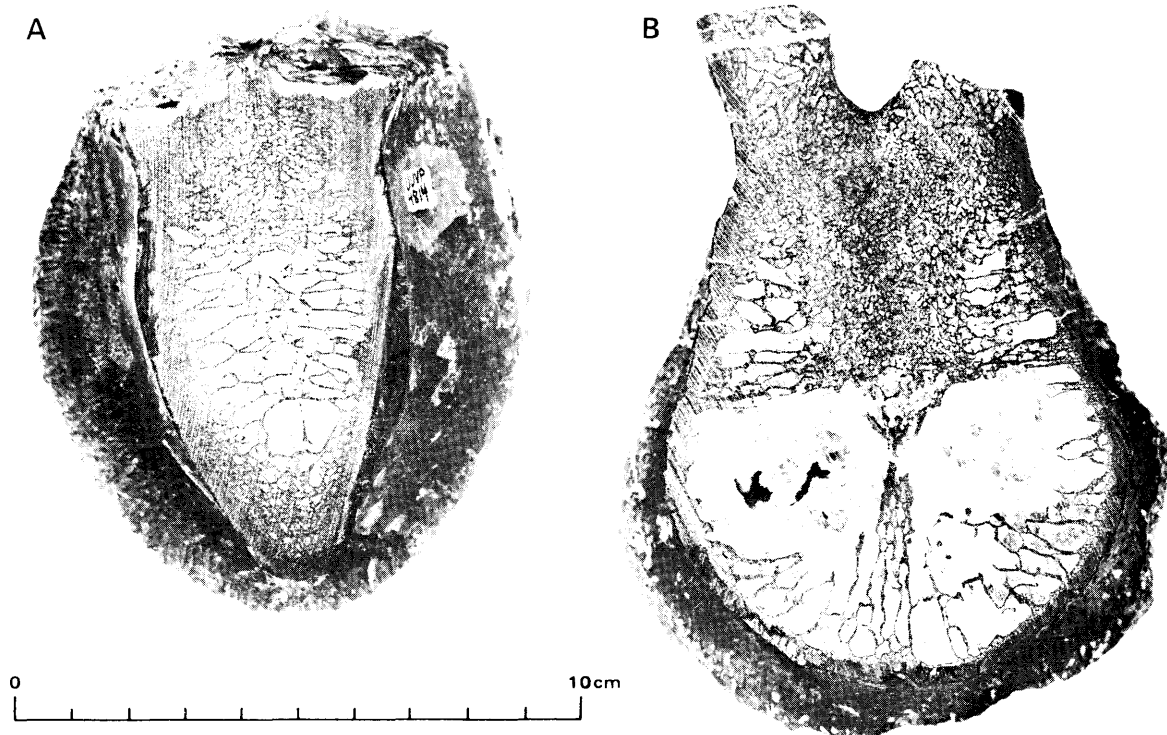
Figure 26. Internal structure of anterior caudal centra of *Allosaurus fragilis* (A, UUVP 4814) and *Ceratosaurus sp.* (B, UUVP 81).

photographs of UUVP 6000 supplied to Stovall and Langston (1950, p. 724) by the late Hyrum Schneider, who was Chairman of the Geology Department at the University of Utah. At that time the skull of UUVP 6000 was incompletely prepared, and many fine details of the specimen were masked by matrix and a thick layer of colorant and shellac. A provisional comparison now supplementing UUVP 6000 with comparative elements from the Cleveland-Lloyd Dinosaur Collection indicates that the skulls of *Acrocanthosaurus atokensis* and *A. fragilis* are closer than Stovall and Langston suspected. A detailed comparison, of course, would be invaluable.

It is interesting that the lachrymal of *Acrocanthosaurus* has two dorsal cavities (Stovall and Langston, 1950, p. 70) as similarly reported by Gilmore (1920, p. 17) for *Allosaurus fragilis.* The internal cavity is variably separated by a small septum in the lachrymal of *A. fragilis,* but the separation is not usually so well defined externally.

A contrast of postcranial skeletons, however, does not reveal similarities consistent with those of the skulls. The centra and the diapophyses and zygapophyses of the neural arches of the presacral vertebrae are close, but the neural spines of *Acrocanthosaurus* are radically unlike those of *Allosaurus fragilis* in their extreme superior elongation. A possible explanation is that there are at least two

options to accomodate a disproportionately large skull on the larger-sized theropods: the cervical vertebrae can become shorter or the cervical neural spines can become elongated to accomodate the greater muscle mass required to support the skull, as also observed by Charig and others (1965, p. 207). Posture may also be a factor; that is, if the head is carried at the end of an outstretched neck rather than in an "S" curve as in *A. fragilis* (frontispiece), then either the vertebrae of the neck must shorten or the neural spines become elongated.

Neural spines in the caudal series of *Acrocanthosaurus* are also extremely long, like *Ceratosaurus*; however, they are similar to *Allosaurus fragilis* in tending toward an anterior-posterior bifurcation in the posterior section of the tail. There the spines become separated dorsally into a shorter, anterior segment and a higher and wider posterior one (plates 28-32). A variation in this curious design of the caudal neural spines is reported by Camp (1936, p. 42 and figure 1) for *Segisaurus* and by Walker (1964, p. 84) for *Ornithosuchus,* and it is apparent in some unassigned caudals of a small nonallosaurid theropod in the Cleveland-Lloyd Dinosaur Collection.

Pointing out other similarities in the pelvic girdle and hindlimbs of *Acrocanthosaurus* and *Allosaurus fragilis,* Stovall and Langston (1950, p. 724) concluded that *Acrocanthosaurus* should be incorporated into the

Family Antrodemidae (Allosauridae of this paper), which seems to be reasonable and consistent with our current knowledge of *Acrocanthosaurus*. Other possibilities should be explored in a restudy of *Acrocanthosaurus*.

Hu (1964) designates two species of a new theropod genus, *Chilantaisaurus*, from Inner Mongolia and effectively isolates the taxa from *A. fragilis*, to which he makes numerous references. Only the second of the two species, *C. maortuensis*, is of Late Jurassic age and is interesting primarily because of its resemblance to *Ceratosaurus* and not to *A. fragilis*.

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PLATES

Plate 1. Composite skull and mandible of *Allosaurus fragilis* in lateral view. Abbreviations: an—angular, aof—antorbital fenestra, ar—articular, de—dentary, ecpt—ectopterygoid, en—external naris, ept—epipterygoid, f ′—posterior surangular foramen, f ″—external mandibular foramen, f ‴—anterior surangular foramen, fr—frontal, ju—jugal, la—lachrymal, lav—lachrymal vacuity, ls—laterosphenoid, ltf—lateral temporal fenestra, mx—maxilla, mxf—maxillary fenestra, na—nasal, naf—nasal foramen, of—orbital fenestra, os—orbitosphenoid, pa—parietal, pal—palatine, pm—premaxilla, po—postorbital, popr—paroccipital process, pr—prootic, pra—prearticular, prf—prefrontal, ps—parasphenoid, pt—pterygoid, qj—quadratojugal, qu—quadrate, sa—surangular, snf—subnarial foramen, soc—supraoccipital, sq—squamosal.

Plate 2. Composite skull of *Allosaurus fragilis* in dorsal (A) and ventral (B) views. Abbreviations: ecpt—ectopterygoid, eo—exoccipital, fr—frontal, in—internal naris, iptv—interpterygoid vacuity, ju—jugal, la—lachrymal, lav—lachrymal vacuity, mx—maxilla, mxf—maxillary fenestra, mxsi—maxillary sinus, na—nasal, oc—occipital condyle, of—orbital fenestra, pa—parietal, pal—palatine, pm—premaxilla, po—postorbital, popr—paroccipital process, prf—prefrontal, ps—parasphenoid, pt—pterygoid, qj—quadratojugal, qu—quadrate, snf—subnarial foramen, soc—supraoccipital, sq—squamosal, stf—subtemporal fenestra, tf—temporal fenestra, vo—vomer.

Plate 3. Posterior skull elements of *Allosaurus fragilis*: left squamosal in medial (A) and ventral (B) views; left postorbital in medial (C) view; left quadrate in medial (D), anterior (E), and lateral (F) views. Abbreviations: jupr—jugal process, ls—contact with laterosphenoid, ltf—lateral temporal fenestra, of—orbital fenestra, papr—parietal process, po—contact with postorbital, pt—contact with pterygoid, qj—contact with quadratojugal, quc—quadrate cotylus, quf—quadrate foramen, sqpr—squamosal process.

Plate 4. Posterior skull elements of *Allosaurus fragilis*: left prefrontal in medial (A) and lateral (B) views; left quadratojugal in medial (C) view; left jugal in lateral (D) and medial (E) views. Abbreviations: fr—contact with frontal, juf—jugular foramen, jupr—jugal process, la—contact with lachrymal, ltf—lateral temporal fenestra, mx—contact with maxilla, of—orbital fenestra, po—contact with postorbital, qj—contact with quadratojugal, qjpr—quadratojugal process, qu—contact with quadrate, sq—contact with squamosal.
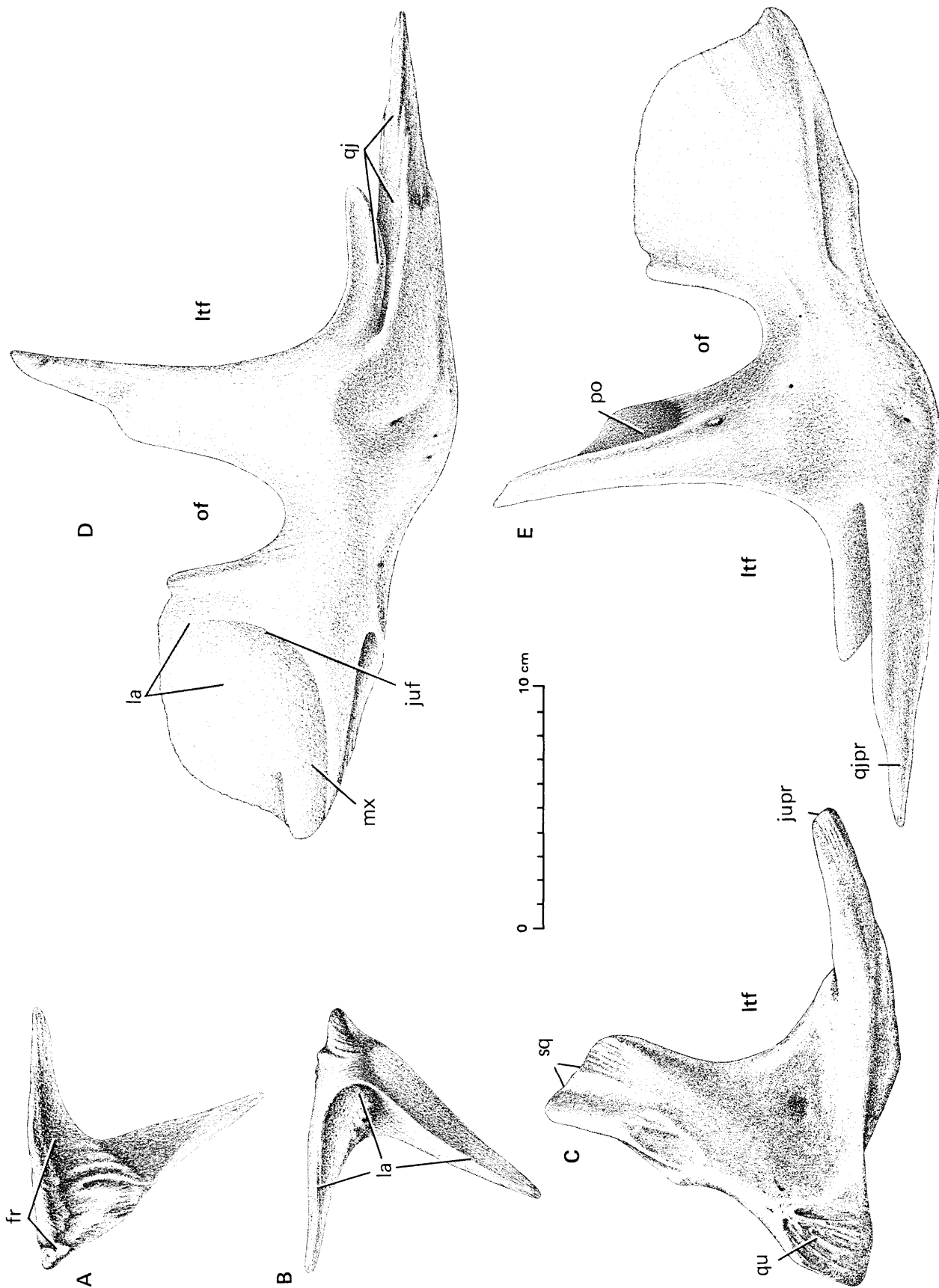
Plate 5. Anterior skull elements of *Allosaurus fragilis*: left lachrymal in medial (A) view; left nasal in ventral (B) and medial (C) views. Abbreviations: aof—antorbital fenestra, en—external naris, fr—contact with frontal, ju—contact with jugal, ms—medial symphysis, mx—contact with maxilla, na—contact with nasal, naf—nasal foramen, pm—contact with premaxilla, prf—contact with prefrontal.
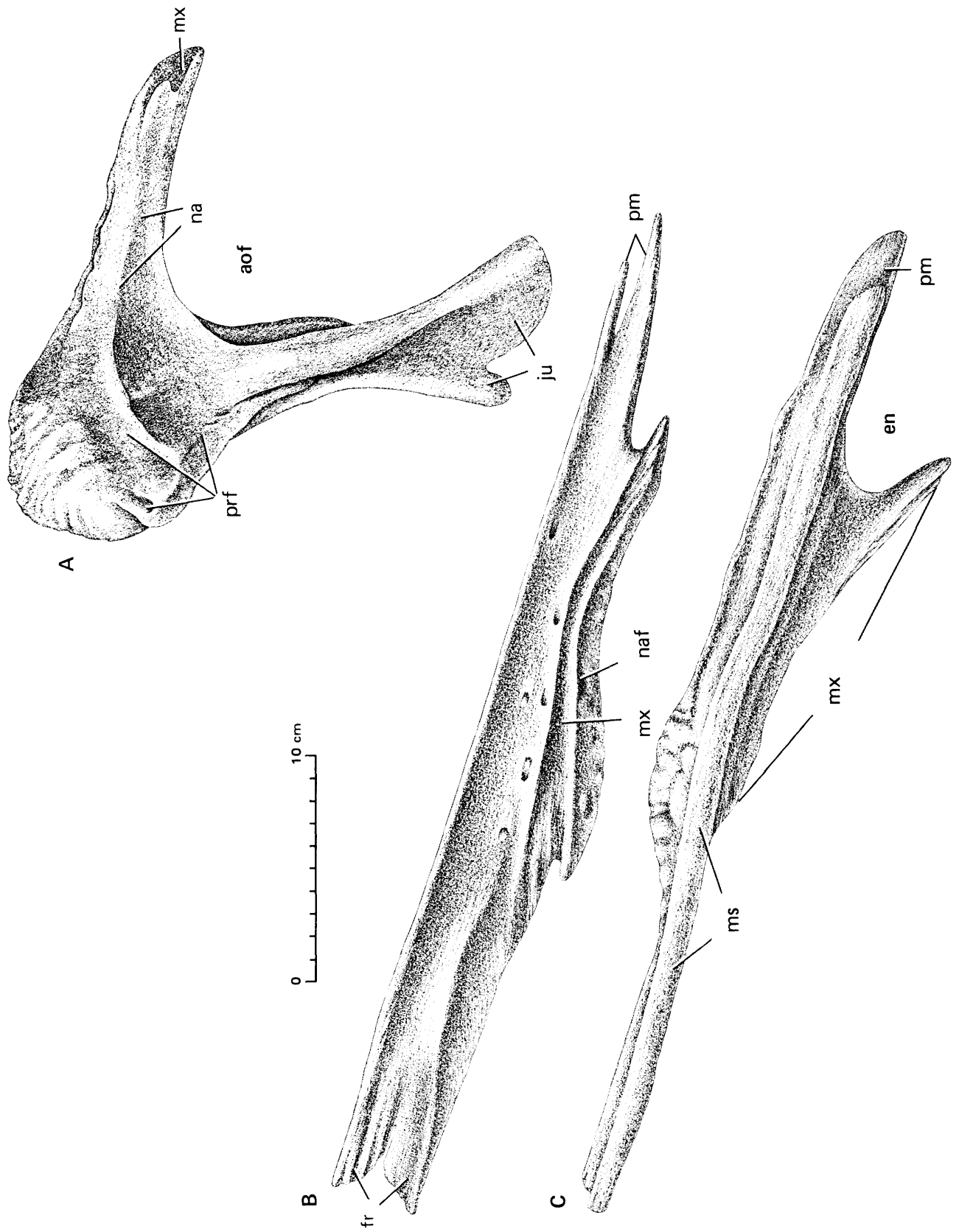
Plate 6. Anterior skull elements of *Allosaurus fragilis*: left maxilla in
dorsal (A) and medial (B) views; left premaxilla in medial (C)
view. Abbreviations: aof—antorbital fenestra, en—external naris,
idp—interdental plates, ju—contact with jugal, la—contact with
lachrymal, ms—medial suture, mx—contact with maxilla,
mxf—maxillary fenestra, mxpr—maxillary process, mxsi—maxillary
sinus, na—contact with nasal, napr—nasal process, pal—contact with
palatine, pm—contact with premaxilla, snf—subnarial foramen,
vo—contact with vomer.
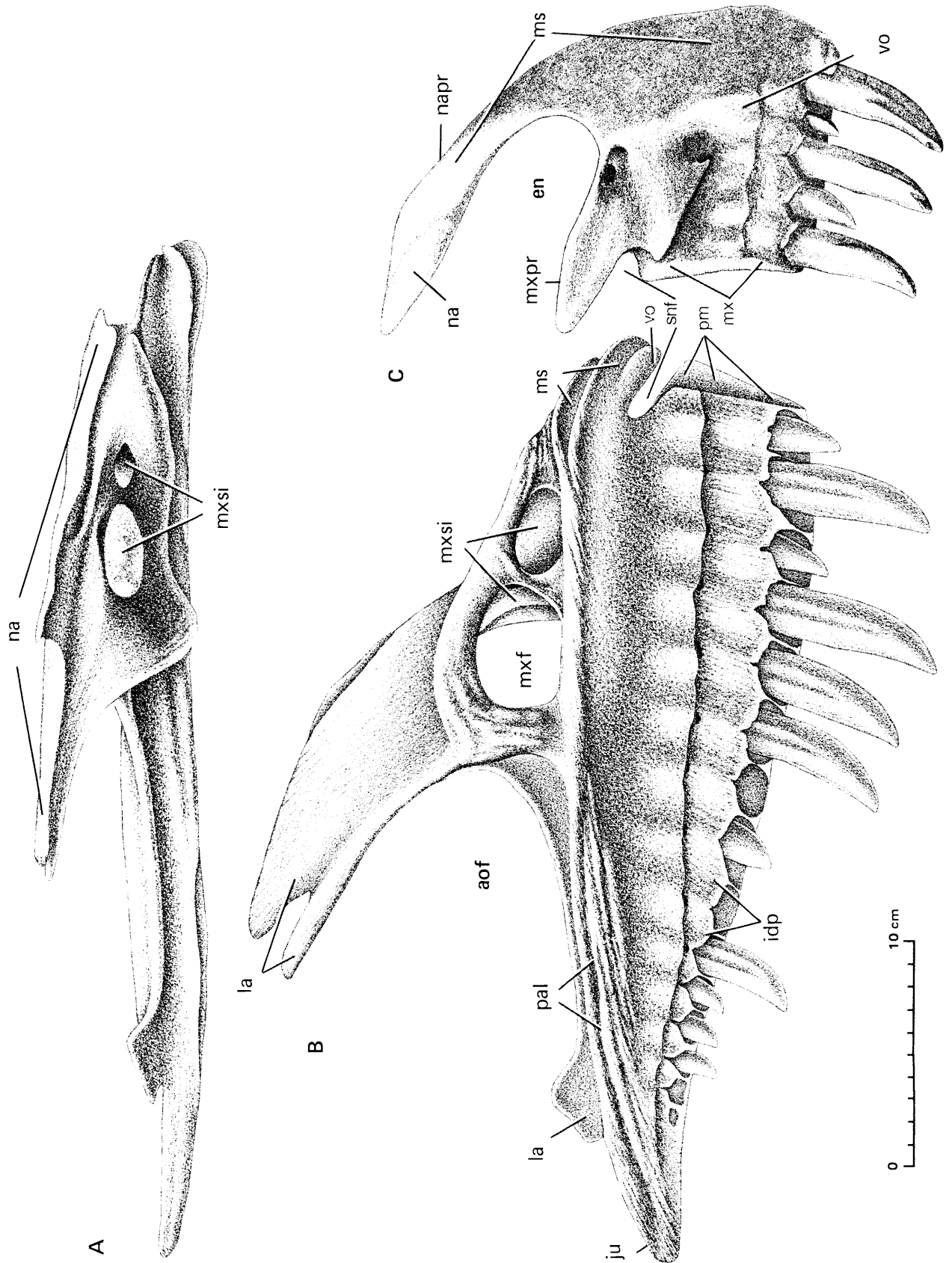
Plate 7. Posterior elements of the mandible of *Allosaurus fragilis*: left coronoid in medial (A) view; left articular in dorsal (B) and ventral (C) views; left angular in lateral (D) and internal (E) views; left prearticular in internal (F) and medial (G) views. Abbreviations: aar—contact with antarticular, an—contact with angular, ar—contact with articular, co—contact with coronoid, de—contact with dentary, gl—glenoid fossa, imf—internal mandibular foramen, repr—retroarticular process, sa—contact with surangular.
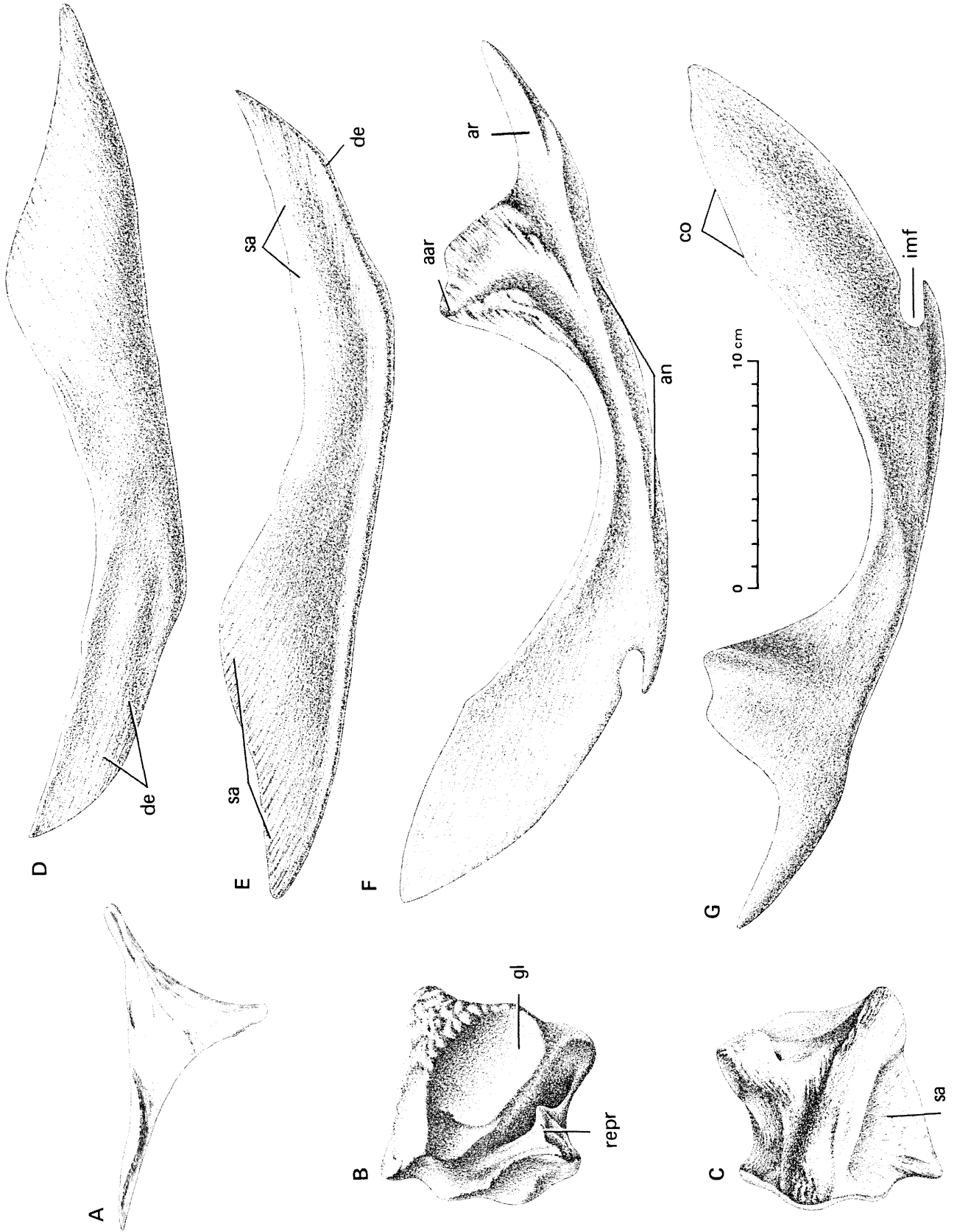
Plate 8. Left surangular of *Allosaurus fragilis* in medial (A), dorsal (B), and lateral (C) views. Abbreviations: aar–contact with antarticular, an–contact with angular, ar–contact with articular, co–contact with coronoid, de–contact with dentary, f '–posterior surangular foramen, f ''–external mandibular foramen, f '''–anterior surangular foramen, gl–glenoid fossa.
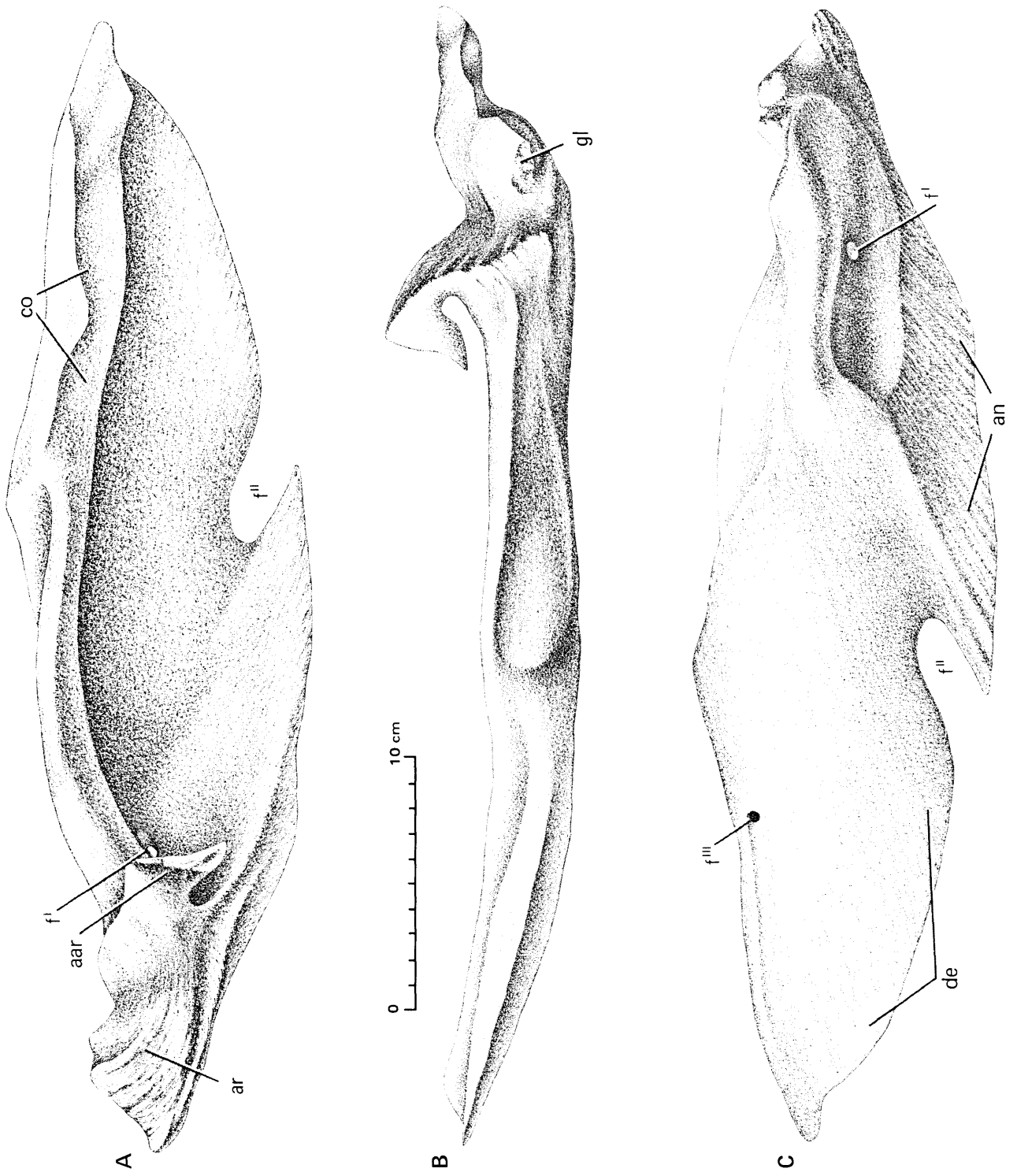
Plate 9. Anterior elements of the mandible of *Allosaurus fragilis*: left splenial in medial (A) and internal (B) views; left dentary in medial (C) view; left supradentary in medial (D) view. Abbreviations: an—contact with angular, de—contact with dentary, f—foramen, idp—interdental plates, mc—Meckelian canal, mg—Meckelian groove, ms—medial symphysis, pra—contact with prearticular, sa—surangular.
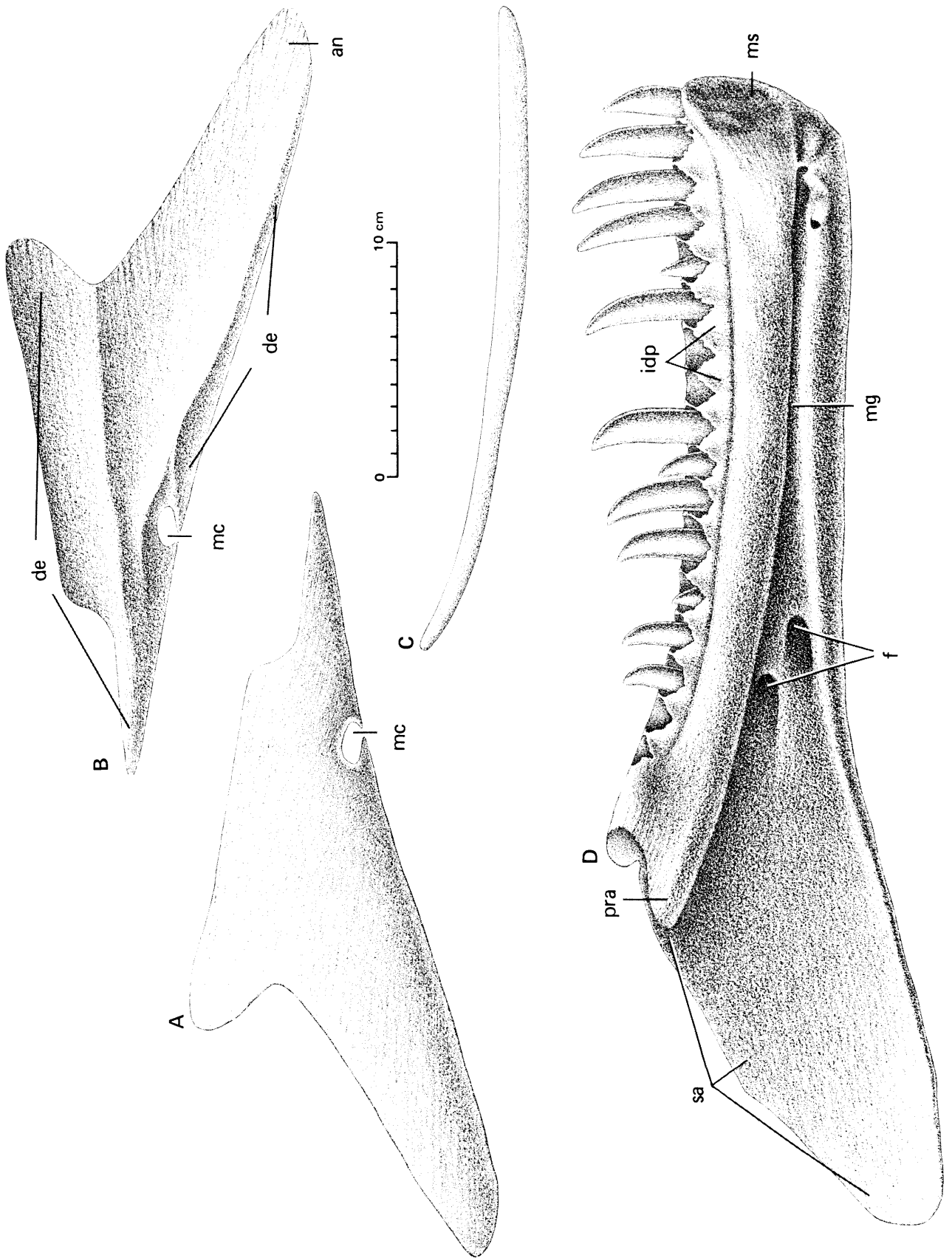
Plate 10. Palate of *Allosaurus fragilis*, elements of left side: palatine in lateral (A) and dorsal (B) views; ectopterygoid in lateral (C) and dorsal (D) views; vomer in lateral (E) and dorsal (F) views; epipterygoid in medial (G) and lateral (H) views; pterygoid in lateral (I) view. Abbreviations: bpt—basipterygoid articulation, ecpt—contact with ectopterygoid, ept—contact with epipterygoid, ju—contact with jugal, ls—contact with laterosphenoid, ms—medial symphysis, mx—contact with maxilla, pal—contact with palatine, pm—contact with premaxilla, pt—contact with pterygoid, qu—contact with quadrate, stf—subtemporal fenestra, vo—contact with vomer.
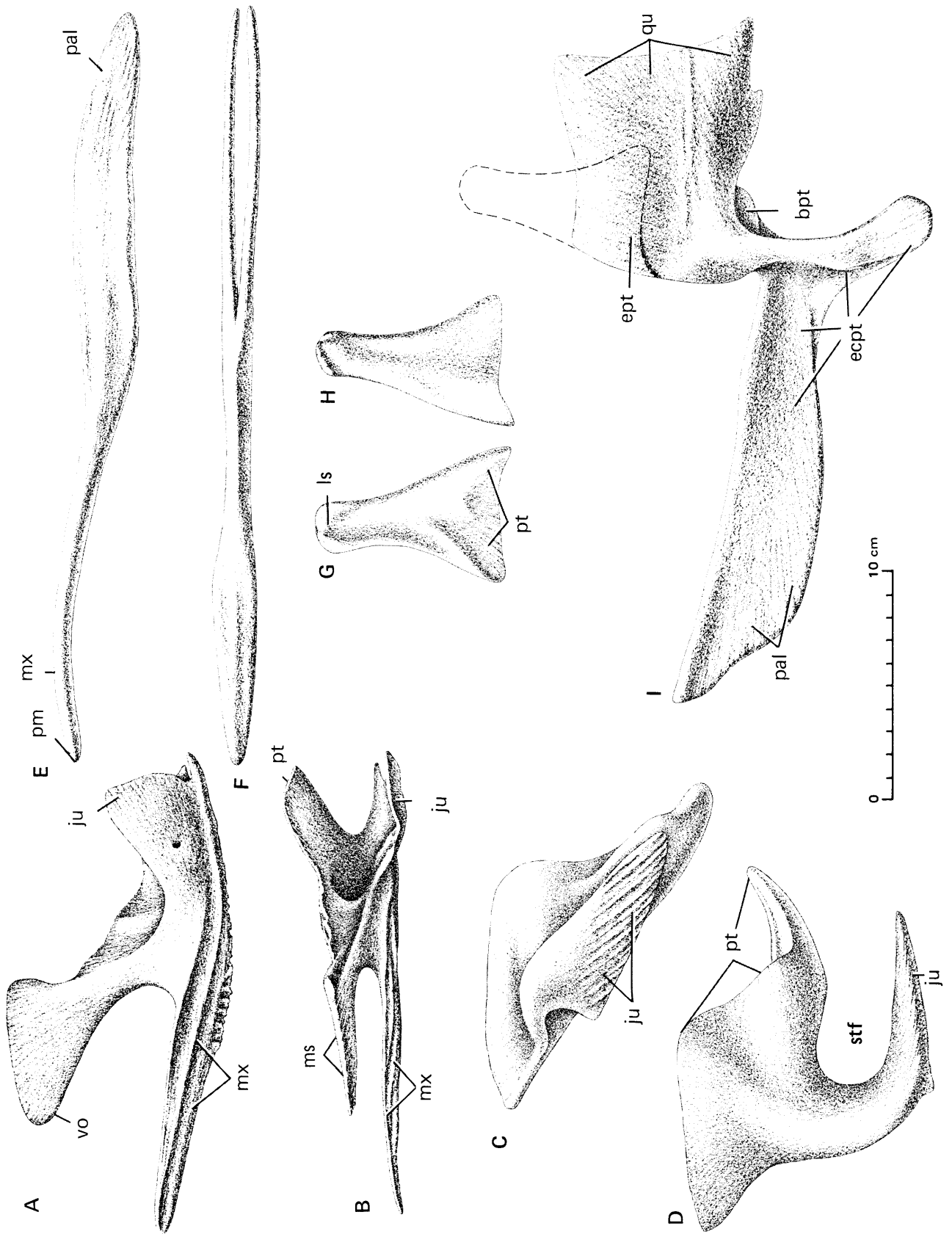
Plate 11. Atlas and axis of *Allosaurus fragilis*: odontoid in posterior (A), dorsal (B), and ventral (C) views; atlantal intercentrum in dorsal (D) and posterior (E) views; axial intercentrum in anterior (F), dorsal (G), and posterior (H) views; left neurapophysis in lateral (I) and medial (J) views; articulated atlas-axis in anterior (K), posterior (L), lateral (M), ventral (N), and dorsal (O) views. Abbreviations: at—facet for atlantal intercentrum, at in—atlantal intercentrum, ax—facet for axial centrum, axi—surface of contact with axial intercentrum, ax in—axial intercentrum, dp—diapophysis, ep—epipophysis, li—scar of interspinous ligament, nc—neural canal, ne—facet for neurapophysis, ns—neural spine, oc—facet for occipital condyle, od—odontoid, odc—concavity for odontoid, pl—pleurocoel, po—postzygapophysis, pof—postzygapophysial facet, pp—parapophysis, pr—prezygapophysis.
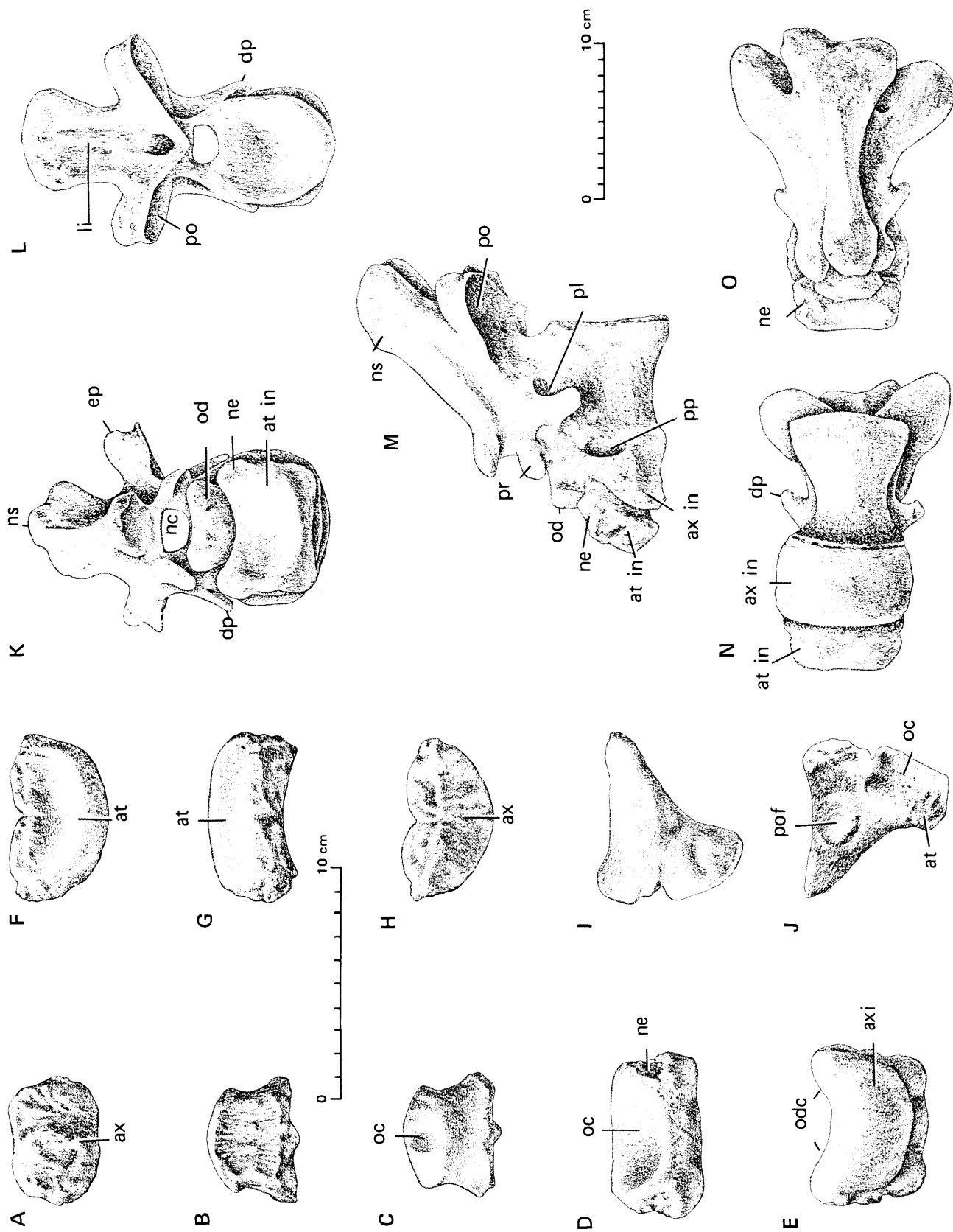
Plate 12. Third (A, B, C) and fourth (D, E, F) cervical vertebrae of *Allosaurus fragilis* in anterior (A, D), lateral (B, E), and posterior (C, F) views. Abbreviations: dp–diapophysis, ep–epipophysis, li–scar of interspinous ligament, nc–neural canal, ns–neural spine, pl–pleurocoel, po–postzygapophysis, pp–parapophysis, pr–prezygapophysis.
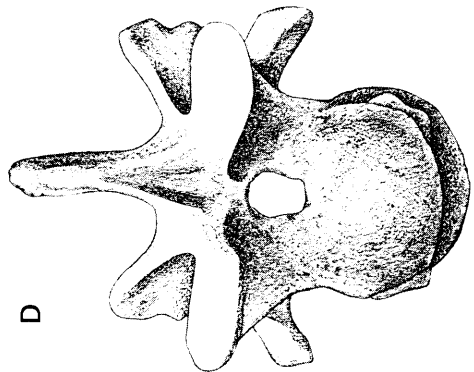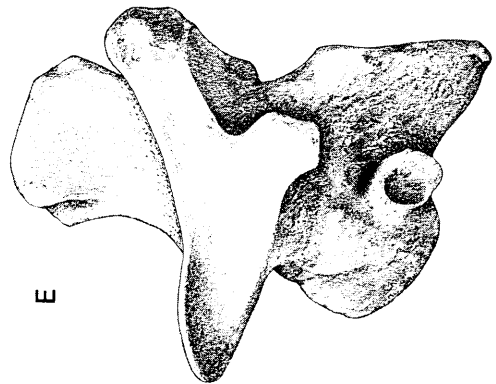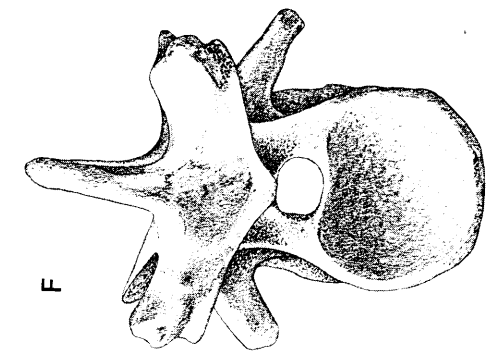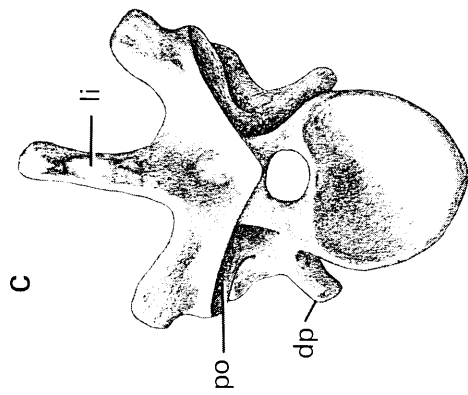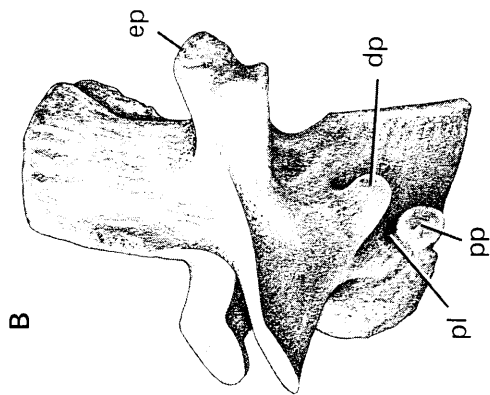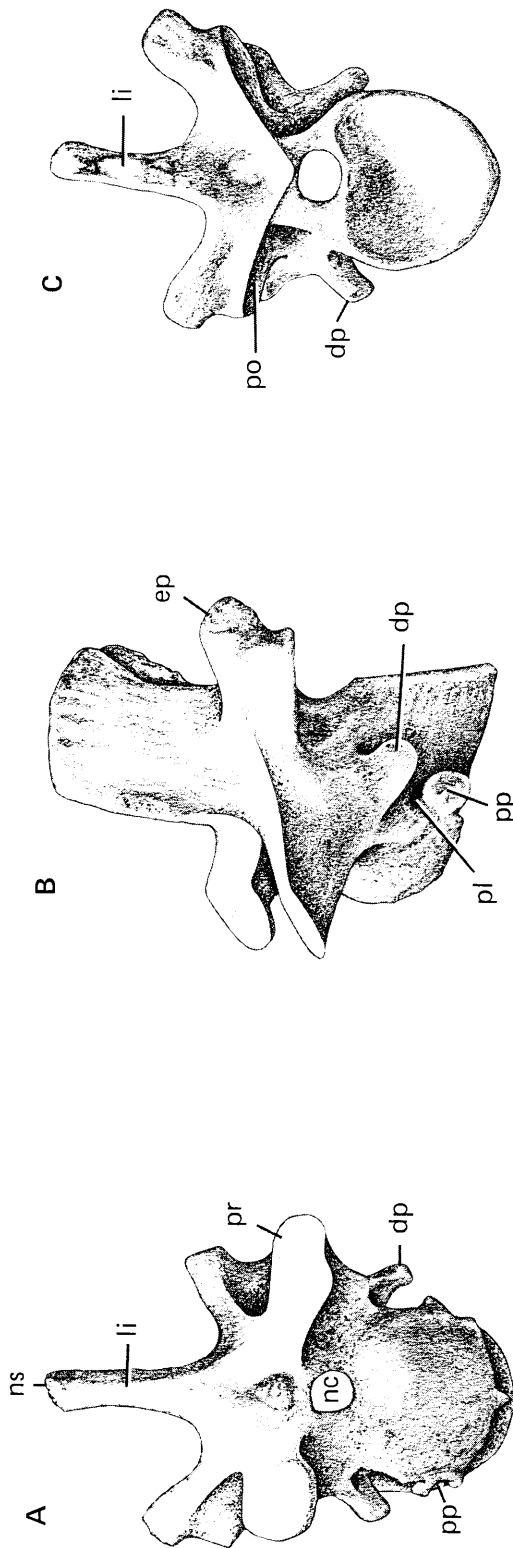
Plate 13. Fifth (A, B, C) and sixth (D, E, F) cervical vertebrae of
Allosaurus fragilis in anterior (A, D), lateral (B, E), and posterior
(C, F) views. Abbreviations: dp–diapophysis, ep–epipophysis,
li–scar of interspinous ligament, nc–neural canal, ns–neural spine,
pl–pleurocoel, po–postzygapophysis, pp–parapophysis,
pr–prezygapophysis.
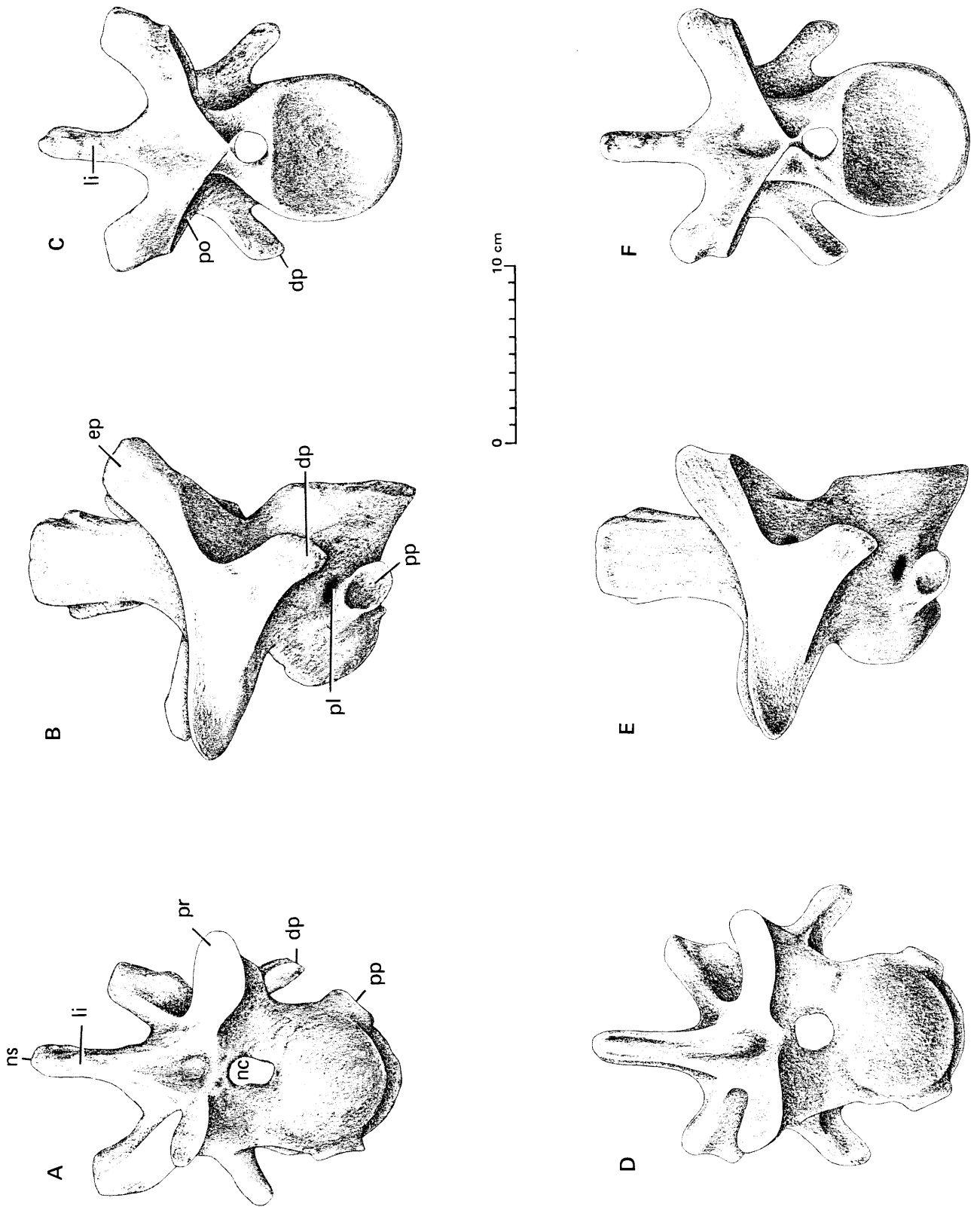
Plate 14. Seventh (A, B, C) and eighth (D, E, F) cervical vertebrae of *Allosaurus fragilis* in anterior (A, D), lateral (B, E), and posterior (C, F) views. Abbreviations: dp—diapophysis, ep—epipophysis, li—scar of interspinous ligament, nc—neural canal, ns—neural spine, pl—pleurocoel, po—postzygapophysis, pp—parapophysis, pr—prezygapophysis.
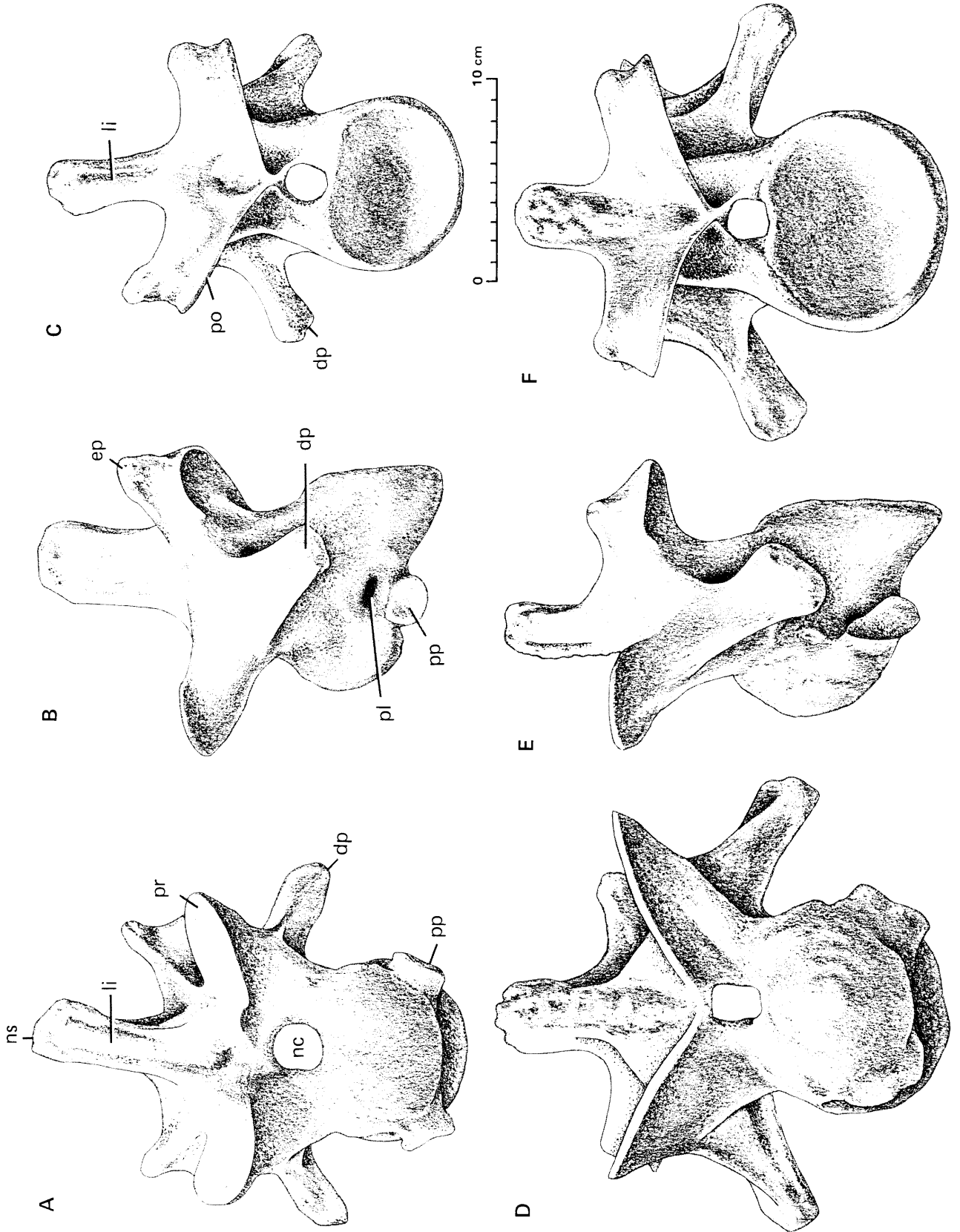
Plate 15. Ninth cervical (A, B, C) and first dorsal (D, E, F) vertebrae
of *Allosaurus fragilis* in anterior (A, D), lateral (B, E), and
posterior (C, F) views. Abbreviations: dp–diapophysis,
ep–epipophysis, li–scar of interspinous ligament, nc–neural canal,
ns–neural spine, pl–pleurocoel, po–postzygapophysis,
pp–parapophysis, pr–prezygapophysis.
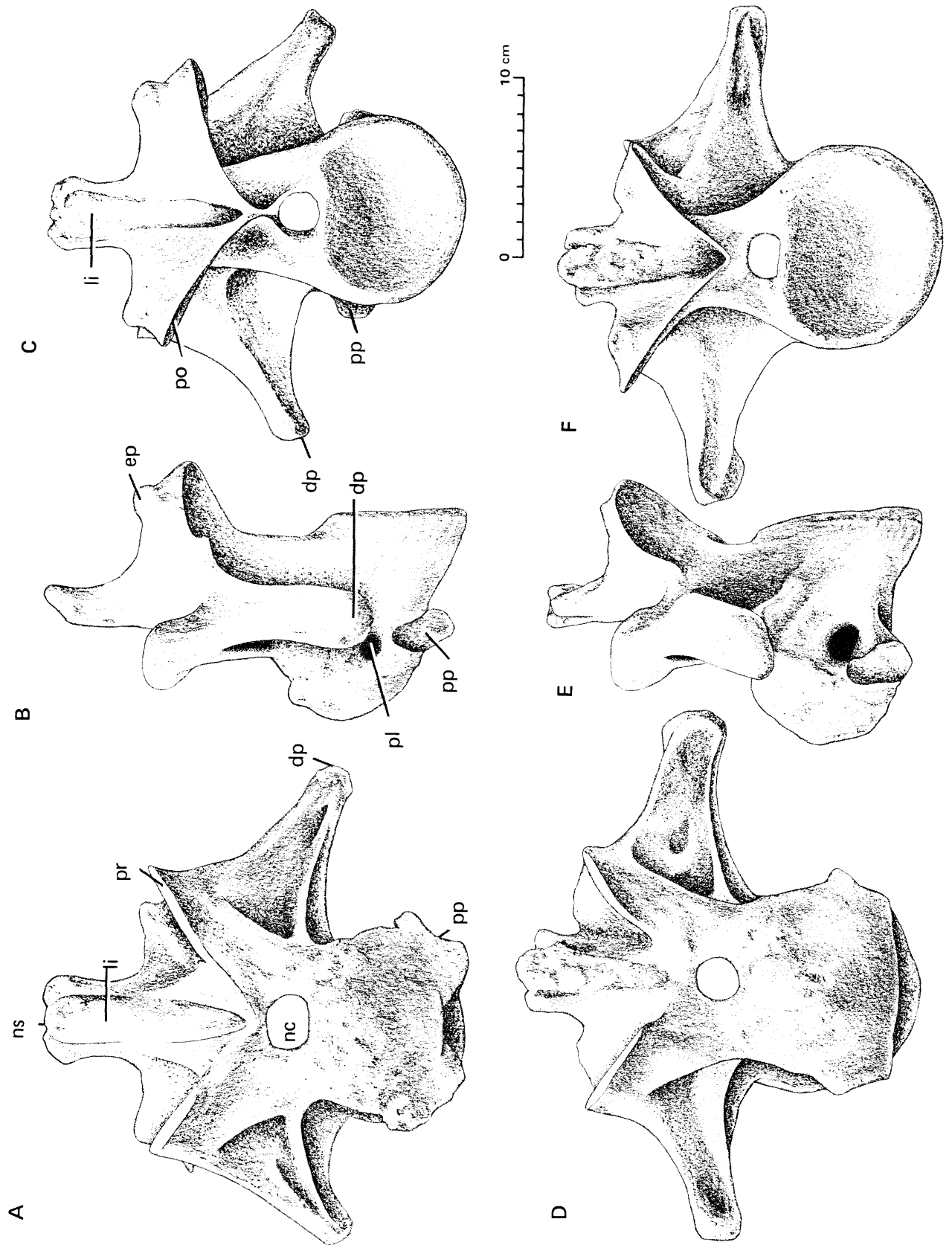
Plate 16. Second (A, B, C) and third (D, E, F) dorsal vertebrae of *Allosaurus fragilis* in anterior (A, D), lateral (B, E), and posterior (C, F) views. Abbreviations: dp—diapophysis, li—scar of interspinous ligament, nc—neural canal, ns—neural spine, pl—pleurocoel, po—postzygapophysis, pp—parapophysis, pr—prezygapophysis.
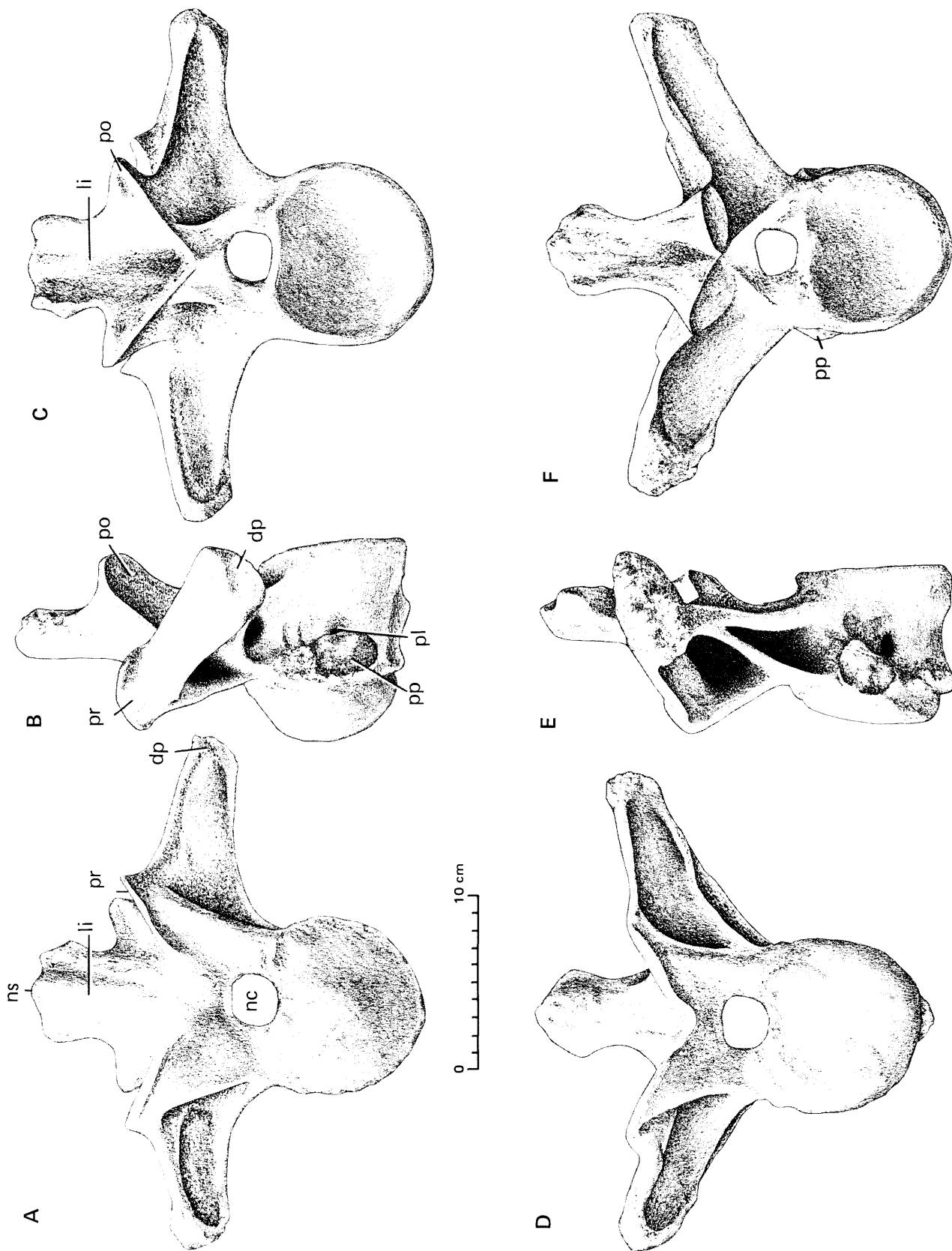
Plate 17. Fourth (A, B, C) and fifth (D, E, F) dorsal vertebrae of
Allosaurus fragilis in anterior (A, D), lateral (B, E), and posterior
(C, F) views. Abbreviations: dp–diapophysis, hy–hyposphene,
li–scar of interspinous ligament, nc–neural canal, ns–neural spine,
pl–pleurocoel, po–postzygapophysis, pp–parapophysis,
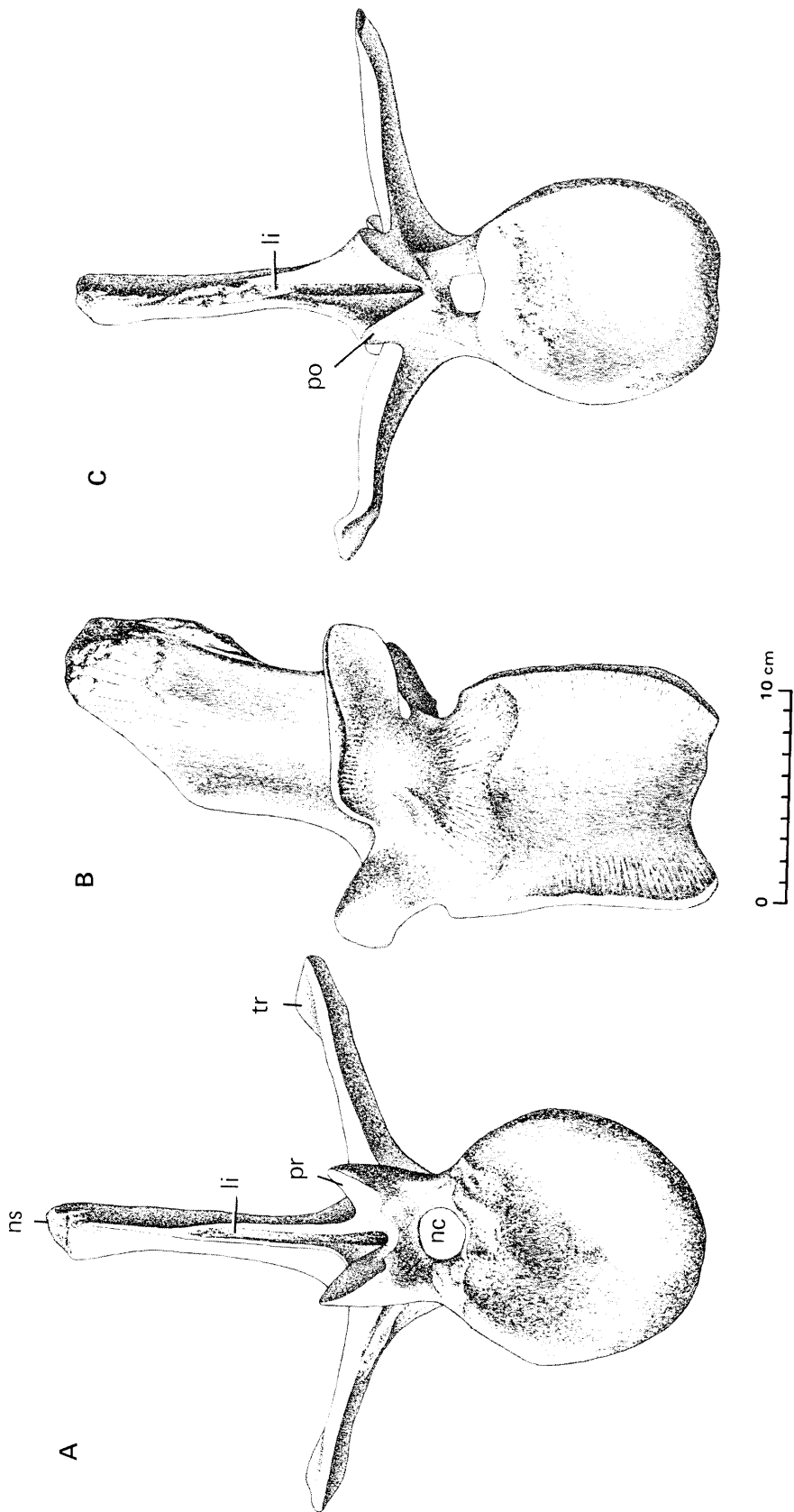pr–prezygapophysis.
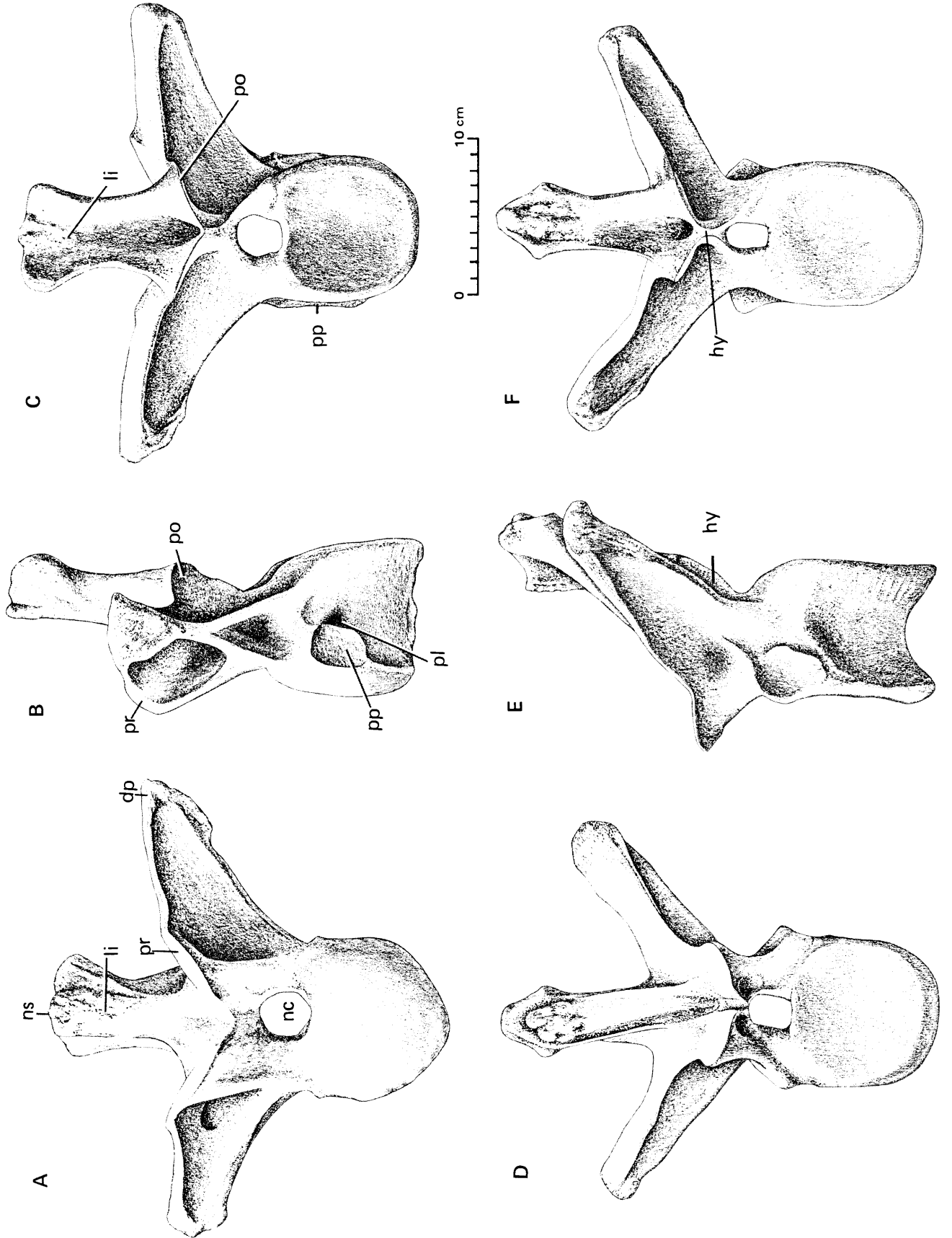
Plate 18. Sixth (A, B, C) and seventh (D, E, F) dorsal vertebrae of *Allosaurus fragilis* in anterior (A, D), lateral (B, E), and posterior (C, F) views. Abbreviations: dp—diapophysis, hy—hyposphene, li—scar of interspinous ligament, nc—neural canal, ns—neural spine, po—postzygapophysis, pp—parapophysis, pr—prezygapophysis.
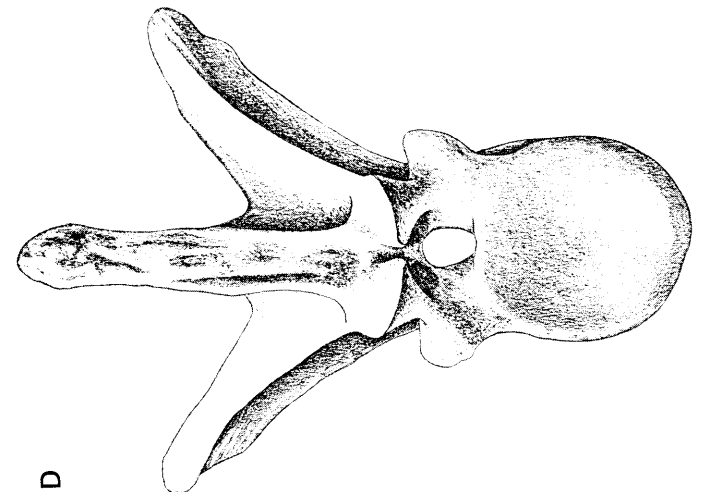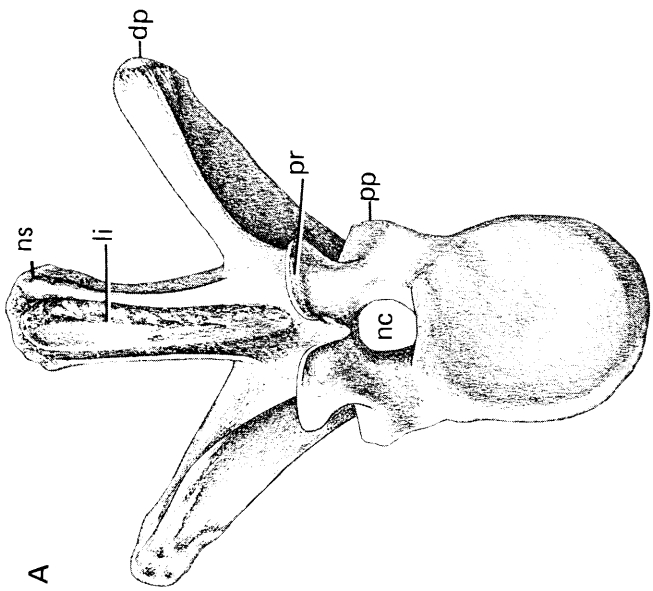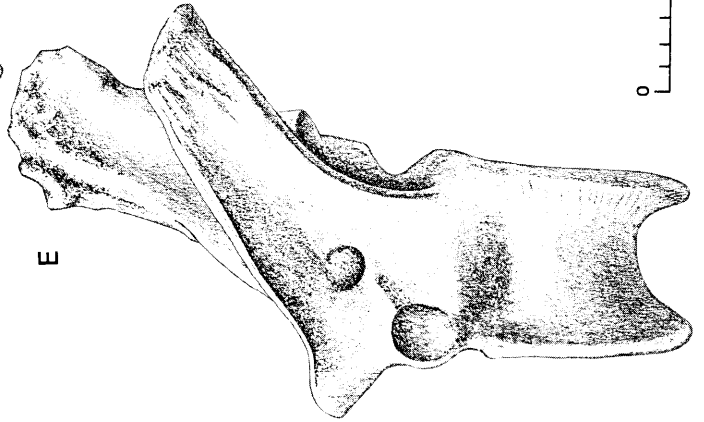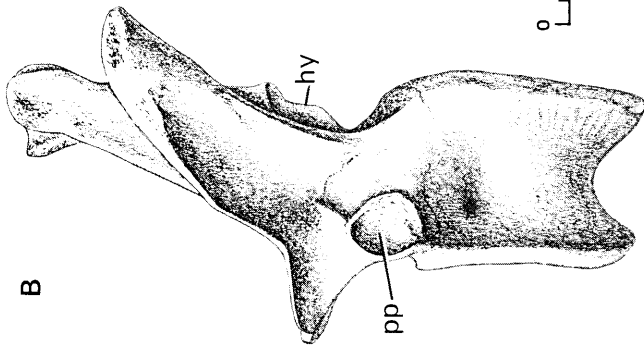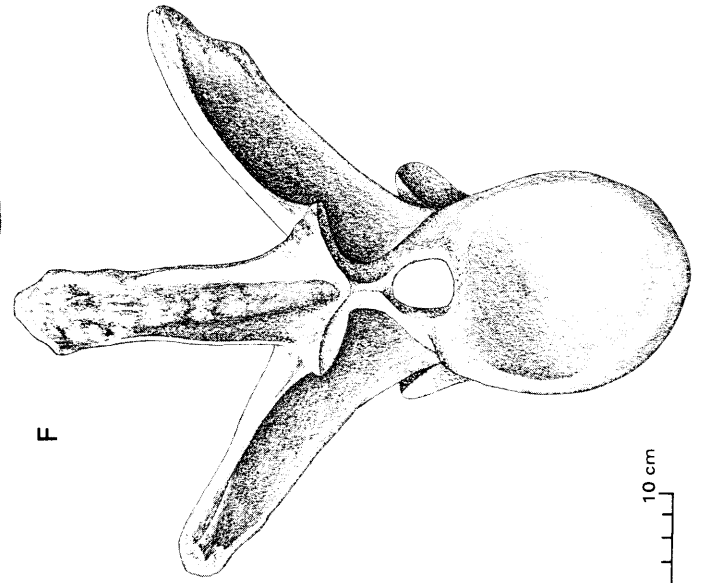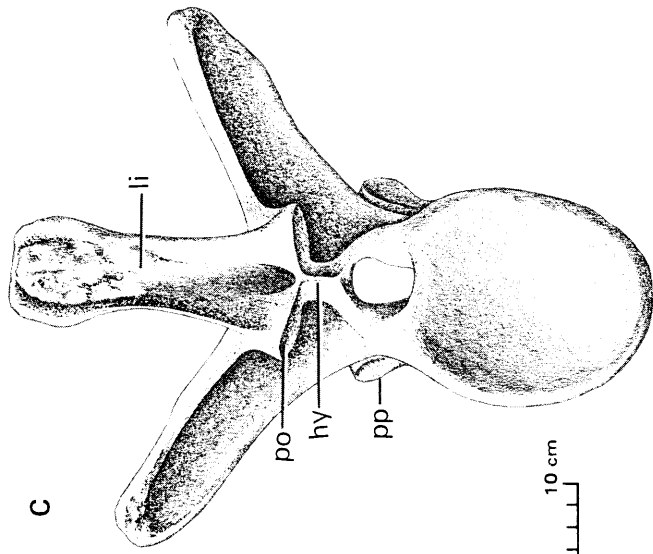
Plate 19. Eighth (A, B, C) and ninth (D, E, F) dorsal vertebrae of
Allosaurus fragilis in anterior (A, D), lateral (B, E), and posterior
(C, F) views. Abbreviations: dp–diapophysis, hy–hyposphene,
li–scar of interspinous ligament, nc–neural canal, ns–neural spine,
po–postzygapophysis, pp–parapophysis, pr–prezygapophysis.
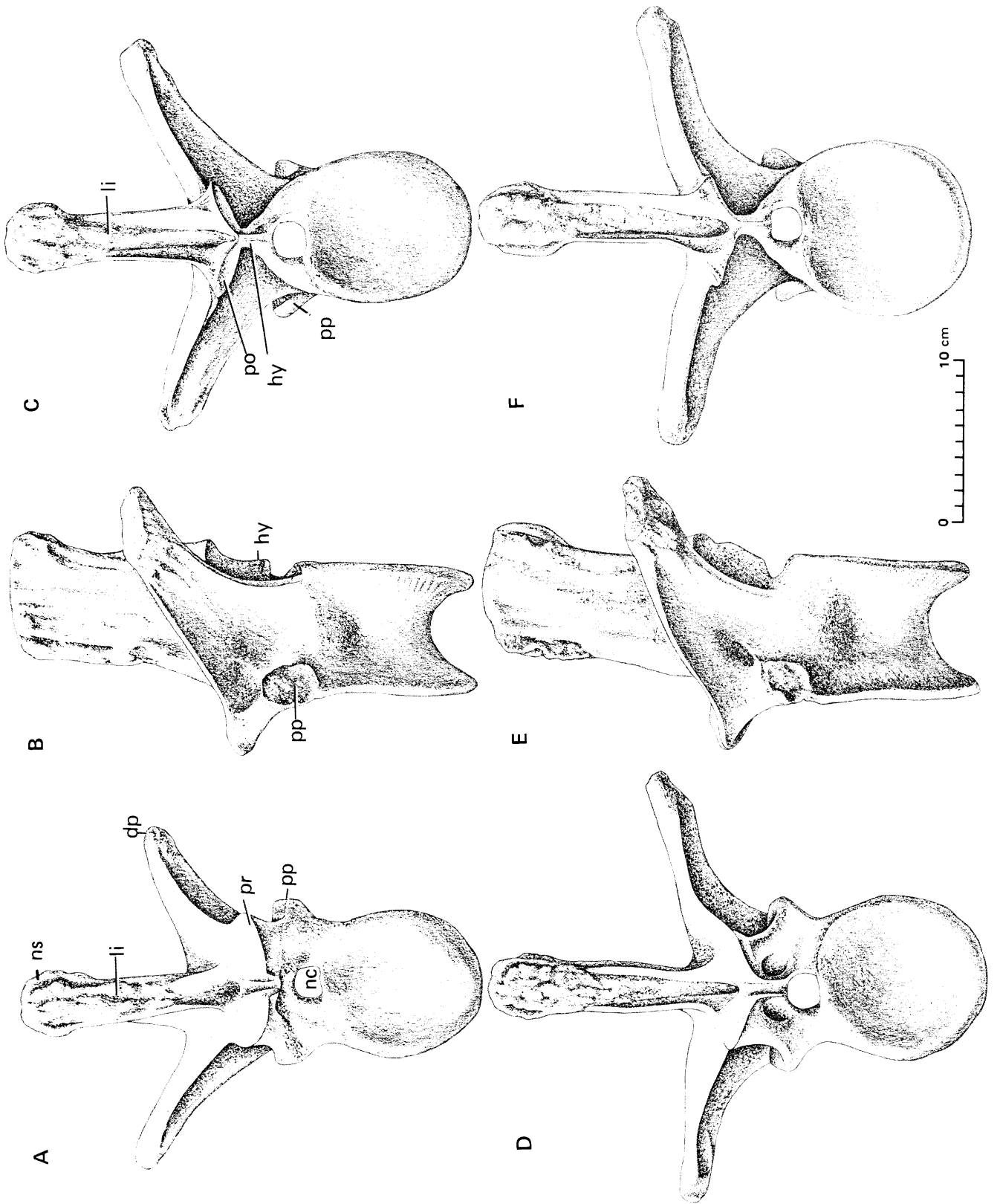
Plate 20. Tenth (A, B, C) and eleventh (D, E, F) dorsal vertebrae of *Allosaurus fragilis* in anterior (A, D), lateral (B, E), and posterior (C, F) views. Abbreviations: dp—diapophysis, hy—hyposphene, li—scar of interspinous ligament, nc—neural canal, ns—neural spine, po—postzygapophysis, pp—parapophysis, pr—prezygapophysis.
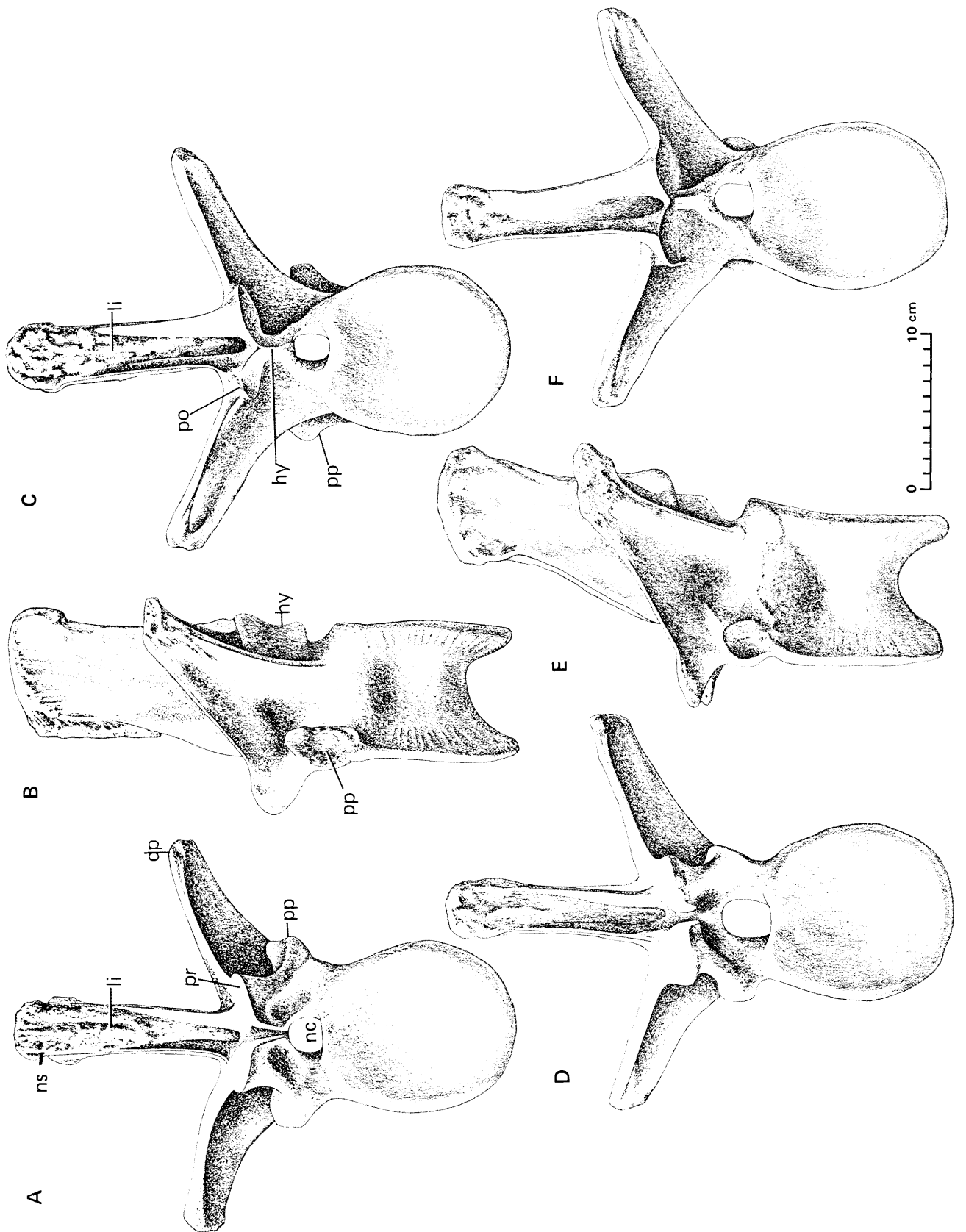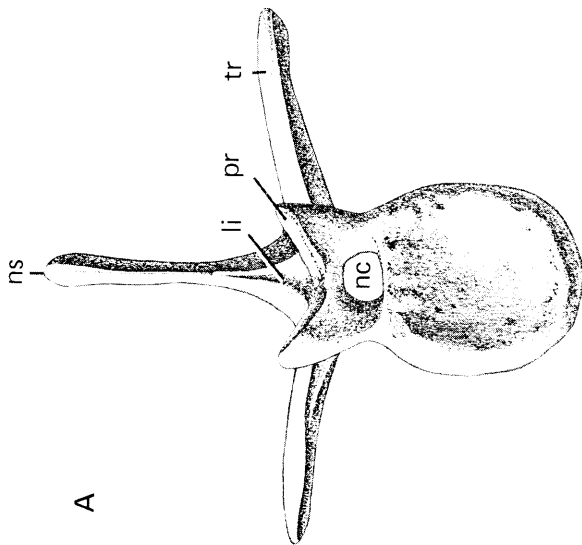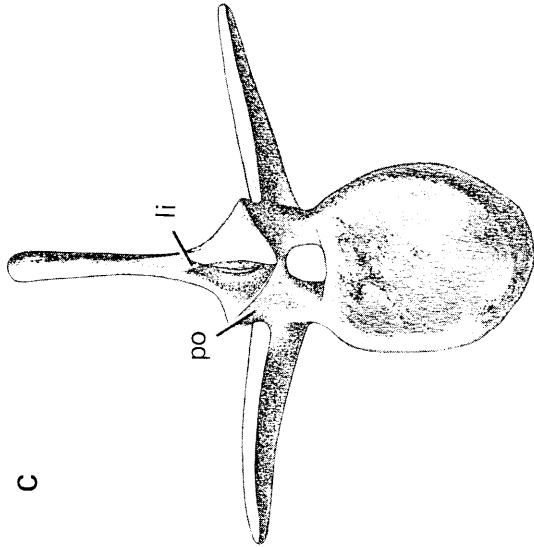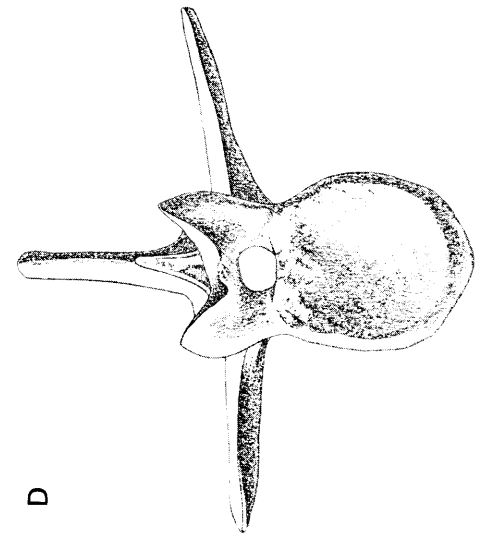
Plate 21. Twelfth dorsal vertebra of *Allosaurus fragilis* in anterior (A),
lateral (B), and posterior (C) views. Abbreviations:
dp–diapophysis, hy–hyposphene, li–scar of interspinous ligament,
nc–neural canal, ns–neural spine, po–postzygapophysis,
pp–parapophysis, pr–prezygapophysis.
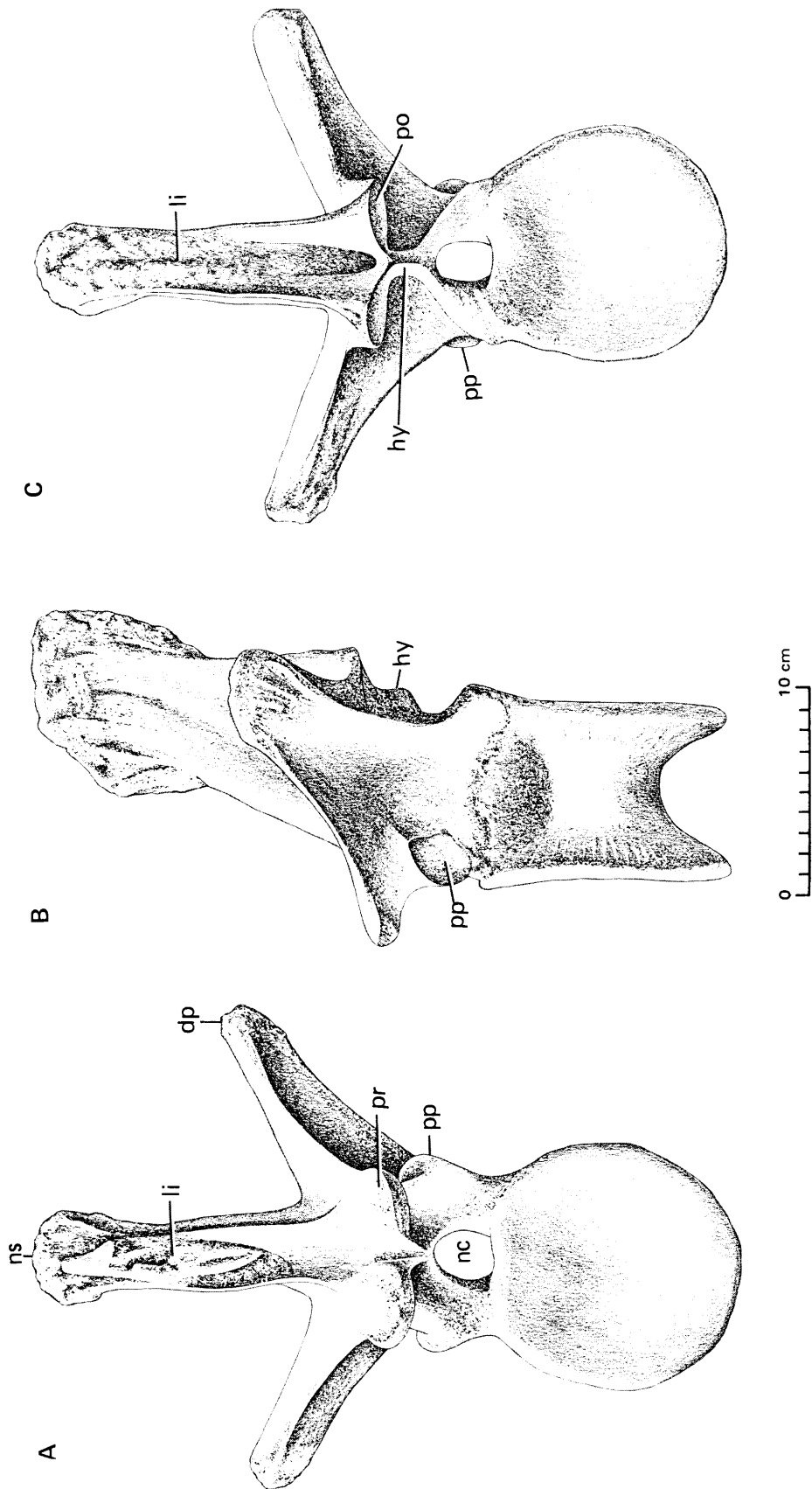
Plate 22. Thirteenth dorsal vertebra of *Allosaurus fragilis* in anterior (A), lateral (B), and posterior (C) views. Abbreviations: dp–diapophysis, hy–hyposphene, li–scar of interspinous ligament, nc–neural canal, ns–neural spine, po–postzygapophysis, pp–parapophysis, pr–prezygapophysis.
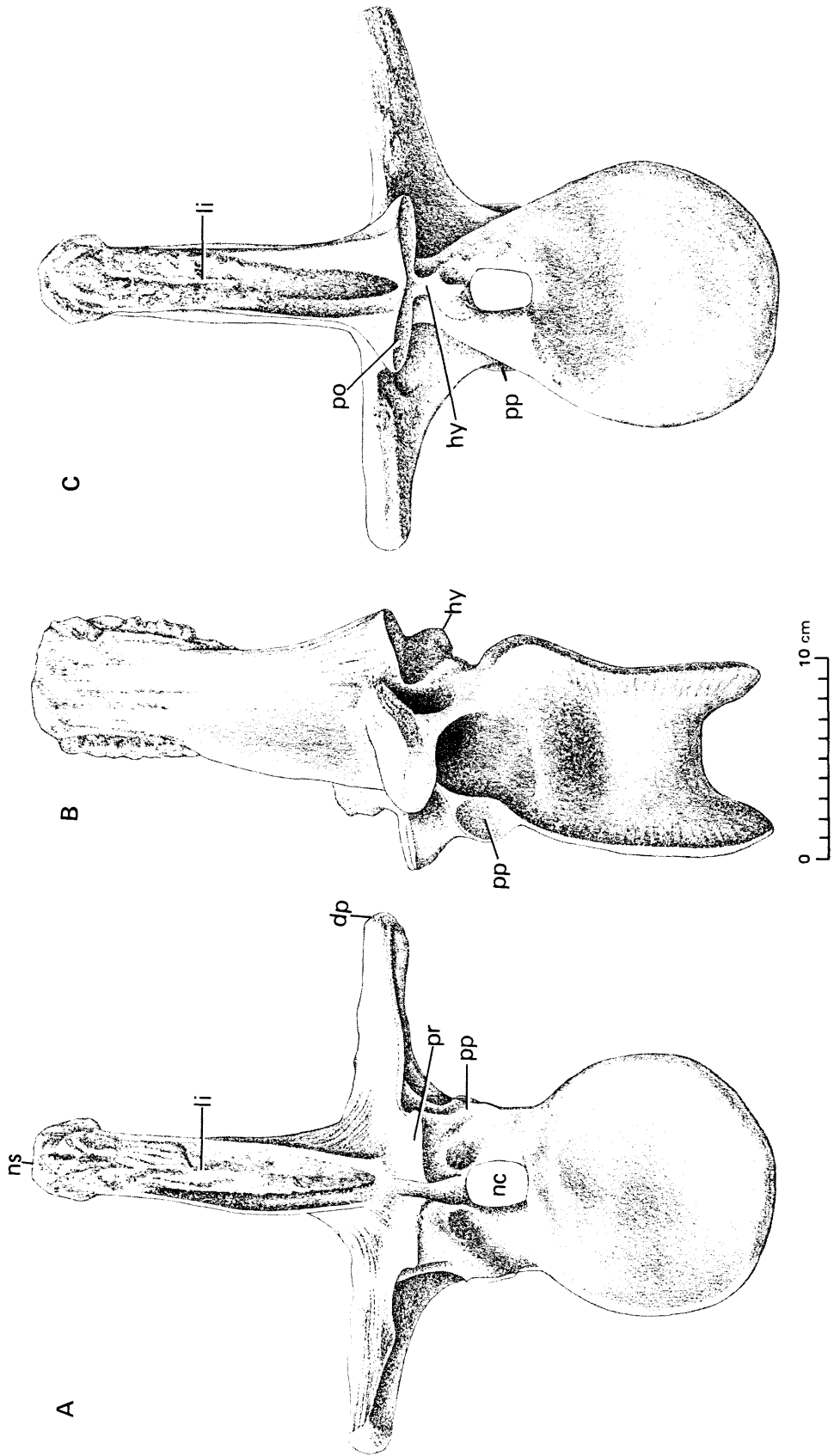
Plate 23. Fourteenth dorsal vertebra of *Allosaurus fragilis* in anterior (A), lateral (B), and posterior (C) views. Abbreviations: dp–diapophysis, hy–hyposphene, li–scar of interspinous ligament, nc–neural canal, ns–neural spine, po–postzygapophysis, pp–parapophysis, pr–prezygapophysis.
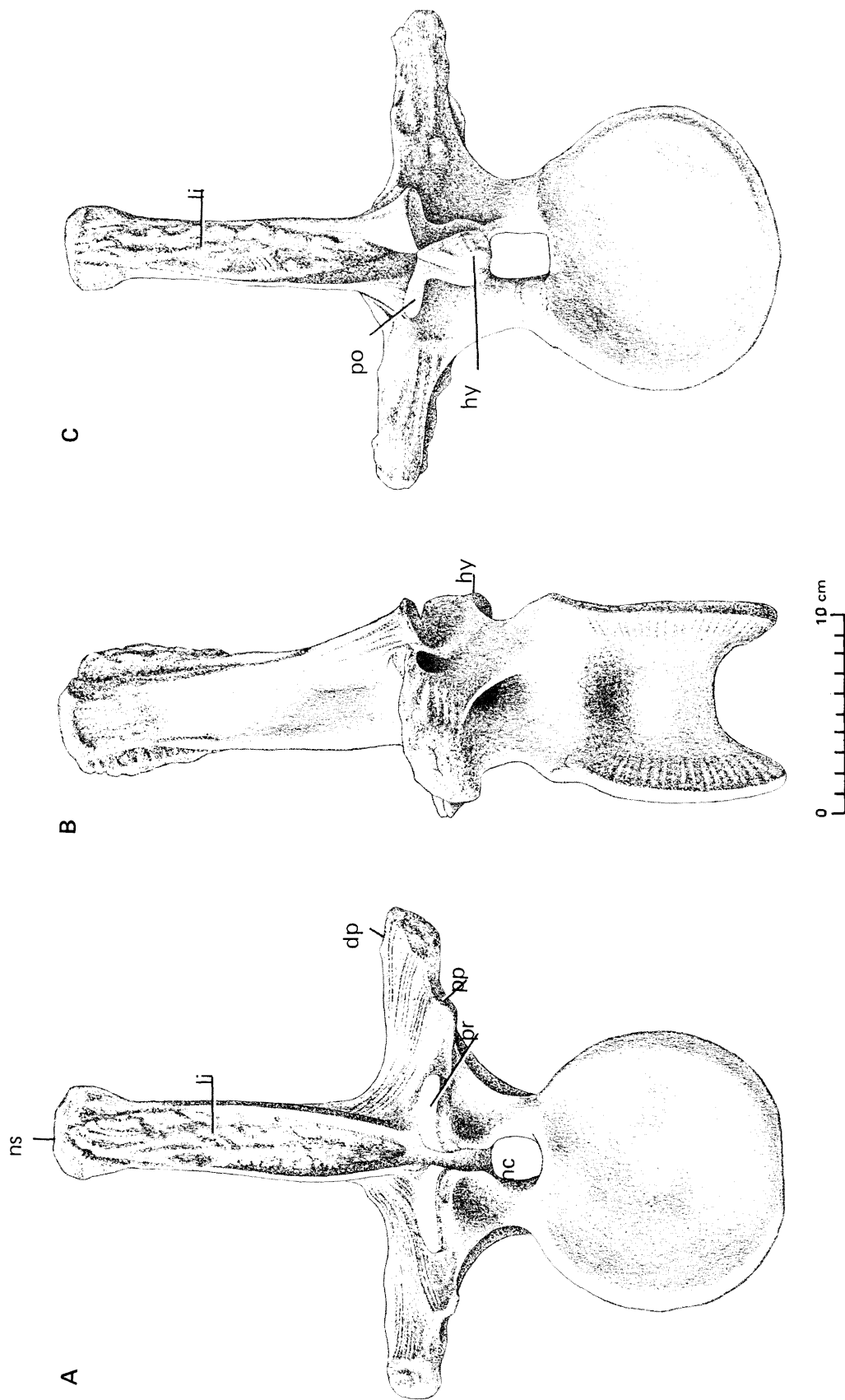
Plate 24. First (A, B, C, D, E, F) and second (G, H, I, J, K, L) sacral vertebrae and ribs (C, D, I, J) of *Allosaurus fragilis* in anterior (A, B), lateral (C, E, F, G, H, J), posterior (K, L), and medial (D, I) views. Abbreviations: li–scar of interspinous ligament, nc–neural canal, ns–neural spine, pr–prezygapophysis, sr_1–contact of first sacral rib, sr_2–contact of second sacral rib, sr_3–contact of third sacral rib, tr_1–transverse process of first sacral vertebra, tr_2–transverse process of second sacral vertebra.
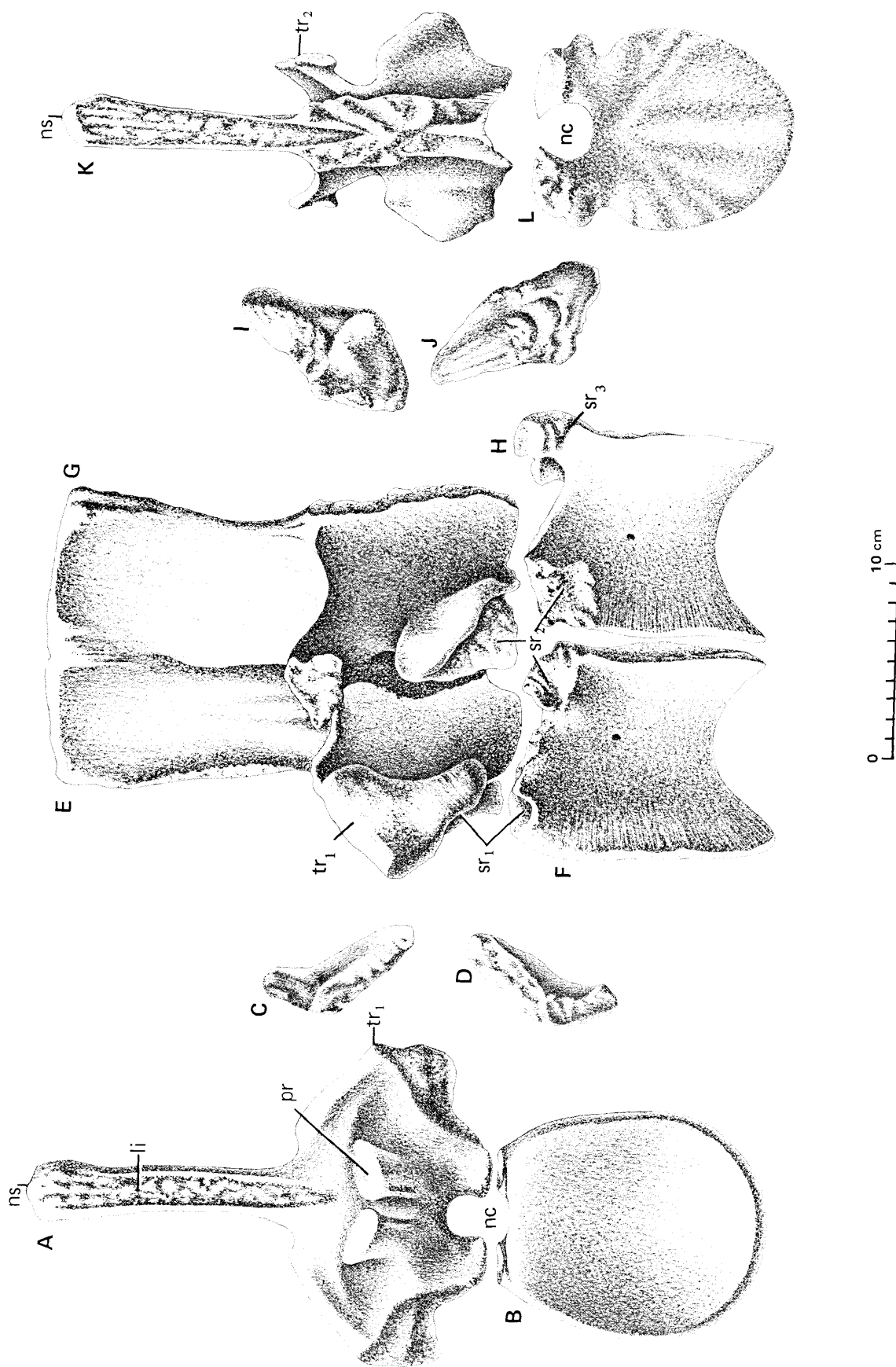
Plate 25. Third sacral vertebra (A, B, C, D, G, H) and rib (E, F) of *Allosaurus fragilis* in anterior (A, B), lateral (C, D, F), posterior (G, H), and medial (E) views. Abbreviations: nc–neural canal, ns–neural spine, sr_3–contact of third sacral rib, sr_4–contact of fourth sacral rib, tr_3–transverse process of third sacral vertebra.
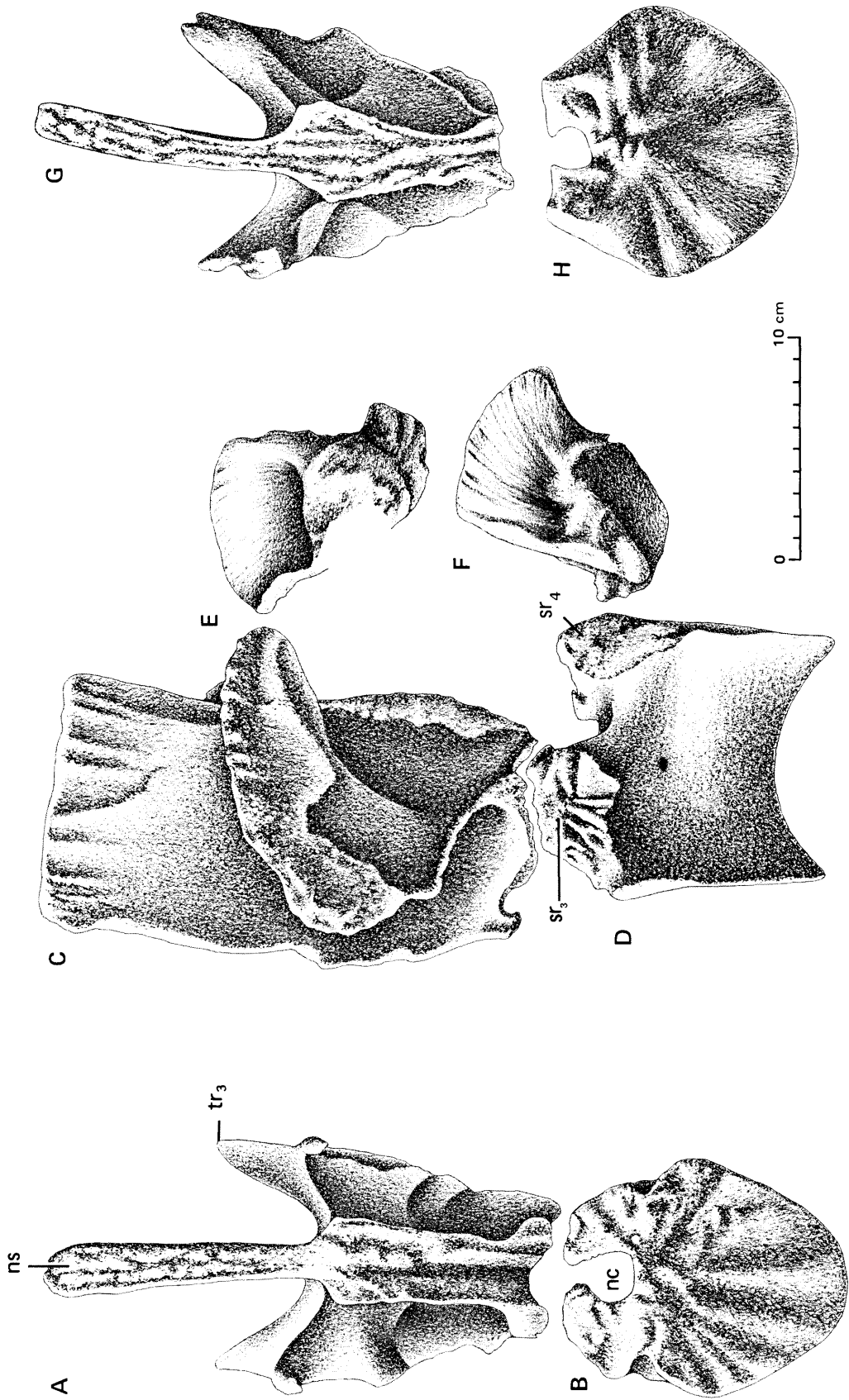
Plate 26. Fourth sacral vertebra (A, B, C, D, G, H) and rib (E, F) of *Allosaurus fragilis* in anterior (A, B), lateral (C, D, F), posterior (G, H), and medial (E) views. Abbreviations: nc–neural canal, ns–neural spine, sr_4–contact of fourth sacral rib, tr_4–transverse process of fourth sacral vertebra.

10 cm
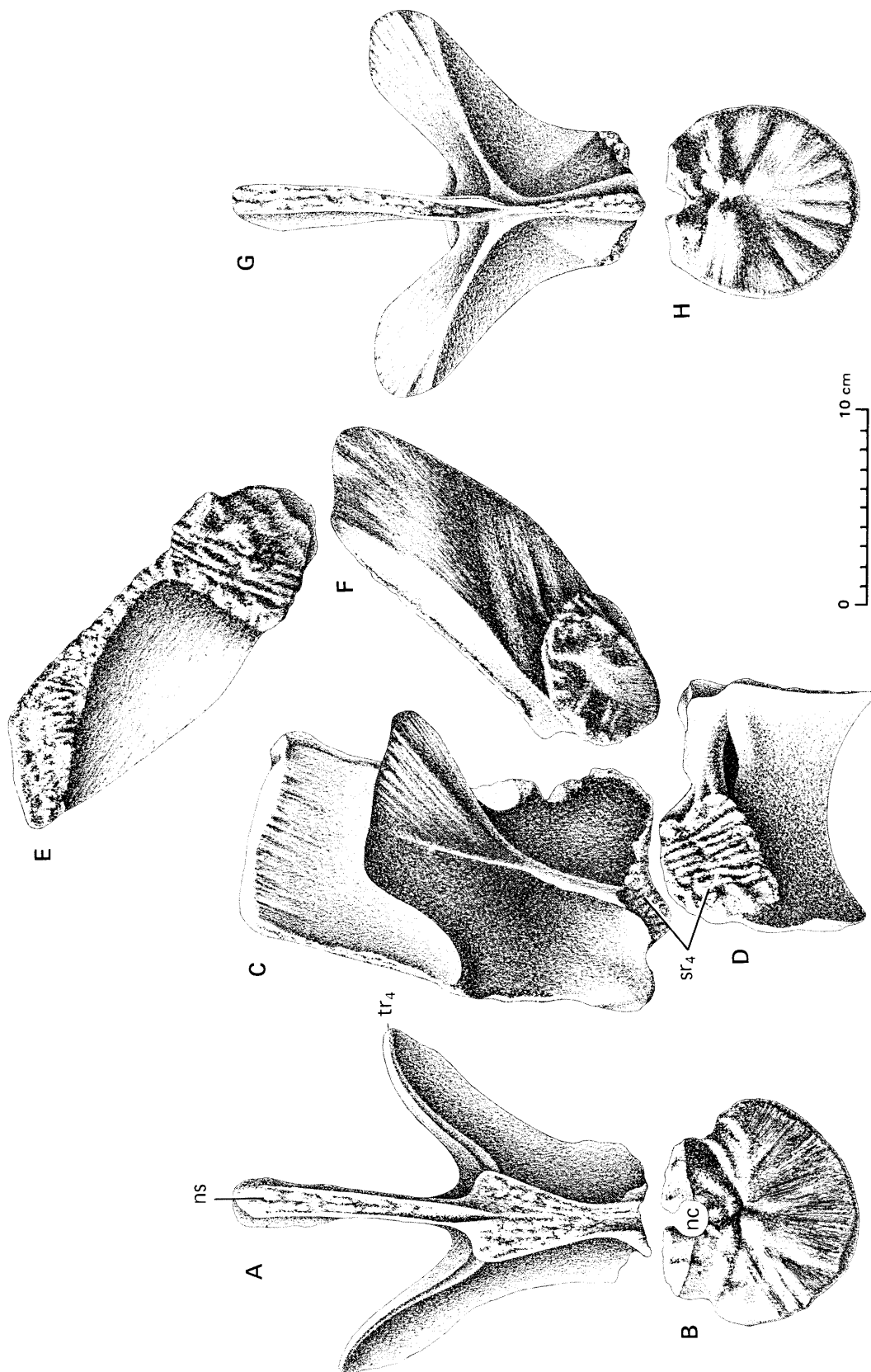
Plate 27. Disarticulated fifth sacral vertebra (A, B, C, D, G, H) and rib (E, F) of *Allosaurus fragilis* in anterior (A, B), lateral (C, D, F), posterior (G, H), and medial (E) views. Abbreviations: li–scar of interspinous ligament, nc–neural canal, ns–neural spine, po–postzygapophysis, sr_5–contact of fifth sacral rib.
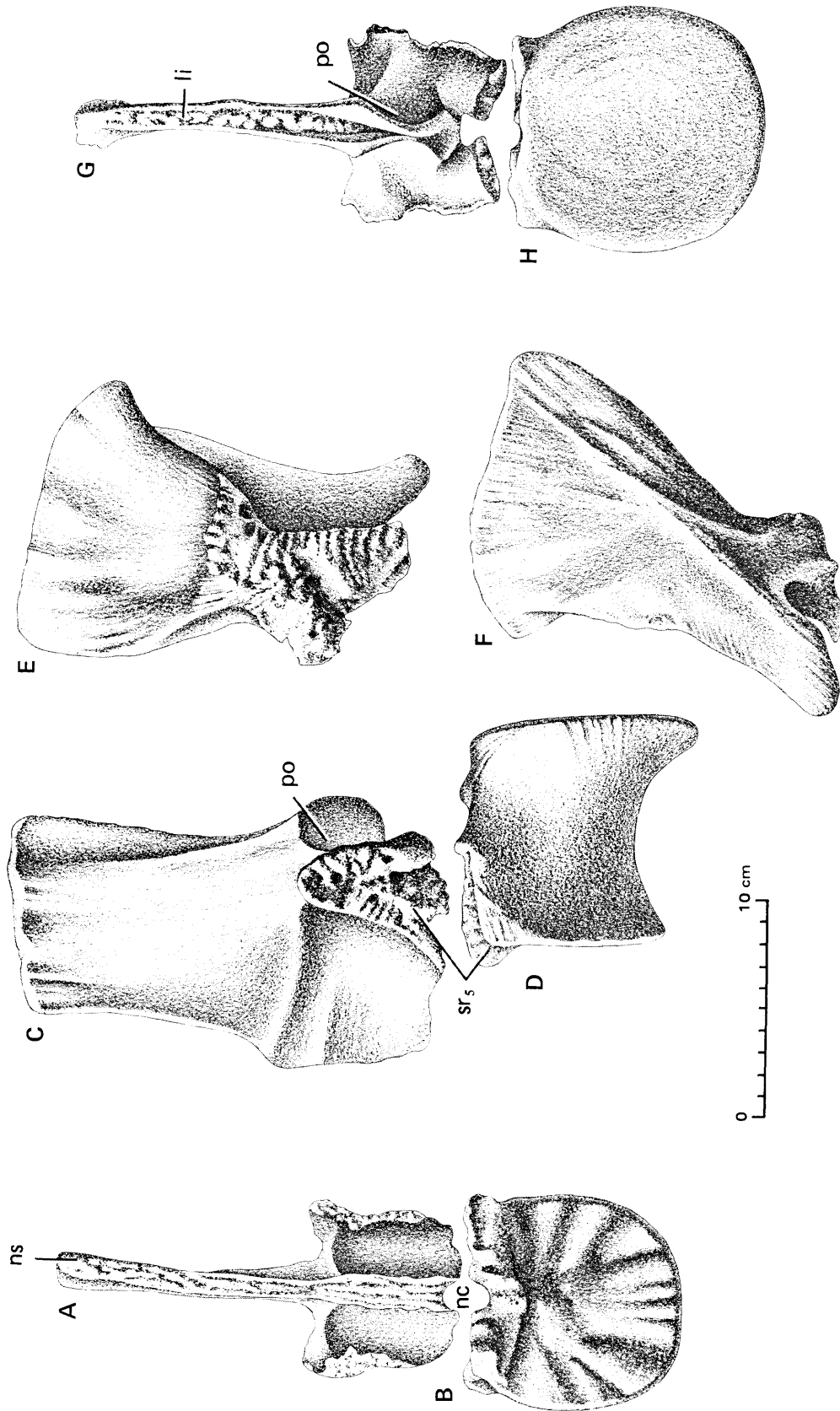
Plate 28. Dorsal view (A) of articulated sacral centra one through five and ventral view (B) of articulated sacral neural spines one through five of *Allosaurus fragilis*. Abbreviations: nc—neural canal, po—postzygapophysis, pr—prezygapophysis, s_1, s_2, s_3, s_4, s_5—sacral vertebrae, tr—transverse process.
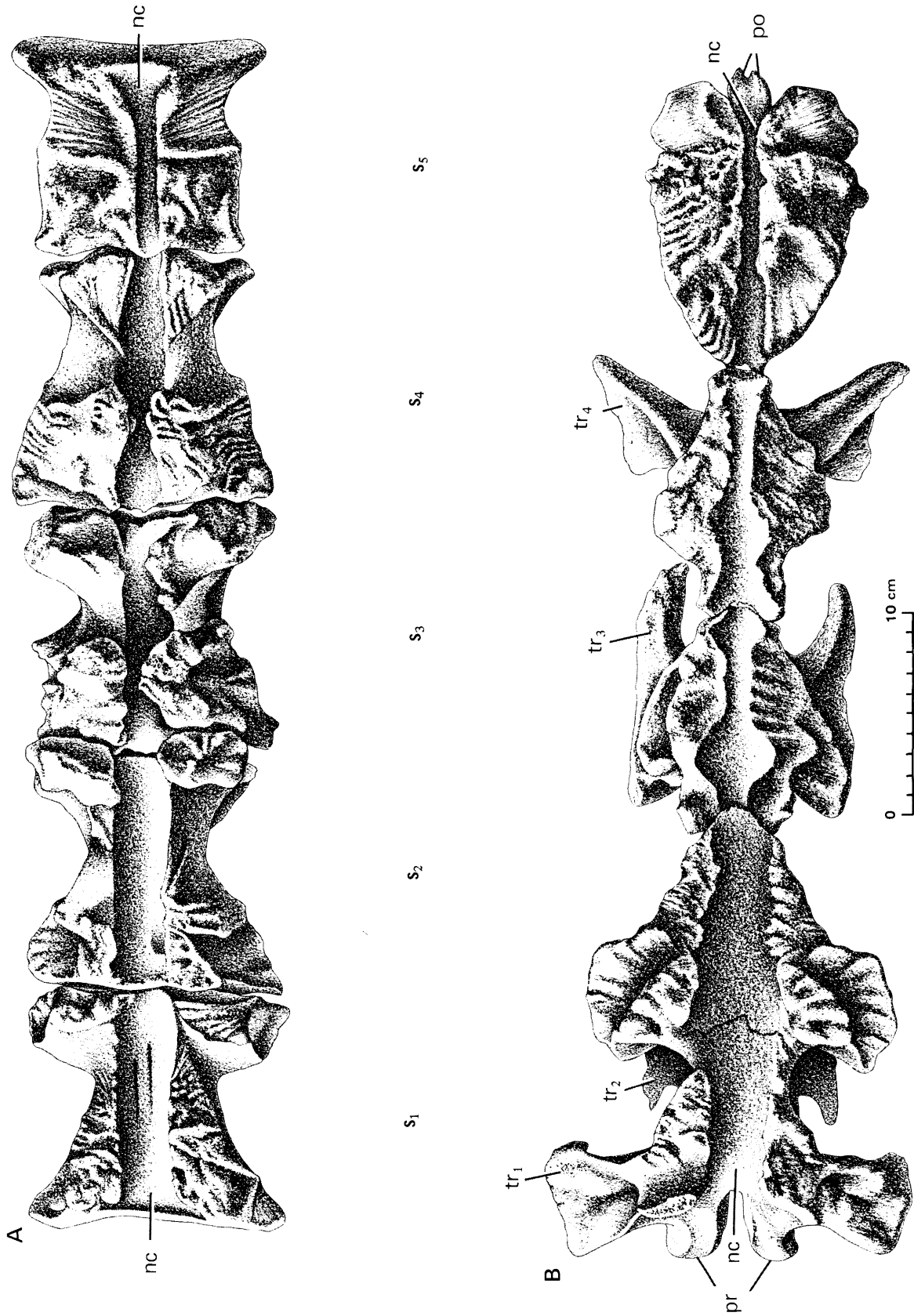
Plate 29. First caudal vertebra of *Allosaurus fragilis* in anterior (A), lateral (B), and posterior (C) views. Abbreviations: li—scar of interspinous ligament, nc—neural canal, ns—neural spine, po—postzygapophysis, pr—prezygapophysis, tr—transverse process.
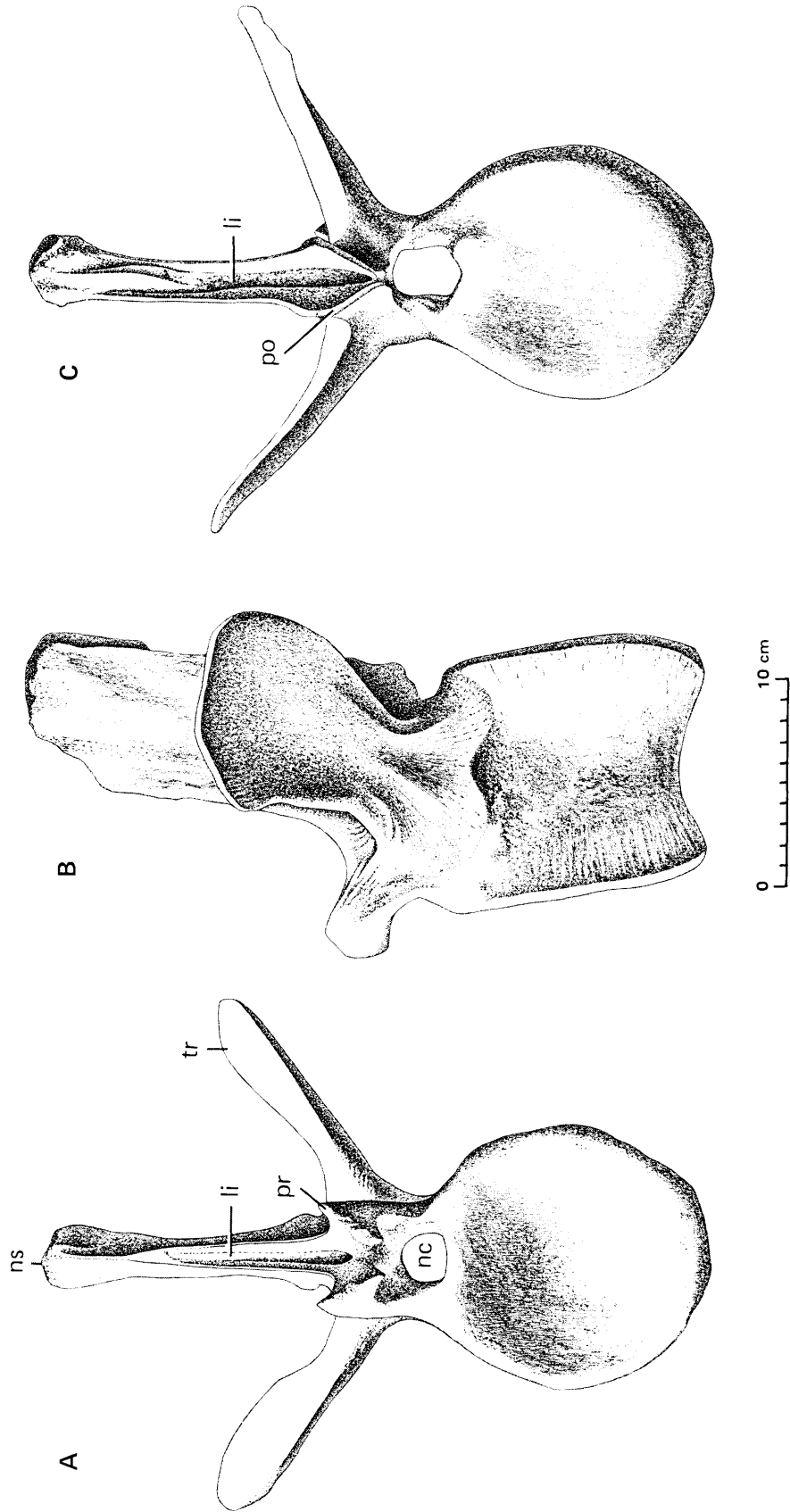
Plate 30. Fourth caudal vertebra of *Allosaurus fragilis* in anterior (A), lateral (B), and posterior (C) views. Abbreviations: li—scar of inter-spinous ligament, nc—neural canal, ns—neural spine, po—postzygapophysis, pr—prezygapophysis, tr—transverse process.

Plate 31. Seventh (A, B, C) and tenth (D, E, F) caudal vertebrae of
   Allosaurus fragilis in anterior (A, D), lateral (B, E), and posterior
   (C, F) views. Abbreviations: li—scar of interspinous ligament,
   nc—neural canal, ns—neural spine, po—postzygapophysis,
   pr—prezygapophysis, tr—transverse process.
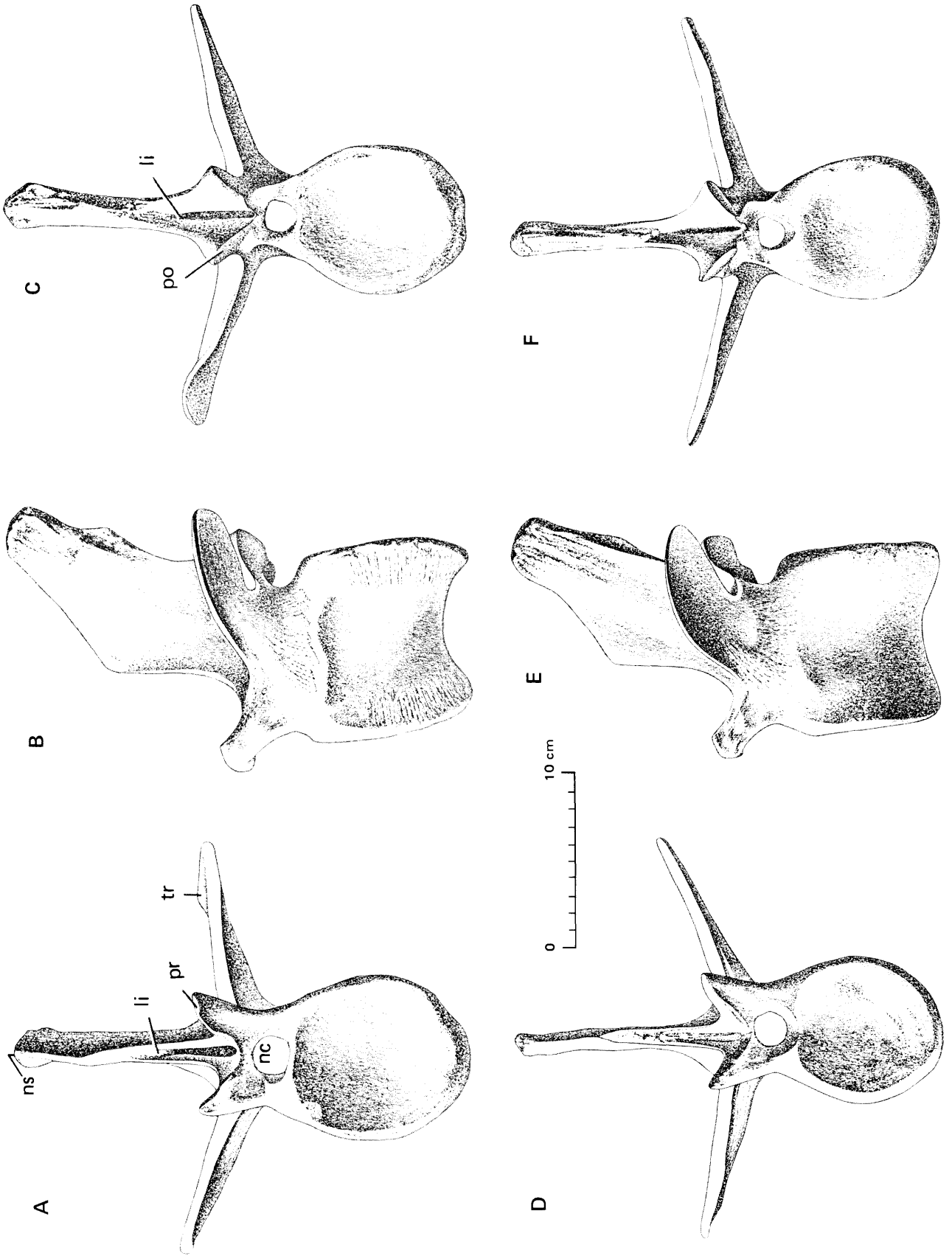
Plate 32. Thirteenth (A, B, C) and sixteenth (D, E, F) caudal vertebrae of *Allosaurus fragilis* in anterior (A, D), lateral (B, E), and posterior (C, F) views. Abbreviations: li–scar of interspinous ligament, nc–neural canal, ns–neural spine, po–postzygapophysis, pr–prezygapophysis, tr–transverse process.
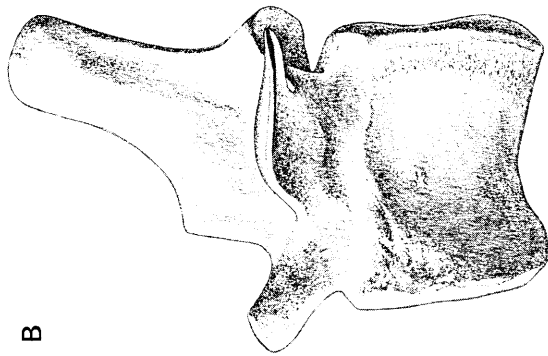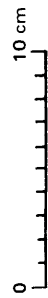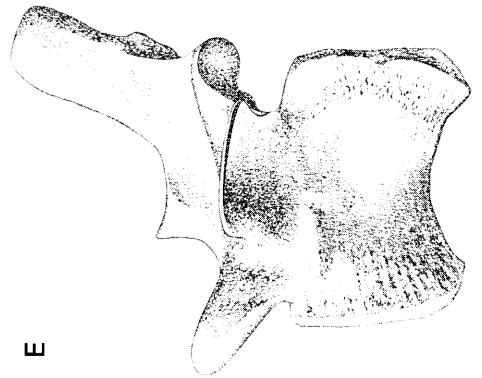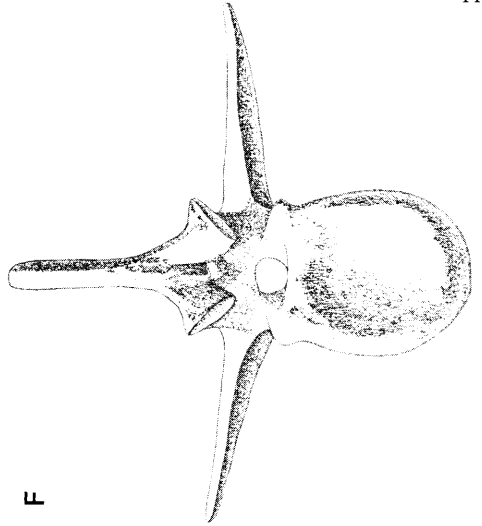
Plate 33. Nineteenth (A, B, C) and twenty-second (D, E, F) caudal vertebrae of *Allosaurus fragilis* in anterior (A, D), lateral (B, E), and posterior (C, F) views. Abbreviations: li—scar of interspinous ligament, nc—neural canal, ns—neural spine, po—postzygapophysis, pr—prezygapophysis, tr—transverse process.
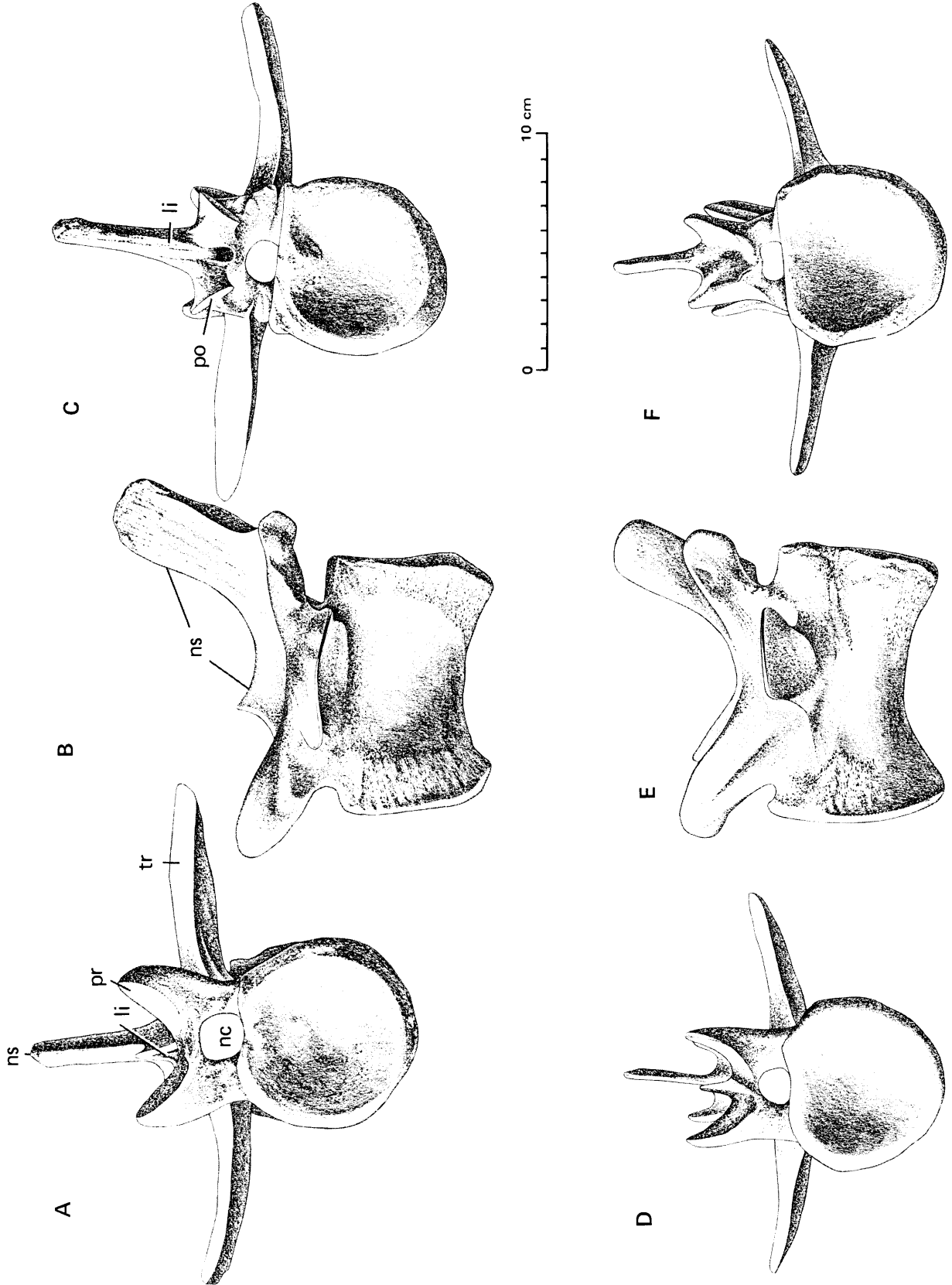
Plate 34. Twenty-fifth (A, B, C) and twenty-eighth (D, E) caudal vertebrae of *Allosaurus fragilis* in anterior (A), lateral (B, E), posterior (C), and dorsal (D) views. Abbreviations: li—scar of inter-spinous ligament, nc—neural canal, ns—neural spine, po—postzygapophysis, pr—prezygapophysis, tr—transverse process.
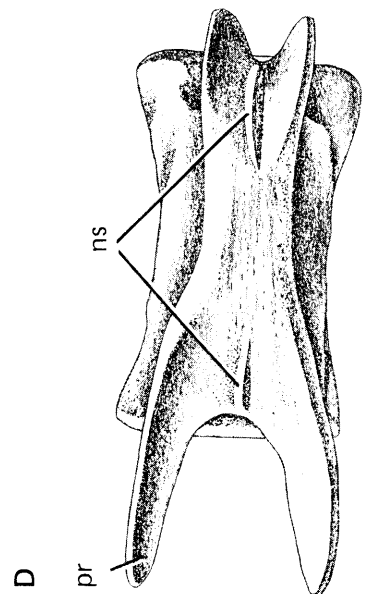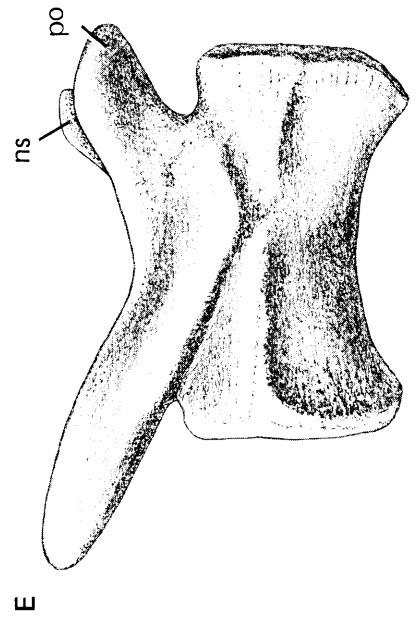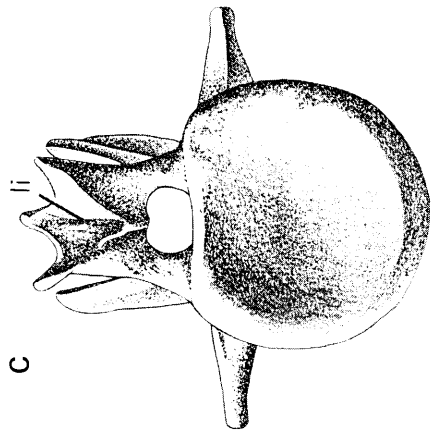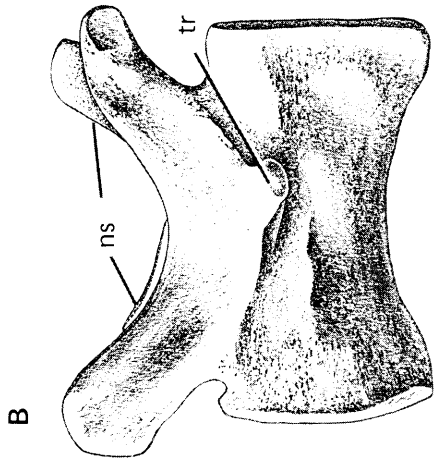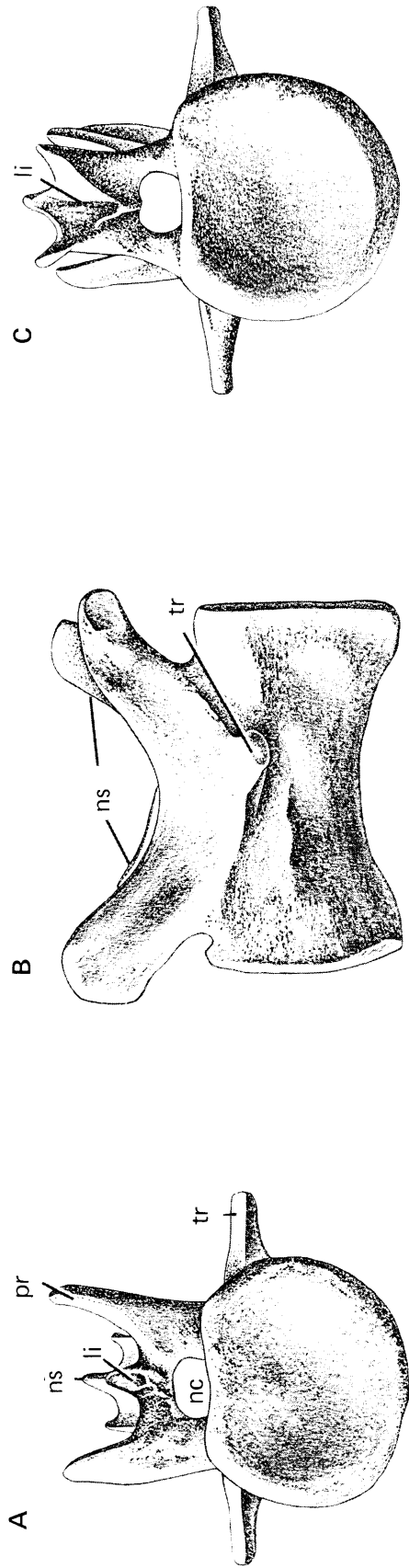
Plate 35. Thirty-first (A, B), thirty-fourth (C, D), thirty-seventh (E, F), and fortieth (G, H) caudal vertebrae of *Allosaurus fragilis* in dorsal (A, C, E, G) and lateral (B, D, F, H) views. Abbreviations: ns—neural spine, po—postzygapophysis, pr—prezygapophysis.
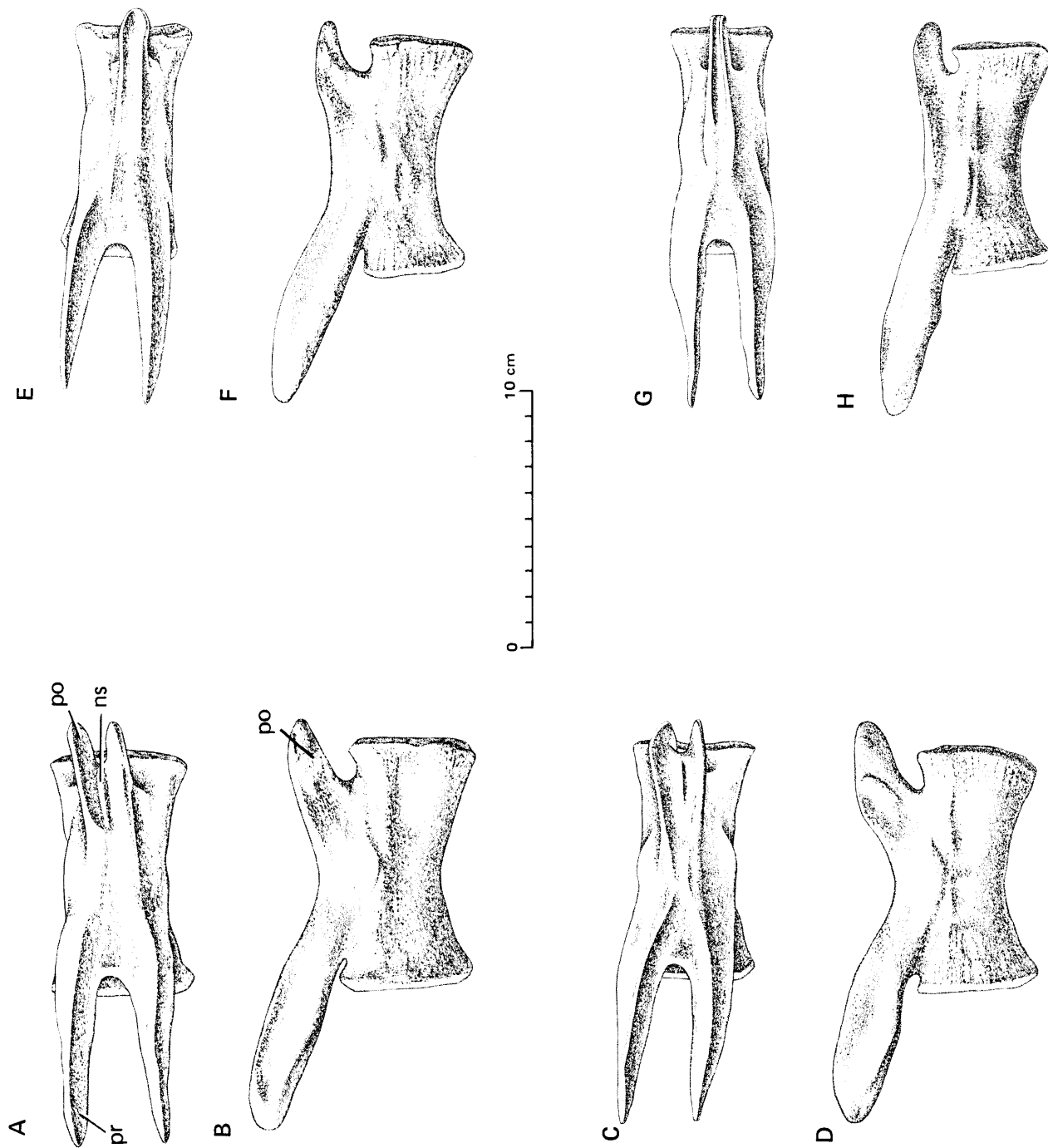
Plate 36. Forty-third (A, B), forty-sixth (C, D), forty-ninth (E, F), and fifty-first (G, H) caudal vertebrae of *Allosaurus fragilis* in dorsal (A, C, E, G) and lateral (B, D, F, H) views. Abbreviations: po—postzygapophysis, pr—prezygapophysis.
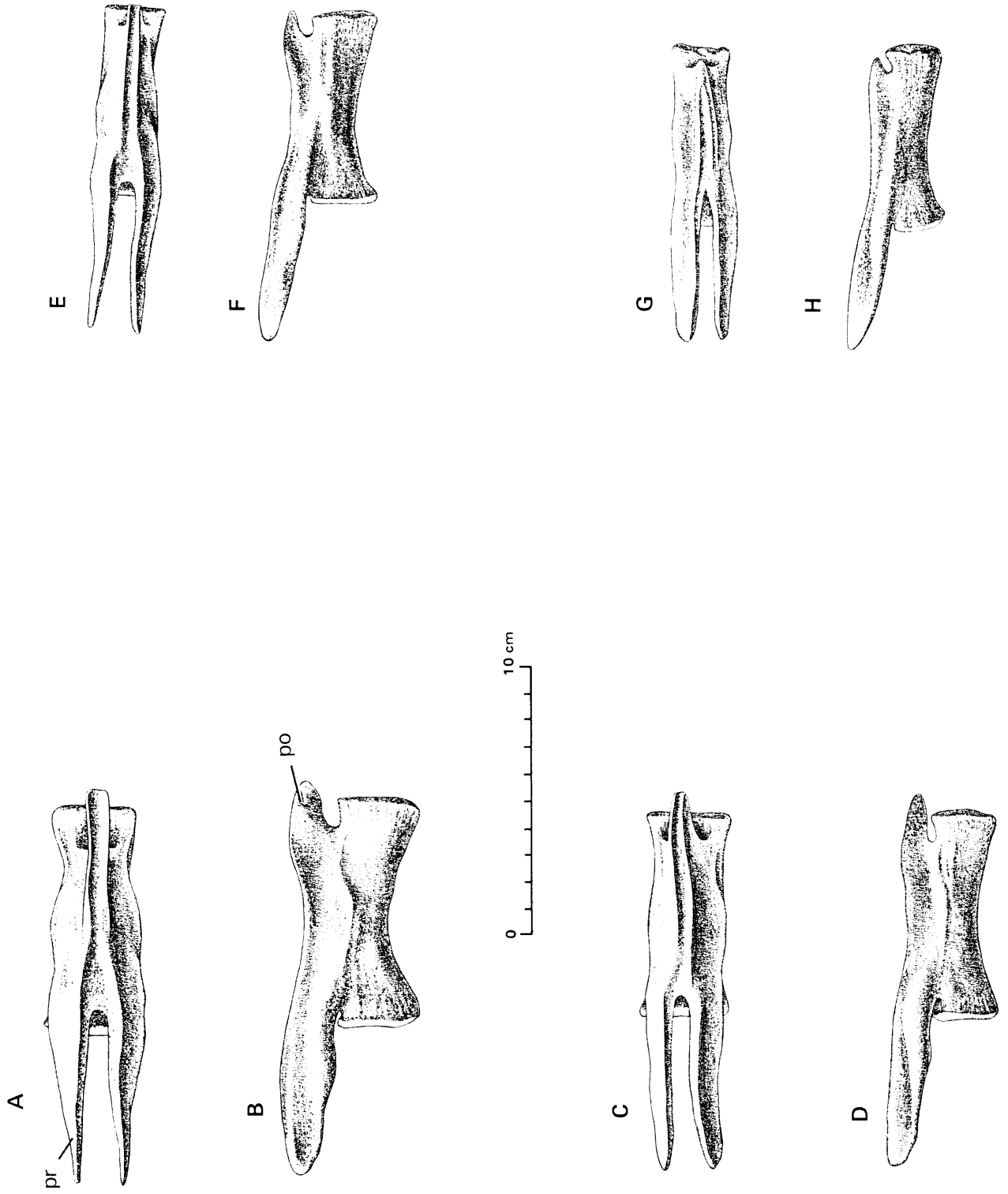
Plate 37. First (A, B, C), fifth (D), tenth (E), fifteenth (F), twentieth
(G, H, I, J), twenty-fifth (K, L, M, N), thirtieth (O), thirty-fifth
(P), fortieth (Q), and forty-fifth (R, S, T, U) chevrons of *Allo-
saurus fragilis* in anterior (A, H, L, S), lateral (B, D, E, F, I, M, O,
P, Q, T), posterior (C, J, N, U), and dorsal (G, K, R) views.
Abbreviation: hc—haemal canal.
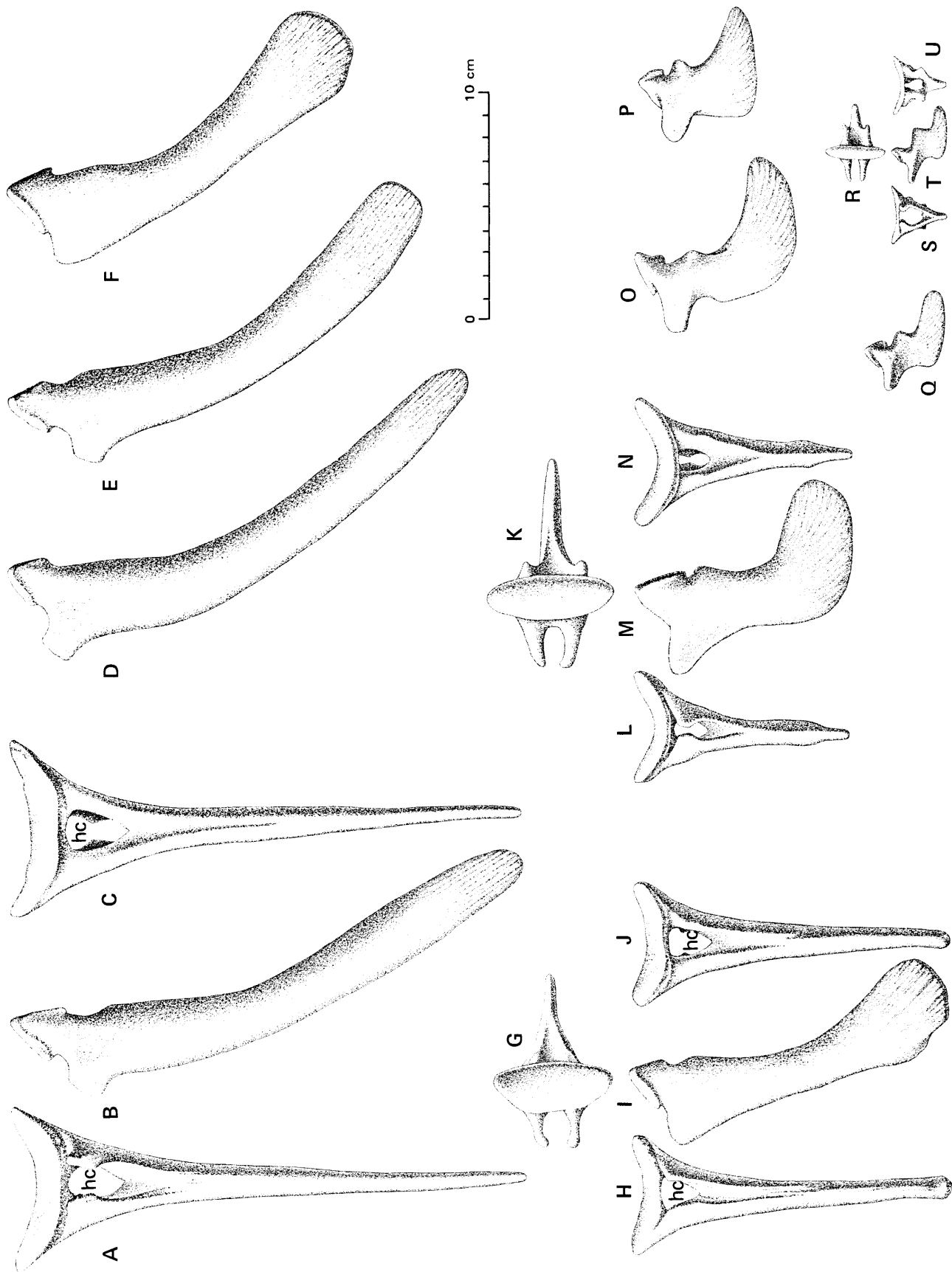
Plate 38. Ribs of the axis (A) and the third (B), fourth (C), fifth (D), sixth (E), seventh (F), eighth (G), and ninth (H) cervical vertebrae of *Allosaurus fragilis* in anterior and lateral views. Abbreviations: c—capitulum, s—shaft, tu—tuberculum.

Plate 39. Ribs of the first (A), third (B), fifth (C), and seventh (D) dorsal vertebrae of *Allosaurus fragilis* in anterior view. Abbreviations: c—capitulum, s—shaft, tu—tuberculum.
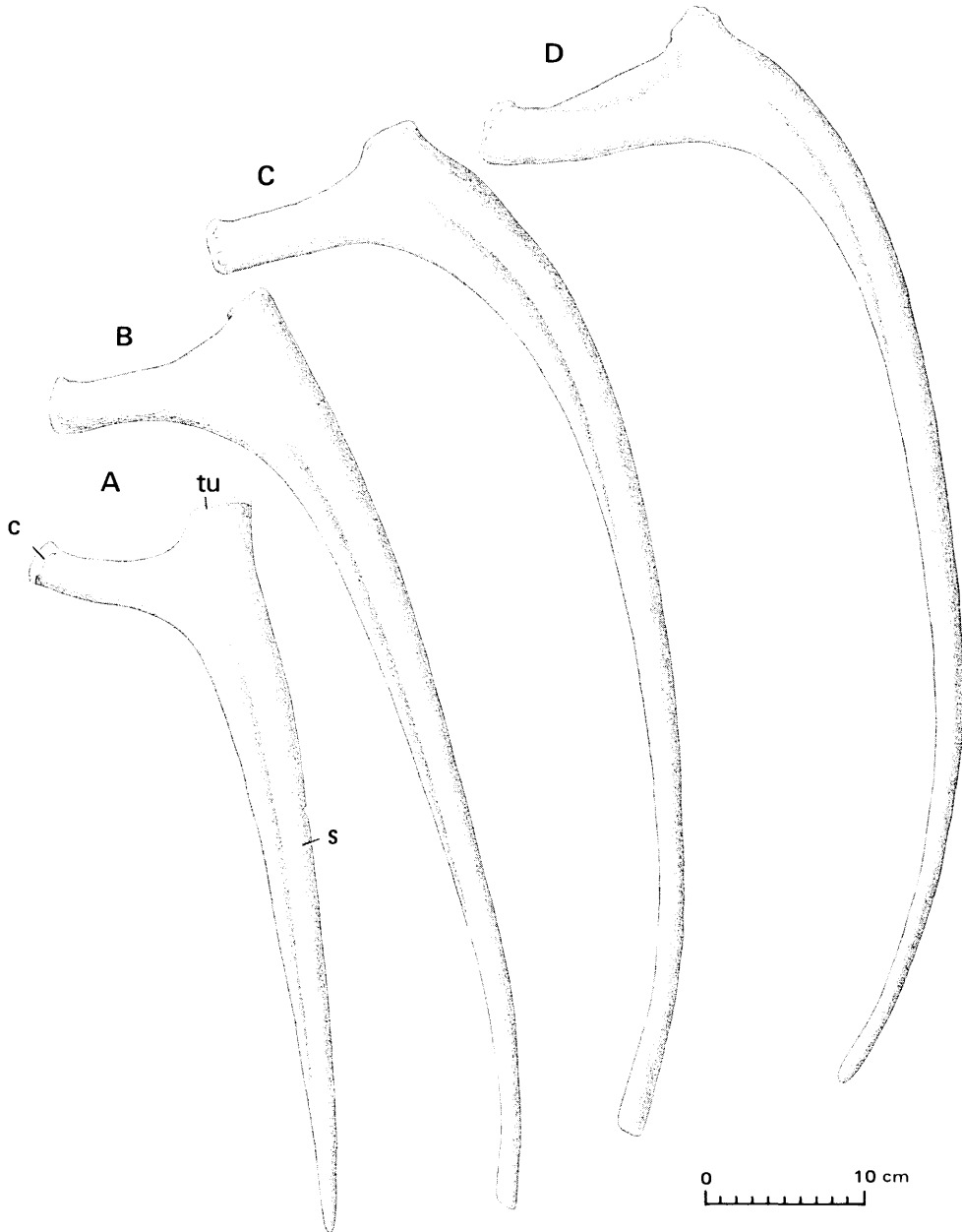
Plate 40. Ribs of the ninth (A), eleventh (B), thirteenth (C), and fourteenth (D, E) dorsal vertebrae of *Allosaurus fragilis* in anterior (A, B, C, D) and posterior (E) views. Abbreviations: c—capitulum, s—shaft, tu—tuberculum.

0   10 cm
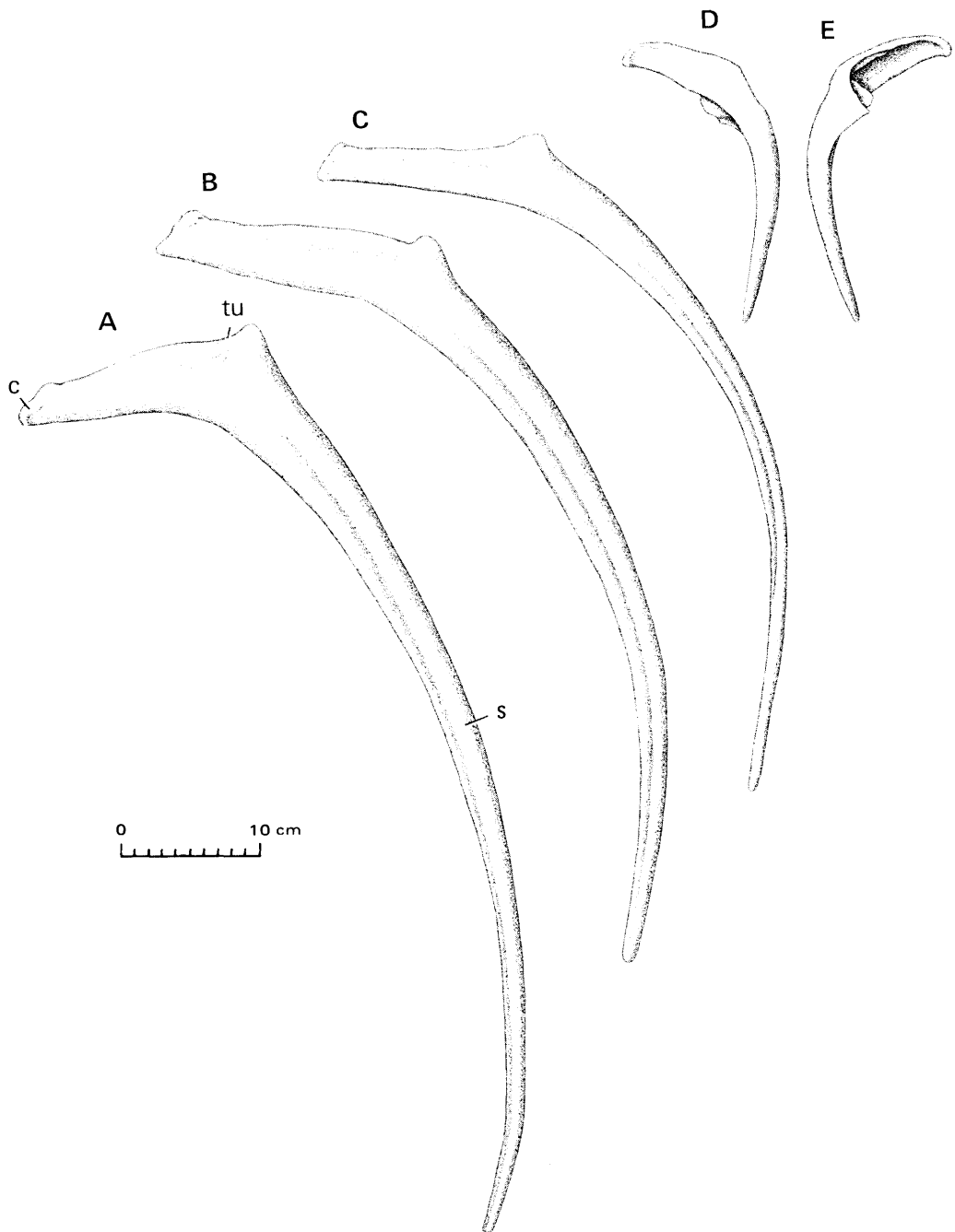
Plate 41. Left coracoid (A, B, D, G) and scapula (C, D, E, F) of *Allosaurus fragilis* in lateral (A, C), medial (E, G), proximal (B, F), and ventral (D) views. Abbreviations: ac—acromial process, bi—biceps tubercle, cf—coracoid foramen, g—glenoid cavity.
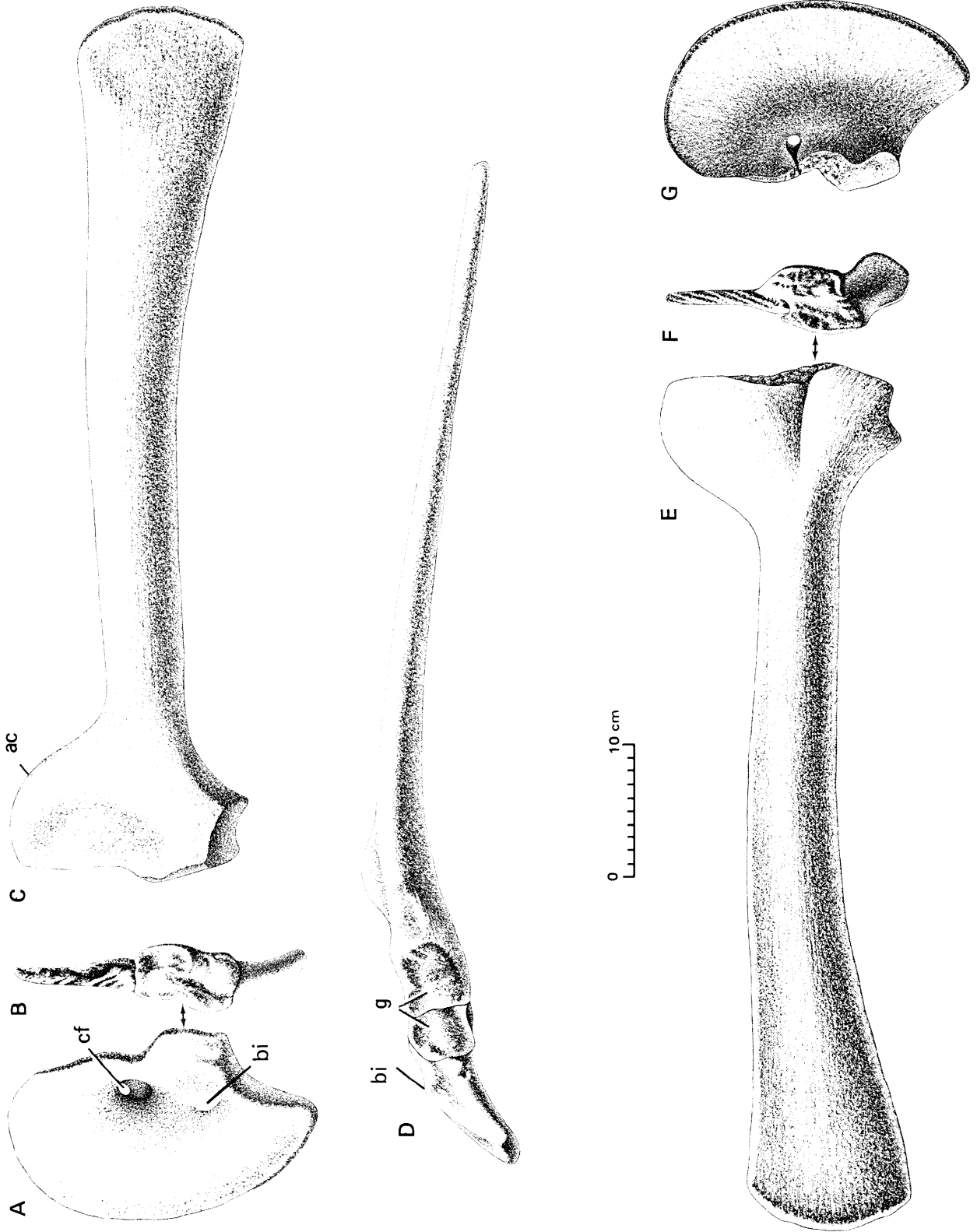
Plate 42. Left humerus (A, B), radius (C, E), and ulna (D, F) of *Allosaurus fragilis* in anterior (A), lateral (C, D), posterior (B), and medial (E, F) views. Abbreviations: dp–deltopectoral crest, f–foramen, he–head of humerus, hu–attachment of humeroradialis muscle, it–internal tuberosity, o–olecranon process, rc–radial condyle, ru–distal articulation of radius and ulna, uc–ulnar condyle.
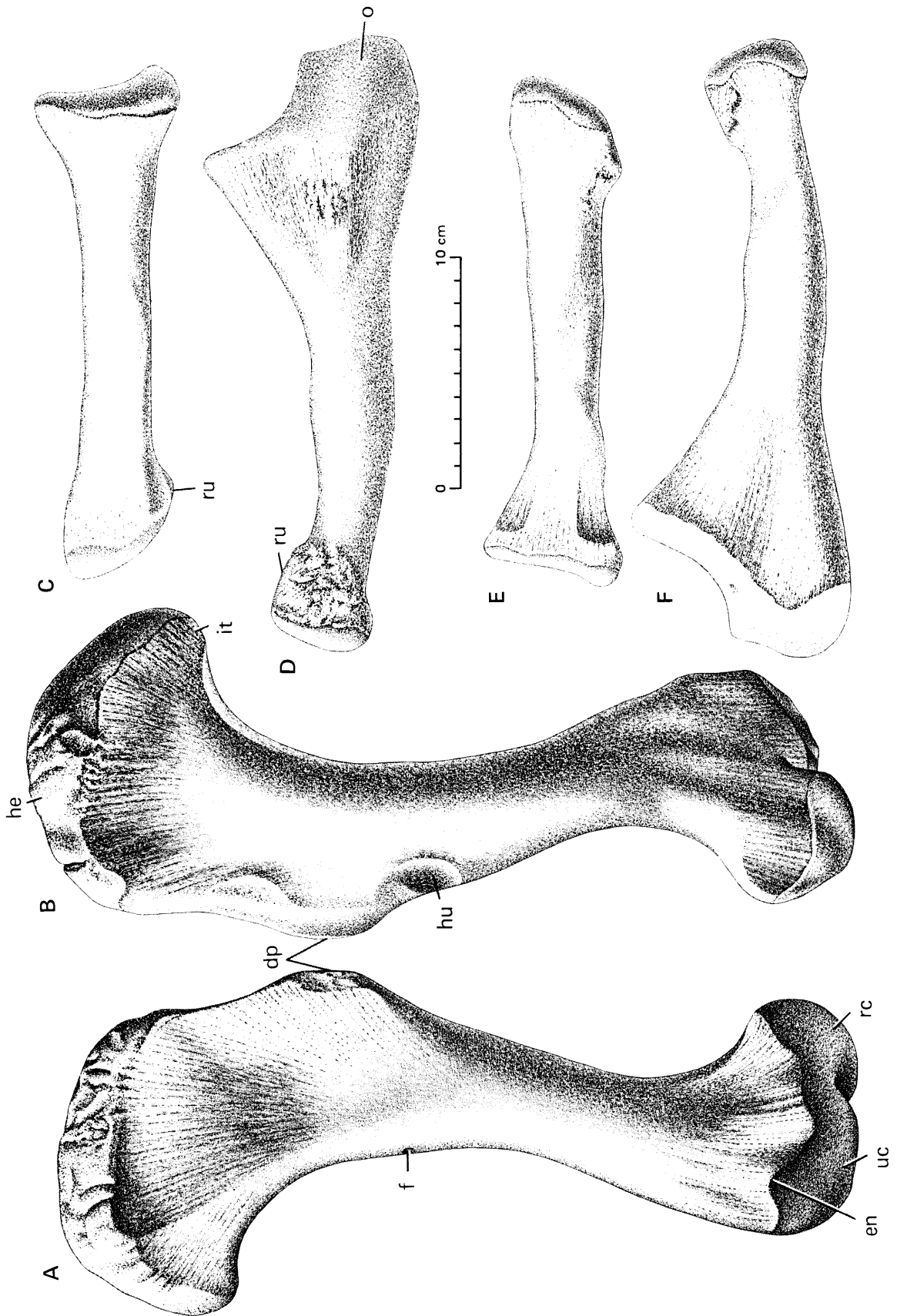
Plate 43. Left manus of *Allosaurus fragilis* in superior (dorsal) view. Abbreviations: 1—carpal 1, 2—carpal 2, mc—metacarpal, ra—radiale, un—ulnare(?).

ra

1

2

un

mc

mc

mc

I

II

III

0   10 cm
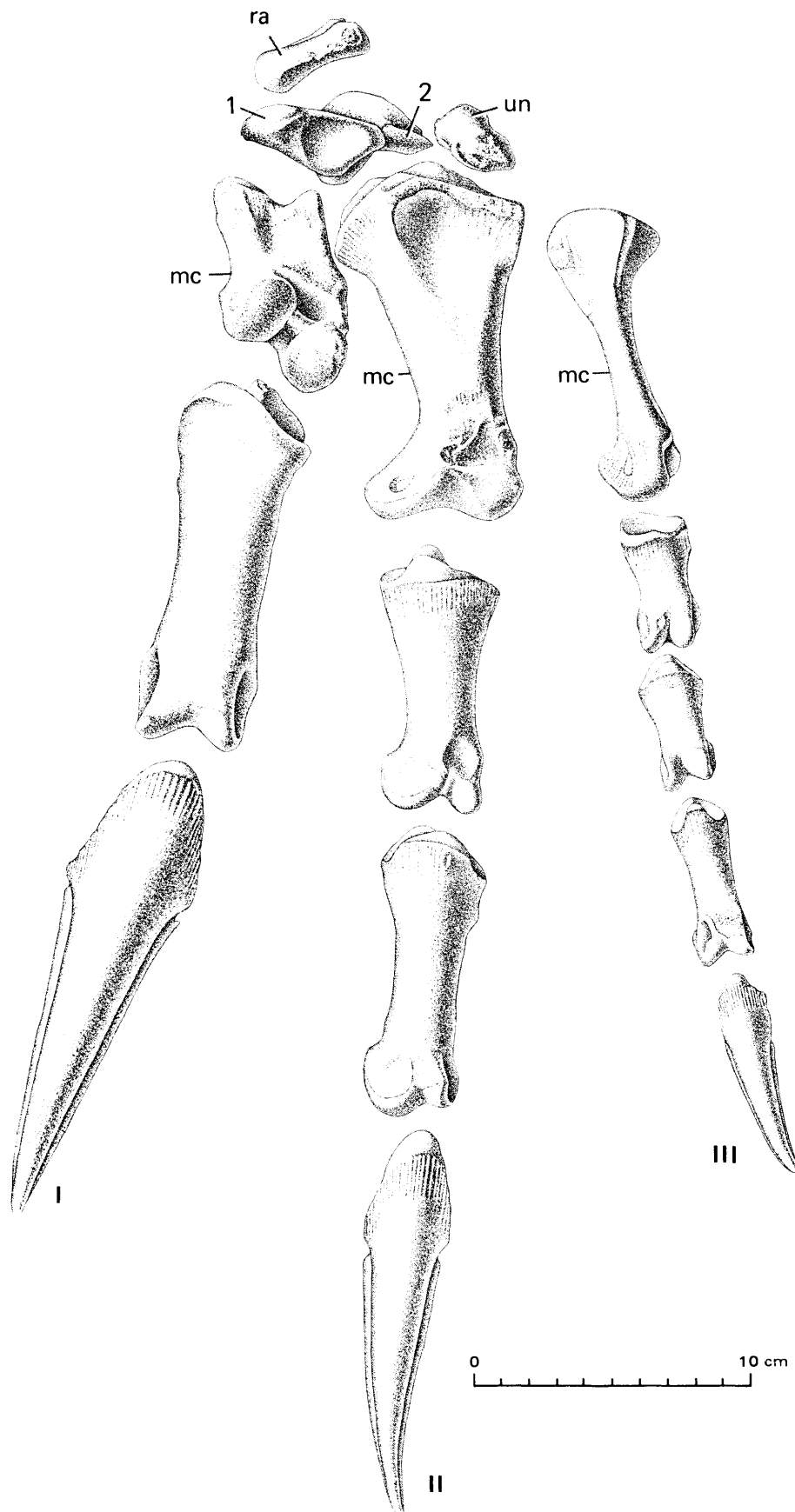
Plate 44. Left manus of *Allosaurus fragilis* in lateral view with articular surfaces shaded. Abbreviation: mc–metacarpal.
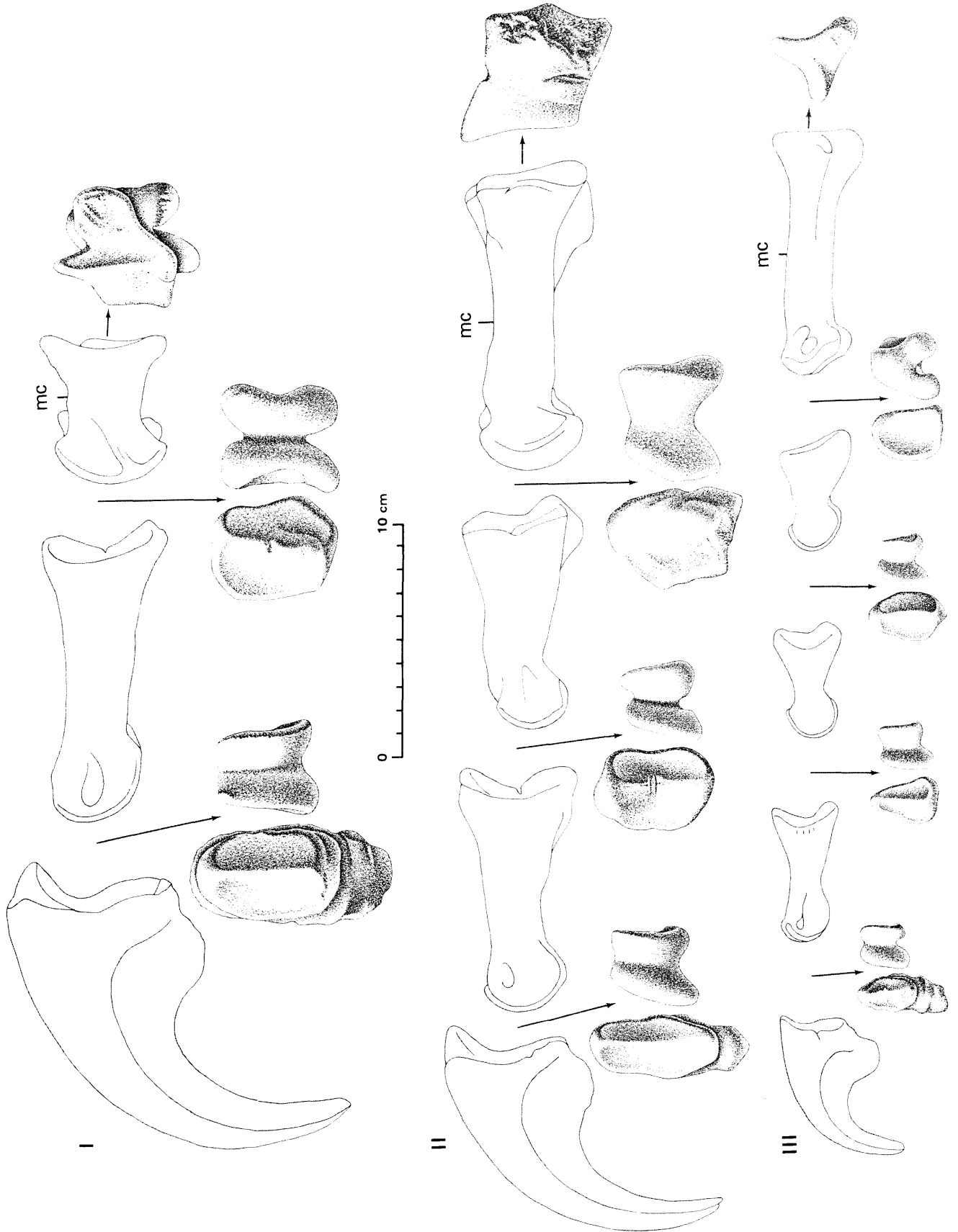
Plate 45. Left manus of *Allosaurus fragilis* in palmar (ventral) view.
Abbreviations: 1—carpal 1, 2—carpal 2, mc—metacarpal, ra—radiale,
un—ulnare(?).
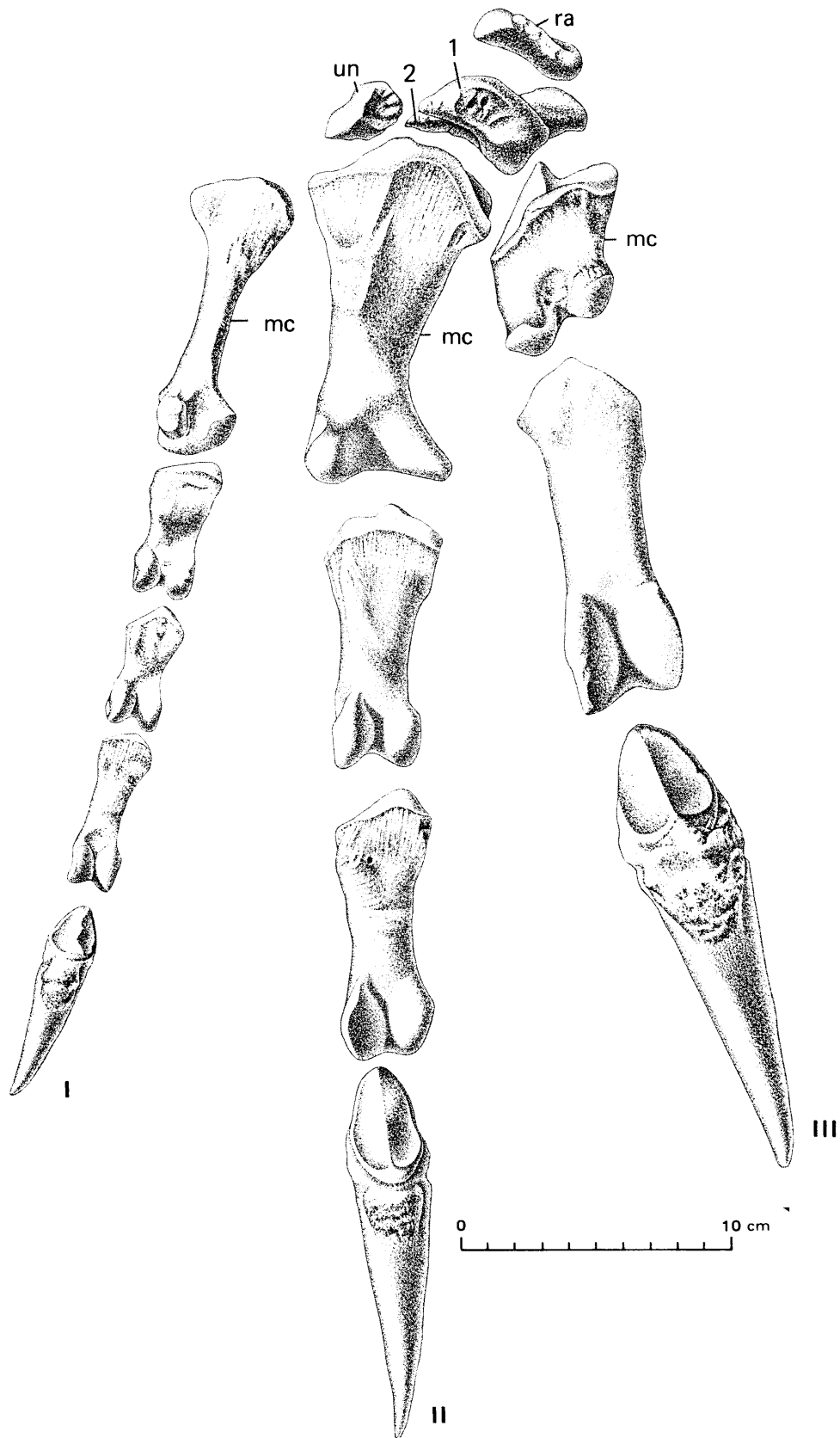
Plate 46. Left ilium of *Allosaurus fragilis* in lateral (A) and ventral (B) views. Abbreviations: act–acetabulum, anb–anterior blade, f–foramen, isc–ischiac peduncle, meb–medial blade, pob–posterior blade, pu–pubic peduncle.
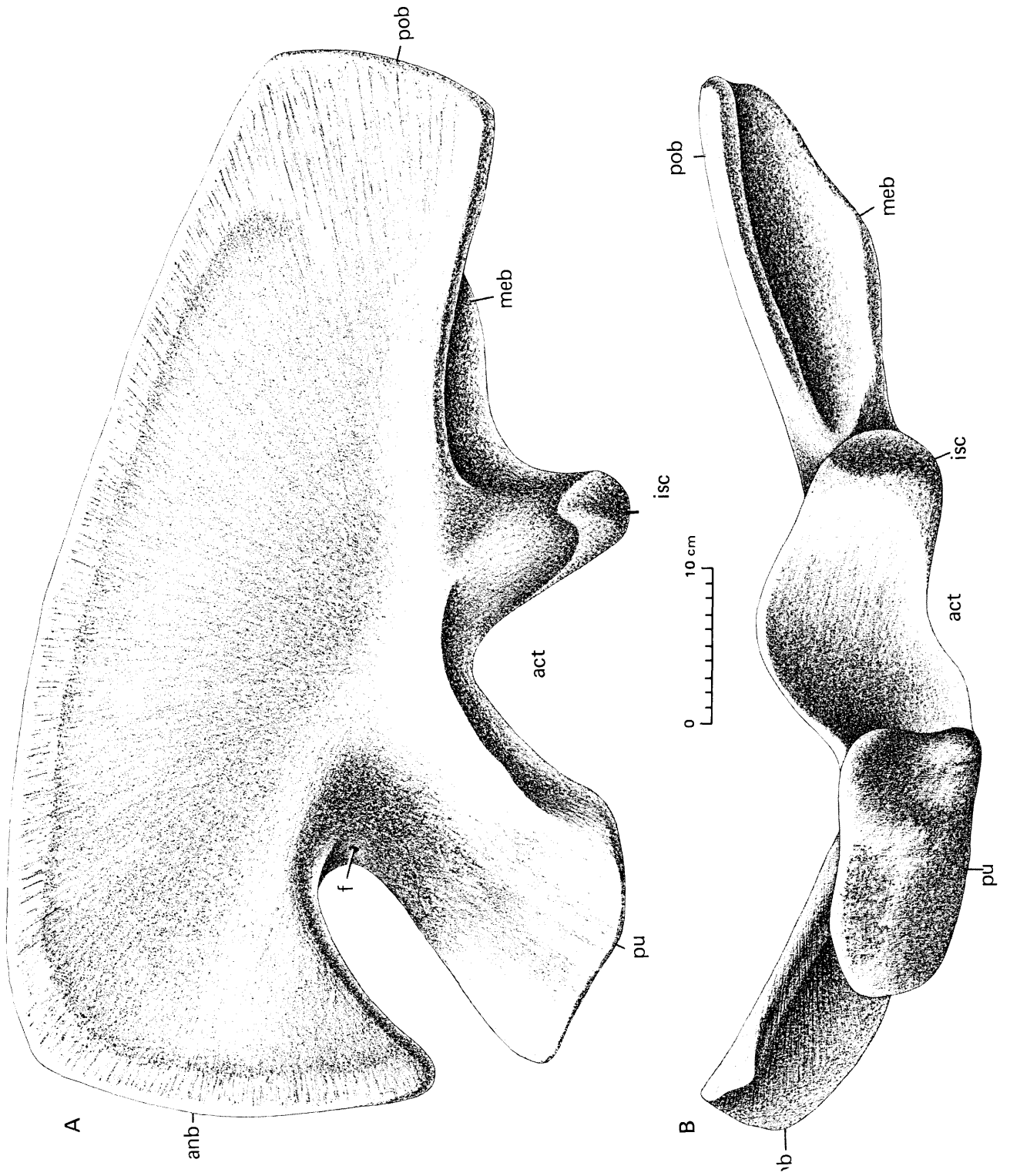
Plate 47. Left ilium of *Allosaurus fragilis* in dorsal (A) and medial (B) views. Abbreviations: act—acetabulum, anb—anterior blade, isc—ischiac peduncle, meb—medial blade, pob—posterior blade, pu—pubic peduncle, sr_2, sr_3, sr_4, sr_5—attachment scars of the sacral ribs, tr_1, tr_2, tr_3, tr_4, tr_5—attachment scars of transverse processes.
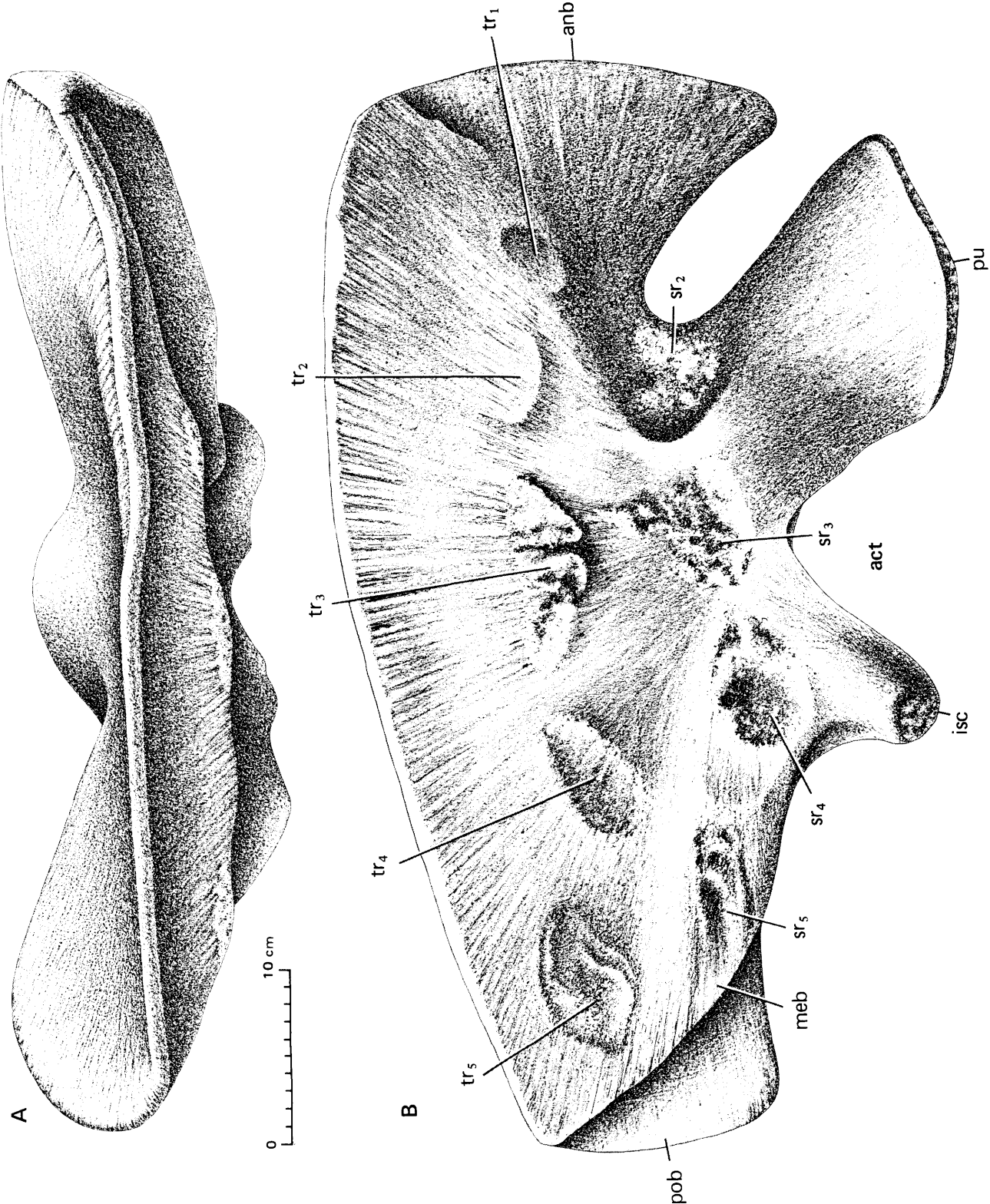
Plate 48. Left pubis (A) and left ischium (B, C) of *Allosaurus fragilis* in lateral (A, B) and proximal (C) views. Abbreviations: act—border of acetabulum, il—iliac articulation, isc—ischiac articulation, on—obturator notch, op—obturator process, pu—pubic articulation.
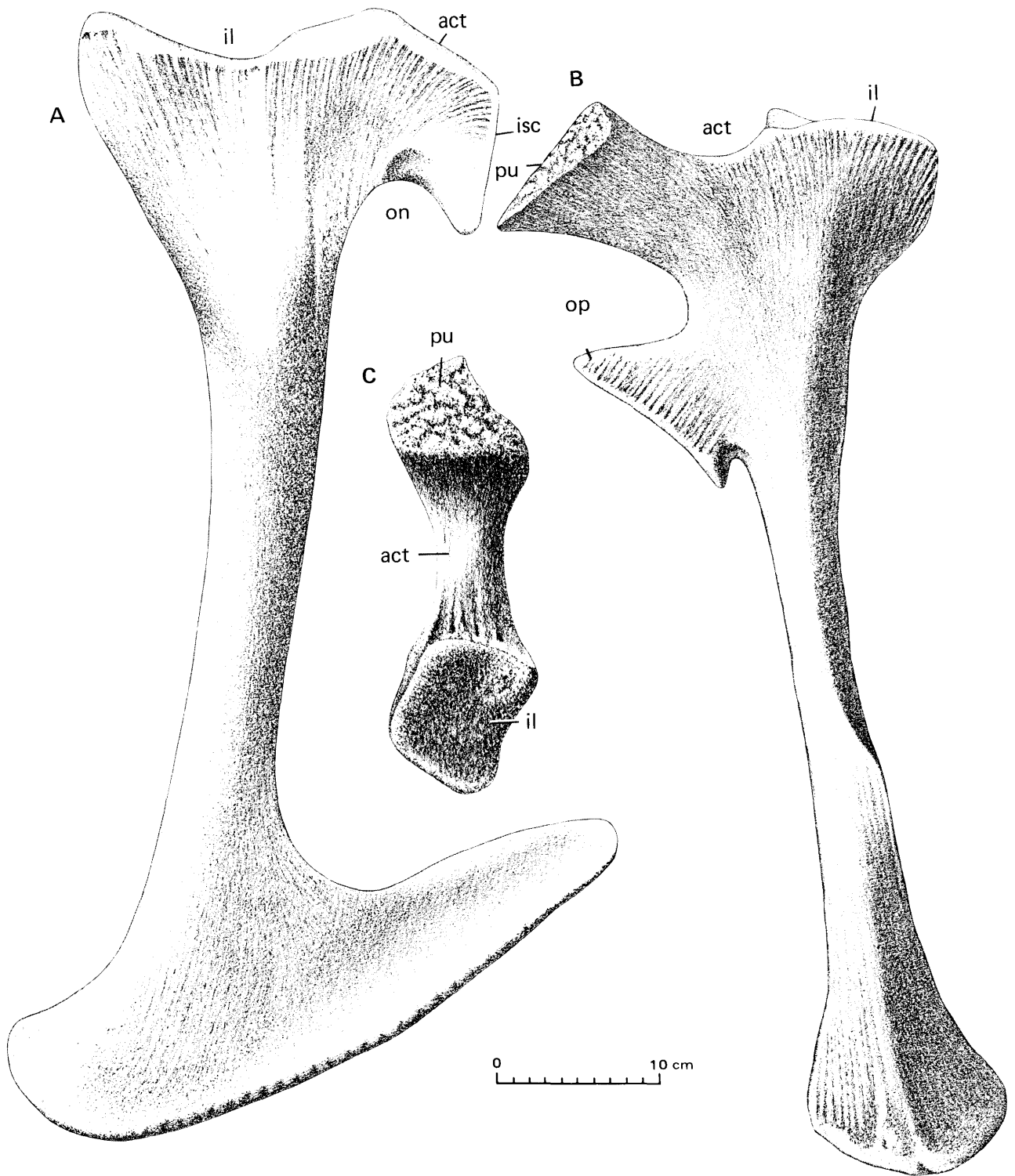
Plate 49. Left ischium (A) and left pubis (B, C) of *Allosaurus fragilis* in medial (A, B) and proximal (C) views. Abbreviations: act—border of acetabulum, ds—distal symphysis, il—iliac articulation, isc—ischiac articulation, ms—medial symphysis, on—obturator notch, op—obturator process, pu—pubic articulation.
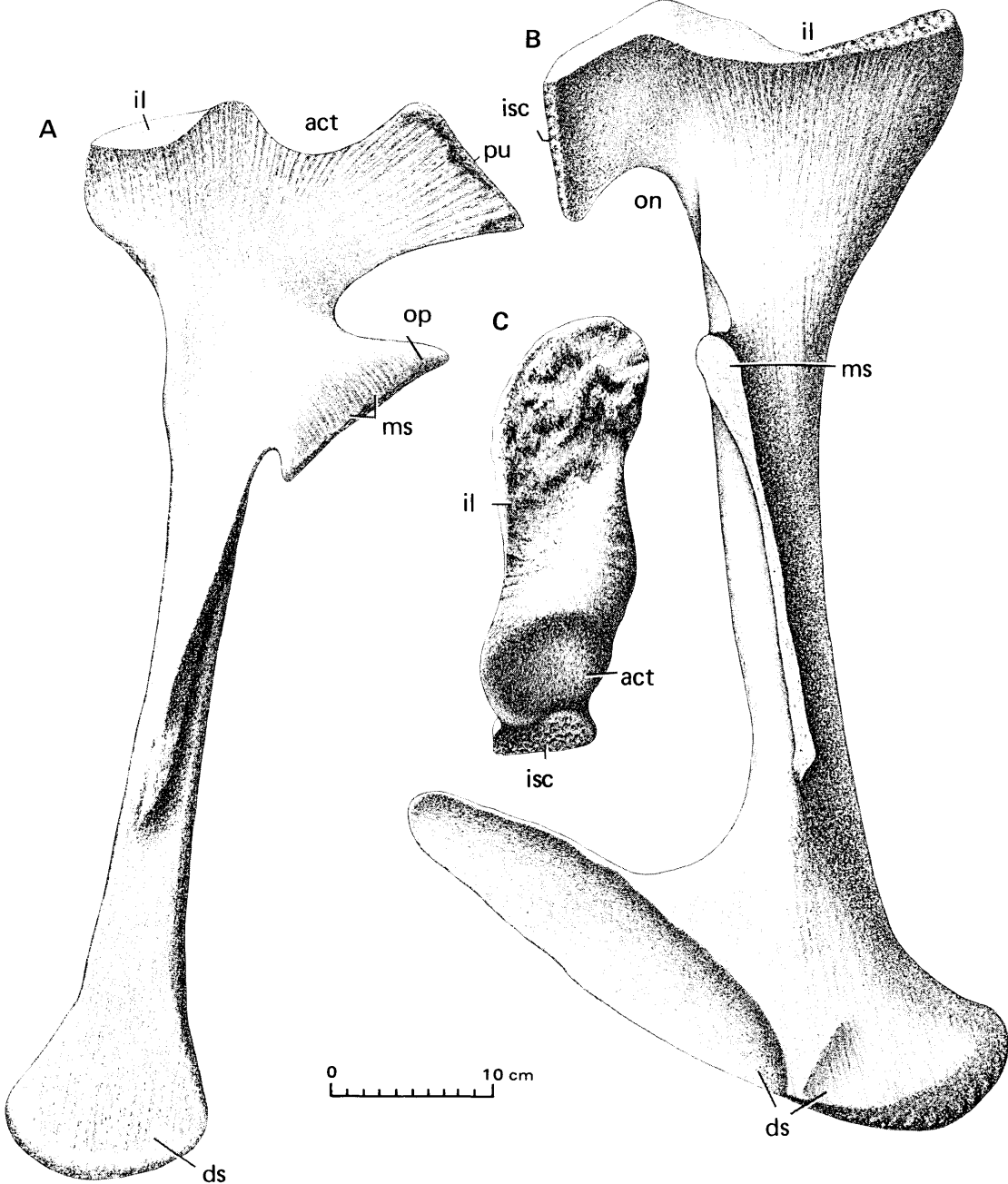
Plate 50. Left femur of *Allosaurus fragilis* in anterior (A), lateral (B), posterior (C), and medial (D) views. Abbreviations: f—foramen, fib—fibular condyle, h—head, lt—lesser trochanter, tib—tibial condyle, tr_4—fourth trochanter.
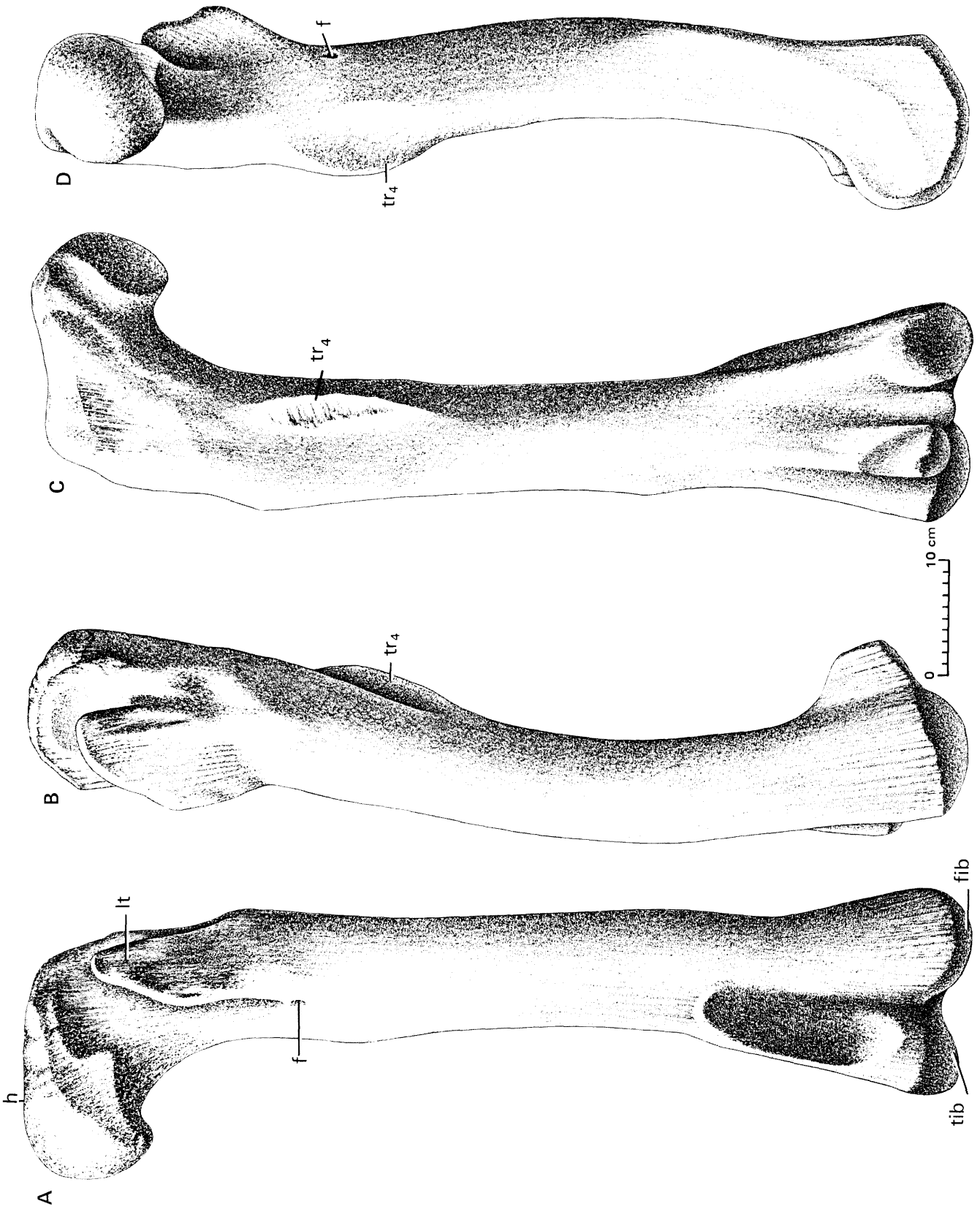
Plate 51. Left tibia (A, B, C, E) and astragalus (D) of *Allosaurus fragilis* in lateral (A, D), anterior (B), medial (C), and distal (E) views. Abbreviations: ast—contact with astragalus, ca—contact with calcaneum, cn—cnemial crest, f—foramen.
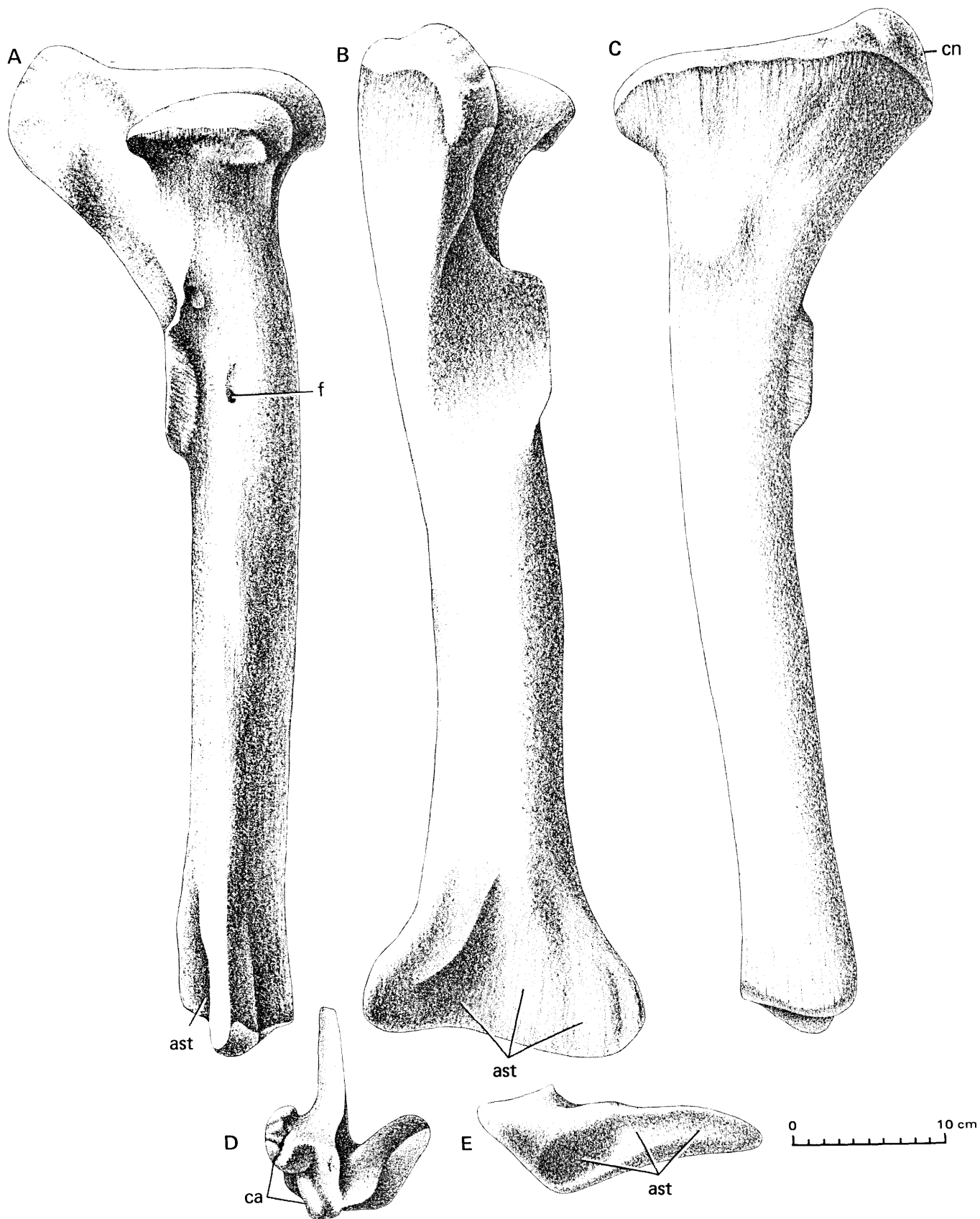
Plate 52. Left tibia (A, D), fibula (A, B, C, D), astragalus (A, E, G), and calcaneum (A, E, F, H) of *Allosaurus fragilis* in anterior (A, G), lateral (B, F), medial (C, H), proximal (D), and distal (E) views. Abbreviations: ast–astragalus, ca–calcaneum, Fi–fibula, T–tibia.
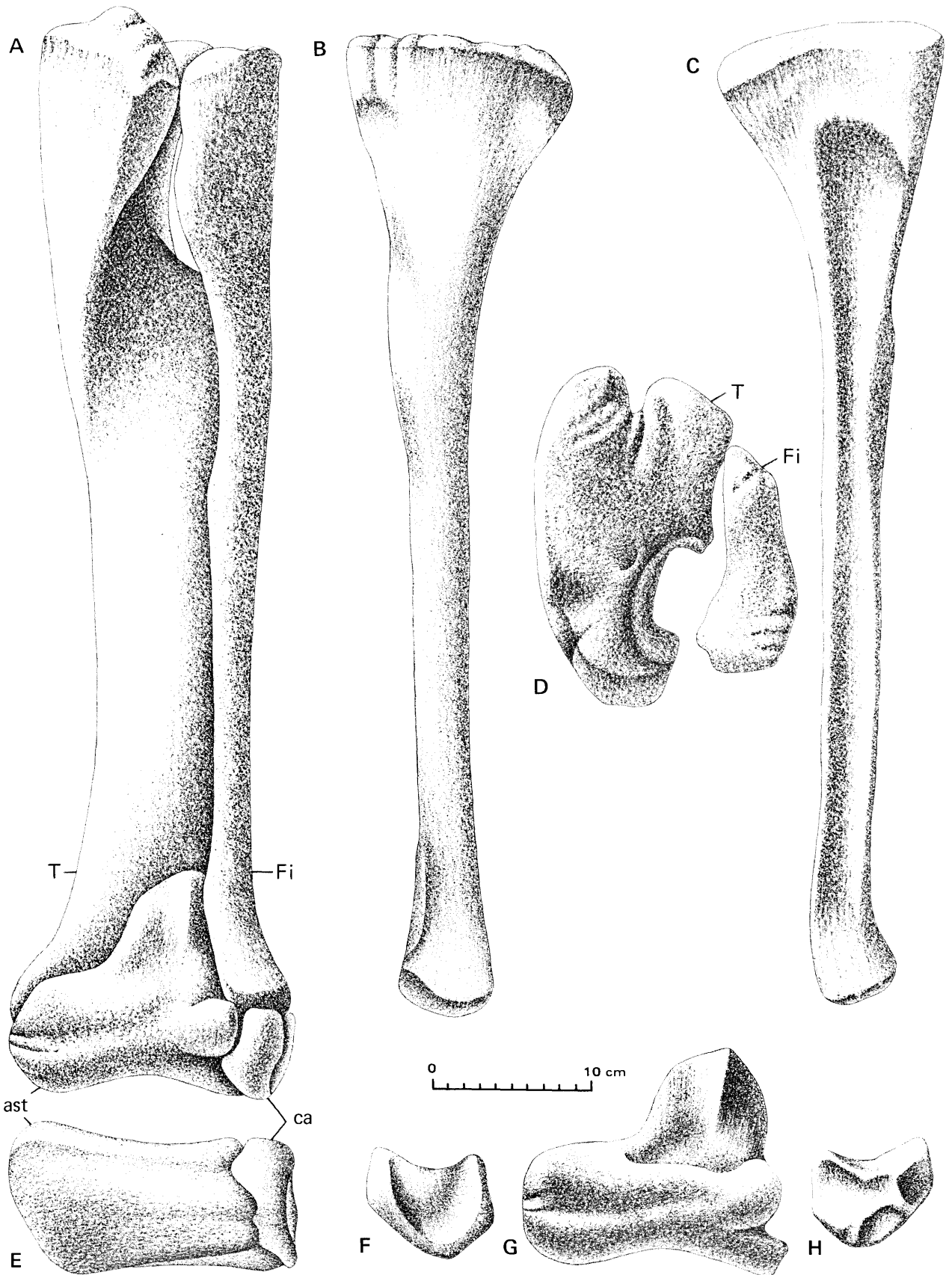
Plate 53. Left pes of *Allosaurus fragilis* in superior view. Abbreviation: mt—metatarsal.

mt

mt

mt

mt

I

II

III

IV

0   10 cm

Plate 54. Left pes of *Allosaurus fragilis* in lateral view with articular surfaces shaded. Abbreviation: mt—metatarsal.
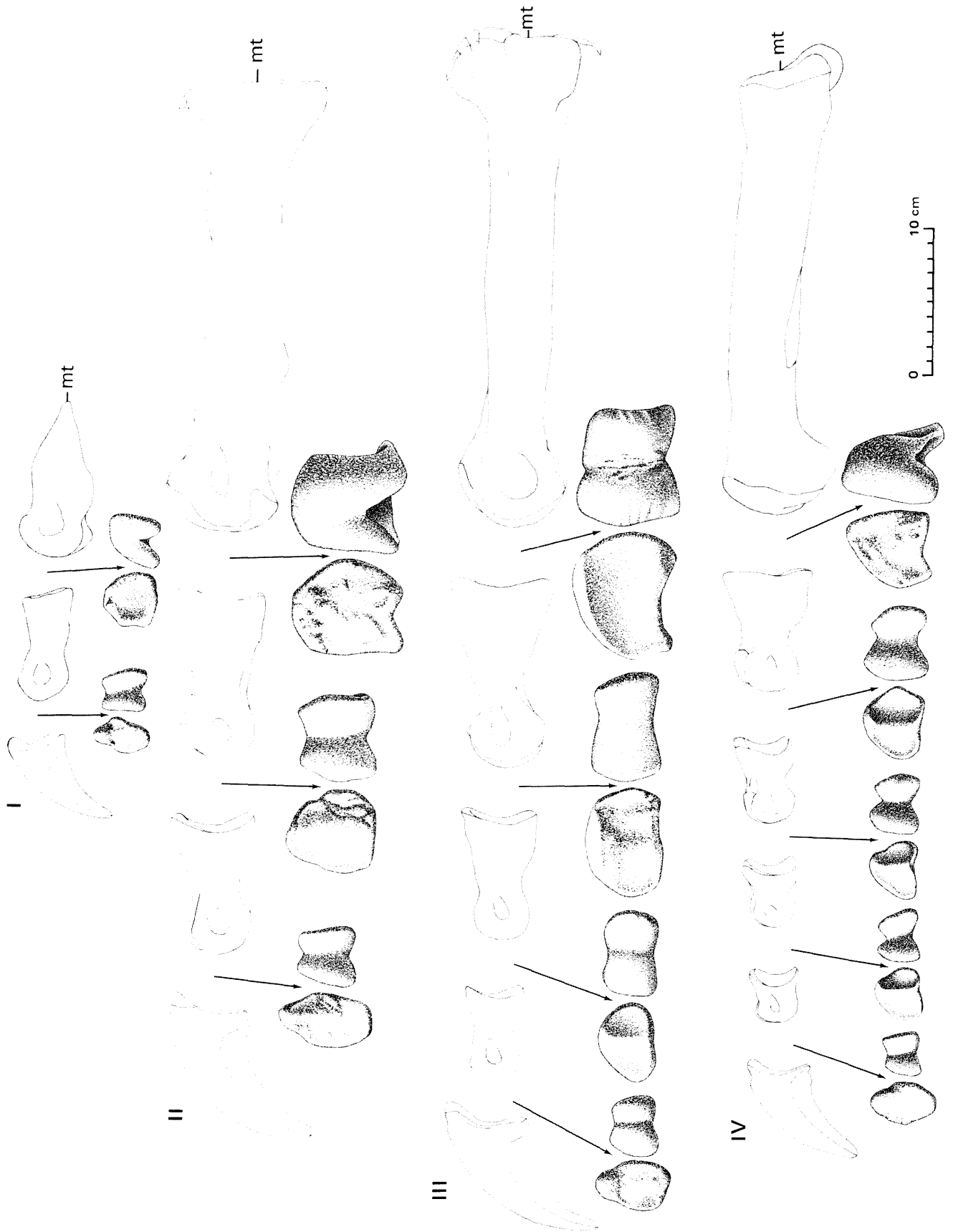
Plate 55. Left pes of *Allosaurus fragilis* in inferior view. Upper left is proximal view of metatarsals in articulation. Abbreviation: mt—metatarsal.

mt

mt

mt

mt

IV

III

II

I

0   10 cm