



Osteology of *Orodromeus makelai* and the phylogeny of basal ornithopod dinosaurs
by Rodney Dwayne Scheetz

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in
Biological Sciences

Montana State University

© Copyright by Rodney Dwayne Scheetz (1999)

Abstract:

The small Upper Cretaceous ornithopod dinosaur *Orodromeus makelai*, possesses many tooth traits reminiscent of Triassic fabrosaur. Determining whether these teeth were retained from a primitive lineage or independently derived within *Orodromeus* prompted a critical examination and ultimate revision of hypsilophodontid and basal ornithopod phylogeny. The revision of the Hypsilophodontidae resulted in a dissolution of the group into a pectinate grade of dinosaurs with a concomitant trend in increased size and herbivorous efficiency. Phylogenetic context reveals *Orodromeus* as nested within ornithopods with established herbivorous adaptations. Anomalous triangular teeth and high angle occlusion in *Orodromeus* is thought indicative of a shift to insectivory, possibly retained from the neonate condition. Other juvenile conditions, such as large orbits and unfused elements in mature specimens, together with rapid deceleration of radial femoral bone growth through ontogeny is suggestive of neoteny. Continued histological studies of fossil taxa, together with a clear understanding of relationships, would help to identify heterochronic shifts in evolution.

Analysis of 20 taxa, using 124 morphological characters, indicates the pandemic distribution of small ornithopod taxa occurred prior to the Upper Jurassic. Although hadrosaurs diversified in the Upper Cretaceous as did angiosperms, most all major herbivorous adaptations were in place within ornithopods prior to the first occurrence of angiosperms in North America.

OSTEOLOGY OF *ORODROMEUS MAKELAI* AND THE
PHYLOGENY OF BASAL ORNITHOPOD DINOSAURS

by

Rodney Dwayne Scheetz

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Biological Sciences

MONTANA STATE UNIVERSITY-BOZEMAN
Bozeman, Montana

April 1999

© COPYRIGHT

by

Rodney Dwayne Scheetz

1999

All Rights Reserved

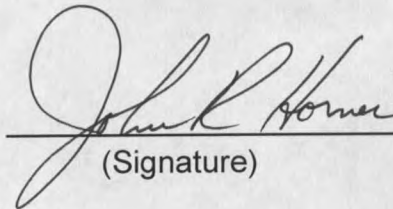
D378
Sch 225

APPROVAL

of a thesis submitted by
Rodney Dwayne Scheetz

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

John R. Horner



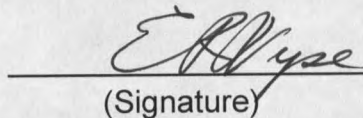
(Signature)

4/23/99

(Date)

Approved for the Department of Biology

Dr. Ernest R. Vyse



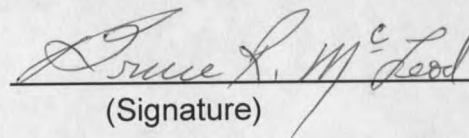
(Signature)

4/23/99

(Date)

Approved for the College of Graduate Studies

Dr. Bruce R. McLeod



(Signature)

5-3-99

(Date)

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a doctoral degree at Montana State University-Bozeman, I agree that the Library shall make it available to borrowers under rules of the Library. I further agree that copying of this thesis is allowable for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for extensive copying or reproduction of this thesis should be referred to University Microfilms International, 300 North Zeeb Road, Ann Arbor, Michigan 48106, to whom I have granted "the exclusive right to reproduce and distribute my dissertation in and from microform along with the non-exclusive right to reproduce and distribute my abstract in any format in whole or part."

Signature Rodney D. Scheetz

Date April 12, 1999

This work is dedicated to my mentor, Dr. James A. Jensen, for his contagious and enthusiastic curiosity. I will be forever grateful to him for sharing his eternal perspective of this world and this life.

ACKNOWLEDGMENTS

Without the merit of the works cited in the references, and the continuing work of Jack Horner and Dave Weishampel, this study would not have been conceived. Much appreciation goes to Jack Horner and the NSF (EAR-9219035) grant funded to him, Barbara Lee, the Dinosaur Society, and Museum of the Rockies for supporting this study. The illustrations were provided through the talents of Frankie Jackson, who together with Jack Horner, Dave Varricchio, Kristin Junette, Mary Schweitzer, Yoshi Katsura, Kristi Currie, Oliver Rauhut, Dan Brinkman, Dale Winkler, and Bob Bakker, served as a sounding board for ideas and discussion. Their insight and suggestions are greatly appreciated. Prompt and meticulous preparation of specimens and histological slides were accomplished through the talents of Carrie Ancell and Ellen Lamb. Brooks Britt and Nita Kroniger provided the nagging and technical support needed to finish, and they deserve much credit. I am grateful to Ken Statdman, Cliff Miles, Lou Jacobs, Mary Dawson, Mark Norell, Hans Peter Schultze, Angela Milner, Jon Storer, Hans-Dieter Sues, Chuck Schaaf, Mary Ann Turner, and Michael Brett-Surman for letting me study specimens in their care. Thanks goes to my committee members: Jack Horner, Dave Weishampel, Kevin O'Neill, Matt Lavin, Jim Schmidt, Lynn Irby, and Sandy Osborne. Most importantly is the support provided by my best friend and wife, Wilfreta, who, among the many things she did, insured I not miss-out on having a life while in the trenches of a dissertation.

TABLE OF CONTENTS

	Page
LIST OF TABLES	ix
LIST OF FIGURES.....	x
LIST OF NOMENCLATURE AND ABBREVIATIONS	xi
LIST OF INSTITUTIONAL ABBREVIATIONS	xiv
ABSTRACT	xv
INTRODUCTION	1
Previous Work on <i>Orodromeus</i>	1
Stratigraphic Context	3
Heterochrony	5
Specimens used for Description	9
<i>ORODROMEUS</i> DESCRIBED	10
<i>Orodromeus</i> Morphology	10
The Skull	10
Premaxilla	13
Maxilla	14
Lacrimal	17
Supraorbital	17
Prefrontal	19
Frontal	19
Parietal	20
Postorbital	21
Jugal	22
Quadratojugal	23
Quadrate	24
Squamosal	25
Supraoccipital	25
Opisthotic and exoccipitals	27
Prootic	28
Laterosphenoid	29
Basisphenoid	29
Pterygoid, palatine, and vomer	30

TABLE OF CONTENTS--Continued

Basioccipital	31
Dentary	31
Elements of the Posterior Jaw	33
The Postcrania	34
Proatlas, Atlas & Axis	34
Cervical Vertebrae	36
Dorsal Vertebrae	41
Sacral Vertebrae	45
Caudal Vertebrae	47
Scapula	50
Coracoid	52
Sternal	53
Humerus	53
Ulna	55
Radius	55
Manus	55
Ilium	55
Ischium	57
Pubis	59
Femur	61
Tibia	65
Fibula	68
Ankle	68
Foot	70
Ontogeny	73
Histology	77
<i>Dryosaurus</i> Ontohistology	79
<i>Orodromeus</i> Ontohistology	85
Comparative Growth Rates	89
PHYLOGENY	92
Ornithopod Classification	92
Methods	95
Results	100
Character Summary	100
Evolutionary Trends	103
REFERENCES CITED	107
APPENDICES	121
Appendix A — <i>Orodromeus</i> Specimens Studied	122
Appendix B — Taxa, Specimens, & References	128

TABLE OF CONTENTS — Continued

Appendix C — Phylogenetic Analysis	134
Cladogram of Basal Ornithopod Phylogeny	135
Phylogram of Basal Ornithopod Phylogeny	136
Apomorphy List	137
Apomorphy Explanations	144
Cranial Characters	144
Postcranial Characters	169
Data Matrix	184

LIST OF TABLES

TABLE 1. Ontogenetic Changes	75
TABLE 2. Transitional Changes	105

LIST OF FIGURES

FIGURE 1. Relative abundance of <i>Orodromeus</i> elements.	3
FIGURE 2. Phylogeny of the basal ornithopods	7
FIGURE 3. Skull of <i>Orodromeus makelai</i> type specimen	11
FIGURE 4. <i>Orodromeus makelai</i> skull reconstruction	12
FIGURE 5. <i>Orodromeus</i> maxilla	14
FIGURE 6. <i>Orodromeus</i> teeth	16
FIGURE 7. <i>Orodromeus</i> skull elements.	18
FIGURE 8. <i>Orodromeus</i> jugal.	22
FIGURE 9. <i>Orodromeus</i> neurocranium.	26
FIGURE 10. <i>Orodromeus</i> mandible without prementary	31
FIGURE 11. <i>Orodromeus</i> anterior cervical vertebrae.	37
FIGURE 12. <i>Orodromeus</i> mid- and posterior cervical vertebrae	38
FIGURE 13. <i>Orodromeus</i> ribs	40
FIGURE 14. <i>Orodromeus</i> anterior and mid-dorsal vertebrae	42
FIGURE 15. <i>Orodromeus</i> posterior dorsal vertebrae	43
FIGURE 16. <i>Orodromeus</i> vertebral measurements	44
FIGURE 17. <i>Orodromeus</i> sacrum	46
FIGURE 18. <i>Orodromeus</i> caudal vertebrae and chevrons	49
FIGURE 19. <i>Orodromeus</i> scapula.	51
FIGURE 20. <i>Orodromeus</i> coracoid and sternal.	52
FIGURE 21. <i>Orodromeus</i> humerus	54
FIGURE 22. <i>Orodromeus</i> ulna and radius	56
FIGURE 23. <i>Orodromeus</i> manus	57
FIGURE 24. <i>Orodromeus</i> ilium	58
FIGURE 25. <i>Orodromeus</i> ischium	59
FIGURE 26. <i>Orodromeus</i> pubis	60
FIGURE 27. <i>Orodromeus</i> femur	63
FIGURE 28. <i>Orodromeus</i> femur ends	64
FIGURE 29. <i>Orodromeus</i> tibia and fibula	66
FIGURE 30. <i>Orodromeus</i> ankle.	69
FIGURE 31. <i>Orodromeus</i> pes.	71
FIGURE 32. <i>Dryosaurus</i> histological sections of femur	83
FIGURE 33. <i>Orodromeus</i> histology of hatchling femur.	86
FIGURE 34. <i>Orodromeus</i> femur histology.	88
FIGURE 35. <i>Orodromeus</i> and <i>Dryosaurus</i> growth rates.	90
FIGURE 36. Previously published basal ornithopod phylogenies.	94
FIGURE 37. <i>Othnielia rex</i> dentary teeth	101

LIST OF NOMENCLATURE AND ABBREVIATIONS

Abbreviations Used in Figures

ac: acetabulum
 an: angular
 ANKYL: Ankylosauria
 ant: anterior
 aof: antorbital fenestra
 bo: basioccipital
 brs: brevis shelf
 C: *Camptosaurus*
 c: cervical vertebra
 c-: indicates contact for given bone.
 For example c-mx is maxillary contact.
 CA: "*Camptosaurus*" *leedsi*
 cap: capitulum
 cdl: caudal vertebra
 cdlr: caudal rib
 CERAT: Ceratopsia
 ch: chevron (haemal arch)
 cn: cnemial crest
 CU: *Cumnoria* ("*Camptosaurus*") *prestwichi*
 D: *Dryosaurus* and *Dysalotosaurus*
 d: dorsal vertebra
 de: dentary
 diap: diapophysis of vertebra
 dp: deltapectoral crest
 E: *Echinodon*
 en: external nares
 F: *Fabrosaurus*
 FABR: Fabrosauridae
 fm: foramen magnum
 fo: foramen ovalis
 fr: frontal
 G: *Geranosaurus* and *Lychorhinus*
 gt: greater trochanter
 H: *Heterodontosaurus*
 HADR: Hadrosauridae
 hc: haemal canal

LIST OF NOMENCLATURE AND ABBREVIATIONS--Continued

hd: head
HETER: Heterodontosauridae
HY: *Hypsilophodon*
HYPsil: Hypsilophodontidae
I: *Iguanodon*
ic: intercentrum of axis
IGUAN: Iguanodontidae
ip: iliac peduncle
isp: ischiac peduncle
ju: jugal
L: *Laosaurus*
lag: line of arrested growth (histology)
lat: lateral
lc: lateral condyle
lcg: line of changed growth (histology)
LM: "*Laosaurus*" *minimus*
lt: lesser trochanter
ltf: laterotemporal fenestra
mec: medial condyle
med: medial
mx: maxilla
na: nasal
ns: neural spine
obf: obturator foramen
obp: obturator process
od: odontoid process
op: opisthotic
P: *Pisanosaurus*
PA: *Pachycephalosaurus*
pa: parietal
PACHY: Pachycephalosauridae
pal: palpebral (supraorbital)
pap: parapophysis of vertebra
pd: predentary
PK: *Parksosaurus*
pmx: premaxilla
po: postorbital
post: posterior
poz: postzygapophysis
PS: *Psittacosaurus*
PSITT: Psittacosauridae

LIST OF NOMENCLATURE AND ABBREVIATIONS--Continued

pp: pubic peduncle
prf: prefrontal
pro: prootic
prp: prepubic process
prz: prezygapophysis
qj: quadratojugal
qu: quadrate
r: rib
S: *Stegoceras*
s: sacral vertebra
sa: surangular
sc: scapula
soc: supraoccipital
sq: squamosal
STEG: Stegosauria
T: *Tenontosaurus*
TH: *Thescelosaurus*
tub: tuberculum
tvp: transverse process
W: Wealden hypsilophodont undescribed
Y: *Yaverlandia*

LIST OF INSTITUTIONAL ABBREVIATIONS

- AM -- Australian Museum, Sydney
AMNH -- American Museum of Natural History, New York
BM(NH) -- British Museum (Natural History), London
BYU -- Brigham Young University Earth Science Museum, Provo, Utah
CM -- Carnegie Museum, Pittsburgh, Pennsylvania
CPS -- Colorado Paleontological Society at University Museum, University
Colorado, Boulder
DNM -- Dinosaur National Monument, Jensen, Utah
HMN -- Humbolt Museum fur Naturkunde, East Berlin
LACM -- Museum of Natural History, Los Angeles County
MCS -- Museum of Cinco Saltos, Rio Negro Province, Argentina
MCZ -- Museum of Comparative Zoology, Harvard University, Cambridge
MIWG -- Museum of the Isle of Wight Geology, United Kingdom
MNA -- Museum of Northern Arizona, Flagstaff
MNHN -- Museum National d'Histoire Naturelle, Paris
MOR -- Museum of the Rockies, Bozeman, Montana
MUCPv -- Museum of the Universidad Nacional de Comahue, Neuque Province,
Argentina
MWC -- Museum of Western Colorado, Grand Junction
NMC -- National Museum of Canada, Ottawa
PU -- Princeton University, New Haven, Connecticut
QM -- Queensland Museum, Brisbane, Australia
ROM -- Royal Ontario Museum, Toronto
SAM -- South African Museum, Cape Town
SDSM -- South Dakota School of Mines and Technology
SMU -- Southern Methodist University, Dallas, Texas
T -- Museum of the Geological College of Chengdu, Peoples' Republic of China
USNM -- United States National Museum, Washington D.C.
YPM -- Peabody Museum Natural History, Yale, New Haven
ZDM -- Zigong Dinosaur Museum, Sichuan Province, Peoples' Republic of China

ABSTRACT

The small Upper Cretaceous ornithopod dinosaur *Orodromeus makelai*, possesses many tooth traits reminiscent of Triassic fabrosaurs. Determining whether these teeth were retained from a primitive lineage or independently derived within *Orodromeus* prompted a critical examination and ultimate revision of hypsilophodontid and basal ornithopod phylogeny. The revision of the Hypsilophodontidae resulted in a dissolution of the group into a pectinate grade of dinosaurs with a concomitant trend in increased size and herbivorous efficiency. Phylogenetic context reveals *Orodromeus* as nested within ornithopods with established herbivorous adaptations. Anomalous triangular teeth and high angle occlusion in *Orodromeus* is thought indicative of a shift to insectivory, possibly retained from the neonate condition. Other juvenile conditions, such as large orbits and unfused elements in mature specimens, together with rapid deacceleration of radial femoral bone growth through ontogeny is suggestive of neoteny. Continued histological studies of fossil taxa, together with a clear understanding of relationships, would help to identify heterochronic shifts in evolution.

Analysis of 20 taxa, using 124 morphological characters, indicates the pandemic distribution of small ornithopod taxa occurred prior to the Upper Jurassic. Although hadrosaurs diversified in the Upper Cretaceous as did angiosperms, most all major herbivorous adaptations were in place within ornithopods prior to the first occurrence of angiosperms in North America.

INTRODUCTION

A small ornithopod dinosaur from the Two Medicine Formation of Montana, *Orodromeus makelai* Horner & Weishampel 1988, demonstrates unusual primitive features for an Upper Cretaceous "hypsilophodontid." The description of its somewhat anomalous characteristics prompted a closer examination and ultimate revision of the group's definition and phylogeny. This small quasi-herbivorous biped is represented by virtually complete skeletons and partial skeletons depicting several growth stages. For paleontological studies, these specimens provide a rare opportunity to compile a large suite of characters needed to run computer-generated phylogenetic analyses and to document variation and ontogenetic change within a taxon. In doing so, this study combines a thorough phylogenetic analysis of basal ornithopods with histological and morphological changes through ontogeny, to demonstrate the utility and the role of heterochrony in the evolution of ornithopod dinosaurs.

Previous Work on *Orodromeus*

Orodromeus makelai was a key taxon in studies comparing life-history syndromes in dinosaurs (Horner, 1982, 1984a, 1987; Horner & Weishampel, 1989; Weishampel & Horner, 1994). Inferred and circumstantial evidence of growth and behavior implied from nesting horizons of this small ornithopod was

compared to evidence found in the hadrosaur *Maisaura peeblesorum* Horner and Makela, 1979. Both of these small and large ornithopods are abundantly preserved within the Late Cretaceous strata of the Two Medicine Formation of Montana. Comparisons of nesting patterns and bone histology between the two ornithopods suggested *Orodromeus* was a relatively precocial animal, developed enough upon hatching to leave the nest (Horner and Weishampel, 1988). Recent discoveries, however, have shown the sites previously assumed as *Orodromeus* nesting areas, to be nests of the small carnivorous dinosaur, *Troodon formosus* Leidy, 1856 (Varricchio and others, 1997).

With the identity of the nests established, an alternative reason for the presence of abundant young *Orodromeus* carcasses in a *Troodon* nesting area may be because *Troodon* adults brought these small herbivores in as prey items for their young. If this were the case, a bias toward a greater number of hind-limb elements would seem likely, as the hind-quarters of the animal would constitute the largest meat mass. A crude assessment of the abundance of element-types indeed show the elements that occurred more frequently were those skeletal regions that would have been covered with more muscle mass (Figure 1). Interestingly, with the exception of only a few elements, the bones representing the broad growth series of *Orodromeus* that come from these sites are not tooth-marked.

Despite the changing views on *Orodromeus* eggs and nests, embryonic and hatchling *Orodromeus* bones remain good standards for a precocial model.

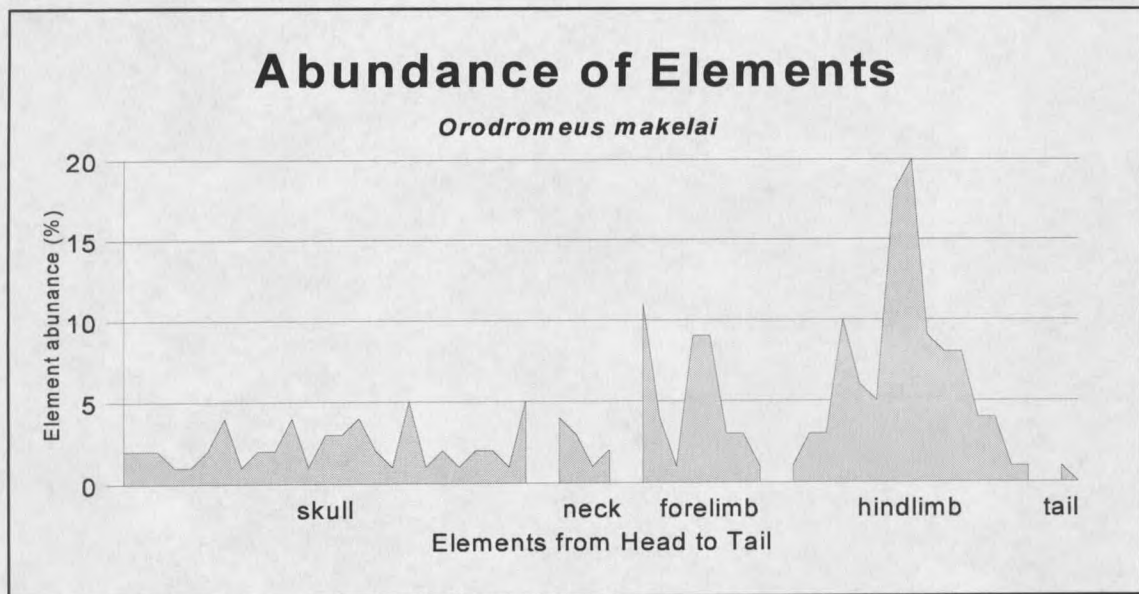


FIGURE 1. Relative abundance of skeletal elements on the Egg Mountain site of the Two Medicine Formation. Highest peak represents femora and tibiae as most abundant, with scapulae and ilia occurring in about 10% of the specimens.

Bone histological studies on embryonic and juvenile *Orodromeus* specimens reveal well-developed limb ends (see histological section), suggestive of an animal capable of active physical activity upon hatching.

Stratigraphic Context

Nearly all the available *Orodromeus* material comes from the Upper Campanian Upper Two Medicine Formation of Teton County, Montana. This formation is an eastward thinning, proximal alluvial facies of the Western Interior foreland basin. Representative of the western upper coastal plain of the north-south Cretaceous seaway, the Two Medicine Formation was bounded to the east by the Cordilleran thrust belt and to the west, by the Sweetgrass Arch and distal coastal plains of the Judith River Formation. The middle portion of the Two

Medicine and Judith River Formations are time-equivalent facies but are separated by the structural high of the Sweetgrass Arch which was active enough during the Campanian to disrupt east-west drainages, but not high enough to shed sediments (Lorenz & Gavin, 1984). Stratigraphically, the Two Medicine Formation is bounded above and below by regional unconformities and transgressive marine and marine-influenced strata. Radioisotopic dates obtained from $^{40}\text{Ar}/^{39}\text{Ar}$ analyses of biotite and plagioclase from bentonitic beds throughout the Two Medicine Formation have bracketed an age of 75 to 80 Ma (Rogers, Swisher, & Horner, 1993).

Within the Willow Creek Anticline, at the Egg Mountain and Egg Island sites, several growth stages of young *Orodromeus* have been discovered among eggs and nests within a soil caliche horizon peripheral to, or on an island within, alkaline lake deposits (Horner, 1984a 1987; 1988; Lorenz & Gavin, 1984). Only a few *Orodromeus* specimens have been recovered from near the top of the Two Medicine Formation in the Landslide Butte area, near the Montana-Alberta border. Here, the upper 100 meters of the Two Medicine Formation is exposed, but it is overlain unconformably by the Bearpaw Shale and has been determined by Lorenz (1981, 1984) as time-equivalent to those strata in the Willow Creek Anticline area.

Other time-equivalent strata of Montana and surrounding areas yield little material referable to *Orodromeus*. About a dozen teeth from the Judith River Formation, originally ascribed as the earliest occurrence of *Thescelosaurus* by

Sahni (1972), has been recently referred to *Orodromeus* by Galton (1995). Galton had previously identified these teeth, as well as an additional tooth (MCZ 3729) found from the Bug Creek anthills of the Maastrichtian Hell Creek Formation (Estes and others, 1969) as from a fabrosaurid ornithomimid (Weishampel & Weishampel, 1983; Russell, 1984; Sullivan, 1987). The cheek teeth (AMNH 8536, 8537; MCZ 3729) illustrated by these authors are very similar to those found in *Orodromeus* in being smoothly triangular, having steep double wear surfaces, and a denticulate cingulum.

The type specimen *Laosaurus minimus* Gilmore (1924) is probably referable to *Orodromeus*, although it is known from little material (Sues & Norman, 1990). Found in the Campanian Belly River Formation of Alberta, Canada, *L. minimus* consists of an incomplete hind-limb and a few vertebral centra. The femoral head extends medial from the posterior half of the greater trochanter and the lateral surface of the greater trochanter is flat, similar to *Orodromeus* and *Parksosaurus*.

Heterochrony

Studies of Upper Crétaceous dinosaur biogeography and paleoecology during eustatic sea level fluctuations has shown possible vicariance due to isolation events (Weishampel and others, 1991), rapid speciation during transgressive events (Bakker, 1977; Horner, 1984b, 1989; Weishampel & Horner, 1987; Horner and others, 1992; Varricchio, 1993), and evidence of

peramorphosis and anagenesis during regressions (Horner, 1984b; Horner and others, 1992). These epeiric seas had profound quantitative and qualitative effects on terrestrial ecosystems while provincializing the continent.

Orodromeus was an interesting inhabitant of the western North American continent during this time. This Late Cretaceous dinosaur is unusual for having retained primitive characters thought lost in its lineage 90 million years prior. Interestingly, this study shows *Orodromeus*, together with *Zephyrosaurus*, to be an offshoot lineage of some of the most primitive ornithopods (Figure 2). However, even in phylogenetic context, *Orodromeus* remains anomalous in its triangular tooth shape and high angled occlusion surfaces (see Morphologic Description) similarly found in Early Jurassic fabrosaurs. Unlike fabrosaurs, the cheek teeth in the first ornithopods are positioned close enough together they touch along the lower half of their crowns. Basal ornithopods like *Yandusaurus*, *Othnielia*, and *Zephyrosaurus* possess teeth with flatter and unidirectional occlusal surfaces than seen in *Orodromeus*. In all basal ornithopods, contacts between lateral skull elements allow limited movement, indicating a pleurokinetic skull has developed (Sues, 1980; Norman, 1984; Weishampel, 1984; Norman & Weishampel, 1991). Although similar contacts between elements are found in *Orodromeus*, independent and high angle occlusal facets on teeth indicate no translational movement of opposing jaws occurred. This occlusal pattern is reminiscent of that seen in mammalian insectivores (Rensberger, 1986). In non-mammalian herbivores insectivory is typical of a neonate state (White, 1985). If

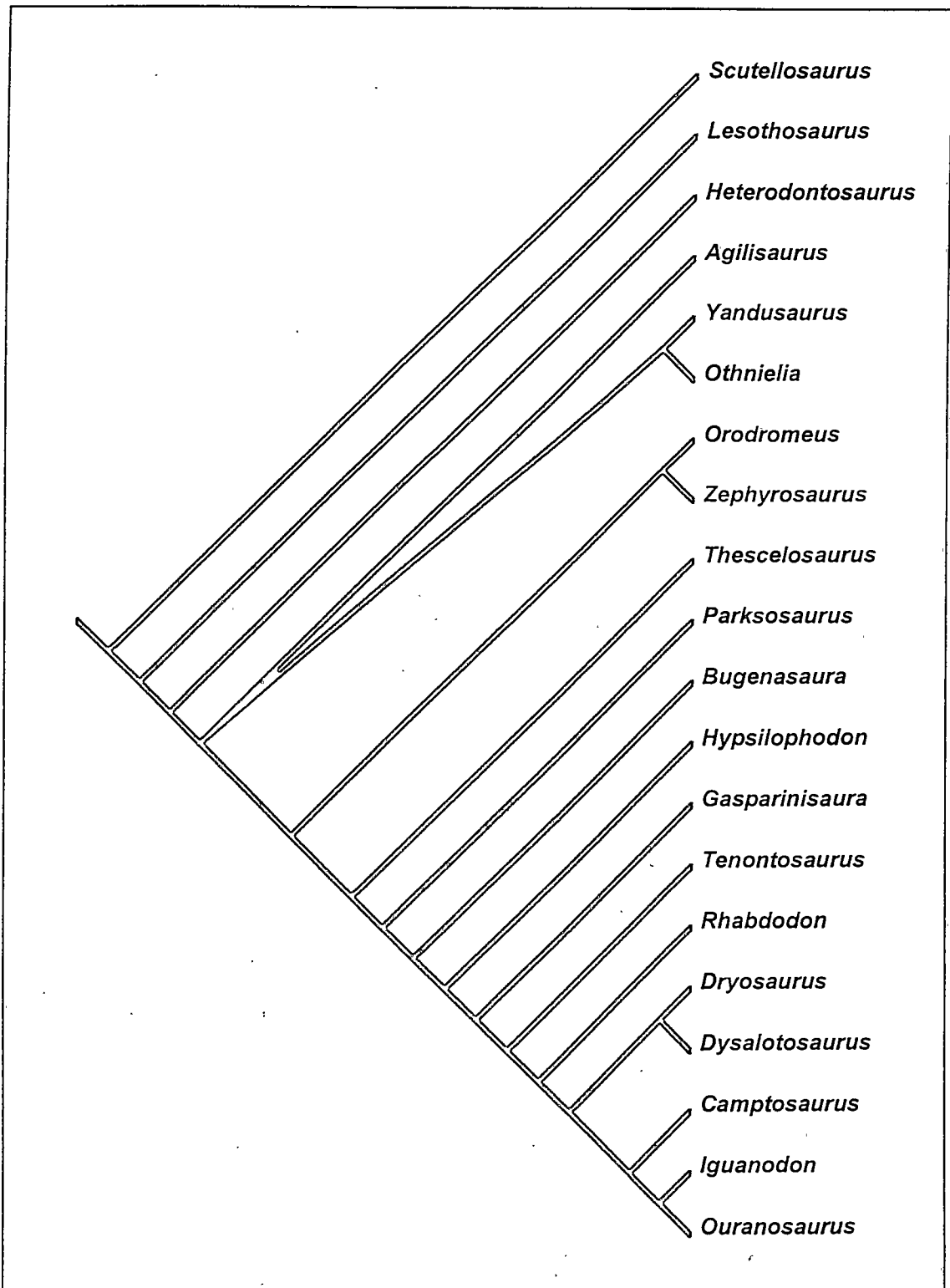


FIGURE 2. Cladogram of the phylogeny of basal ornithopods based on this study.

insectivory was the neonate condition in herbivorous dinosaurs, and if *Orodromeus* was insectivorous as the teeth suggest, then the known specimens of *Orodromeus* are either young animals, or, adult animals that have retained the juvenile state throughout their growth. Retention of juvenile traits would suggest *Orodromeus* was neoteneous, where traits experienced a decreased rate of development, or progenic, having features arrested earlier than the ancestral condition. The cause for such developmental changes is speculative. However, it is conceivable that in context to the habitat bottlenecks during transgressive stages of the Cretaceous Sea, competition with low browsing hadrosaurs, ceratopsians, and ankylosaurs could have imposed adaptive pressures on diminutive herbivores like *Orodromeus*.

Identifying evolutionary shifts in the timing of growth and development is difficult. Indeed, even to determine whether fossil remains are from a young larger animal or an older small animal has been subjective. Size does not always correspond well to age. Age classes have traditionally been determined based on allometry relative to known trajectories of other taxa, degree of ossification and fusion, and shape of articular ends (Ostrom, 1978; Callison & Quimby, 1984). Brinkman (1988) observed a substantial overlap in size relative to development, even in closely related taxa. This could be an especially confusing application when dealing with small animals like *Orodromeus*.

One approach in assessing an ontogenetic stage is by documenting histological development. Even though *exact* skeletal chronology has not been

determined for the Dinosauria as it has been in other many other vertebrates (see Peabody, 1961), a *relative* ontogenetic stage is discernable (Reid, 1981; Ricqles, 1983; Chinsamy, 1991, 1993; Varricchio, 1993). When projected growth rates are compared across taxa, bearing in mind their phylogenetic context, a clearer understanding of adaptive changes will appear (see Histology).

Specimens used for Description

Primarily, four specimens were used for descriptive and comparative purposes: the type specimen, MOR 294, consists of a nearly complete juvenile skeleton without hands and tail; the smaller MOR 661 postcranial skeleton is about 60% complete, and probably represents a near-hatchling stage; MOR 473 is a disarticulated skeleton with a crushed skull and represents a mature animal; and MOR 663, a fairly mature disarticulated individual, has nearly every portion of the skeleton represented at least in part. Description of elements was enhanced by important comparative material of 99 other *Orodromeus* specimens (See Appendix A), consisting mostly of partial individual animals, or several elements of many individuals collected in a specific area.

ORODROMEUS DESCRIBED

Orodromeus Morphology

The Skull

An excellent, although somewhat flattened juvenile *Orodromeus* skull exists for the holotype specimen MOR 294 (Figure 3). Most cranial elements are clearly visible in this specimen, although the rostrum is missing. Except for important clues from a crushed premaxilla in MOR 436, little can be determined of the tip of the skull. No evidence is provided by any other specimen as to the shape and extent of the nasals or prementary, so the rostral architecture of this area is hypothetical. Preparation of several broken and disarticulated skull elements of MOR 473 provided a more mature cranial reconstruction (Figure 4) than the juvenile holotype.

The overall skull is triangular in lateral view, with a large orbit. The postorbitals extend laterally to produce a wider orbit posteriorly, and together with the frontals and prefrontals, are laterally sharp with a smoothly beveled orbital border, indicating the eye filled the orbit and bulged somewhat from the face. A supraorbital bone extends half-way across the orbit, directly opposite an inflated tabular extension of the postorbital. A large infratemporal fenestra occupies most of the posterolateral skull behind a prominent horn-like jugal boss. Most of the cranial elements are relatively slender. Even in dorsal view, the

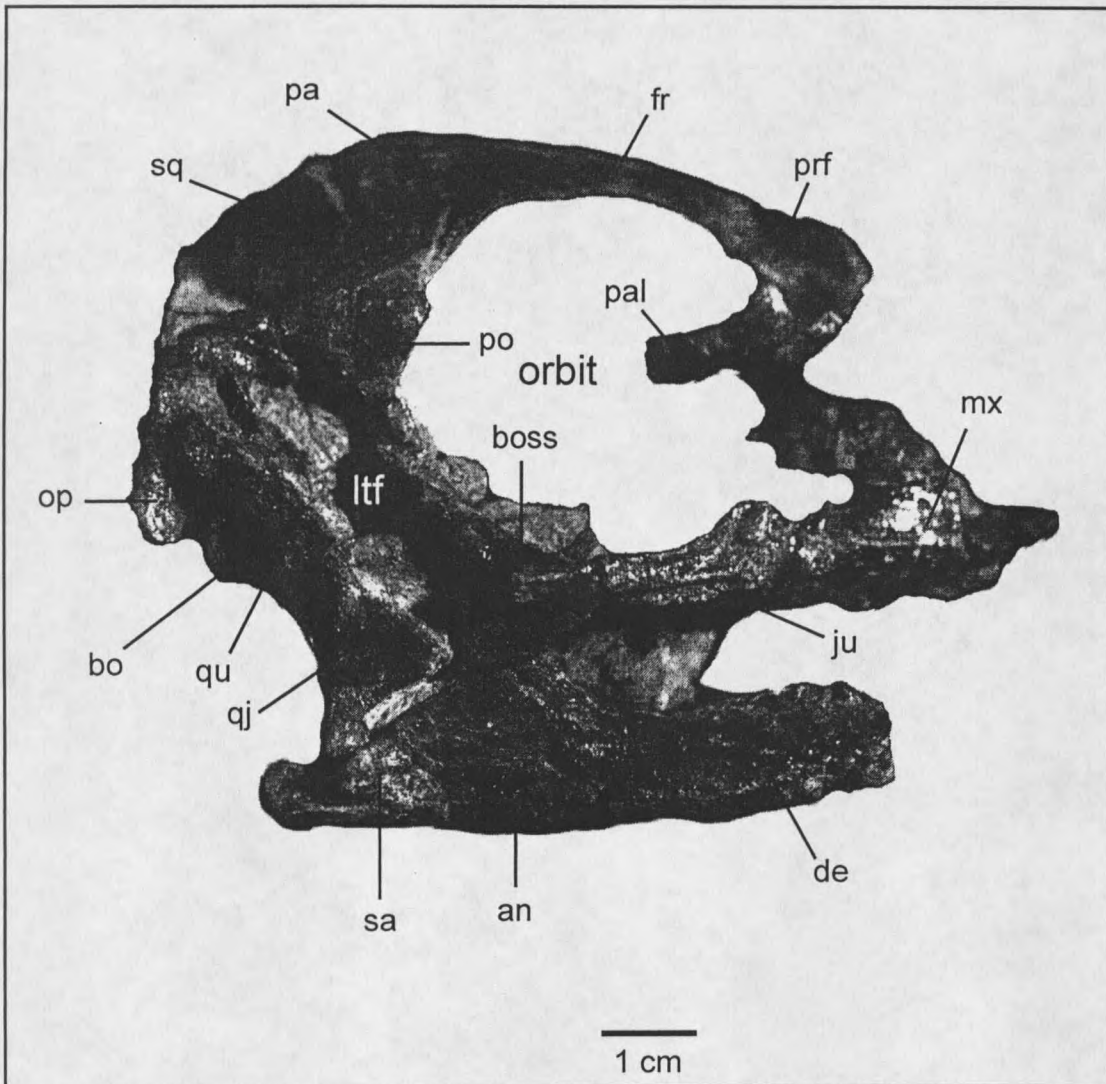


FIGURE 3. Skull of *Orodromeus makelai* type specimen. Skull of juvenile in right lateral view (MOR 294). Rostrum is missing. Key to abbreviations is given in List of Nomenclature.

posterior skull is moderately narrow, tapering further towards the rostrum.

The dentaries have roughly parallel upper and lower margins and the relatively long mandibular elements posterior to the coronoid slope gently to the glenoid fossa. Teeth are noticeably pointed and are not packed within the upper and lower jaws. The tip of the premaxilla comes to a blunt point with the first of five premaxillary teeth erupting from the front of a modestly everted oral margin.

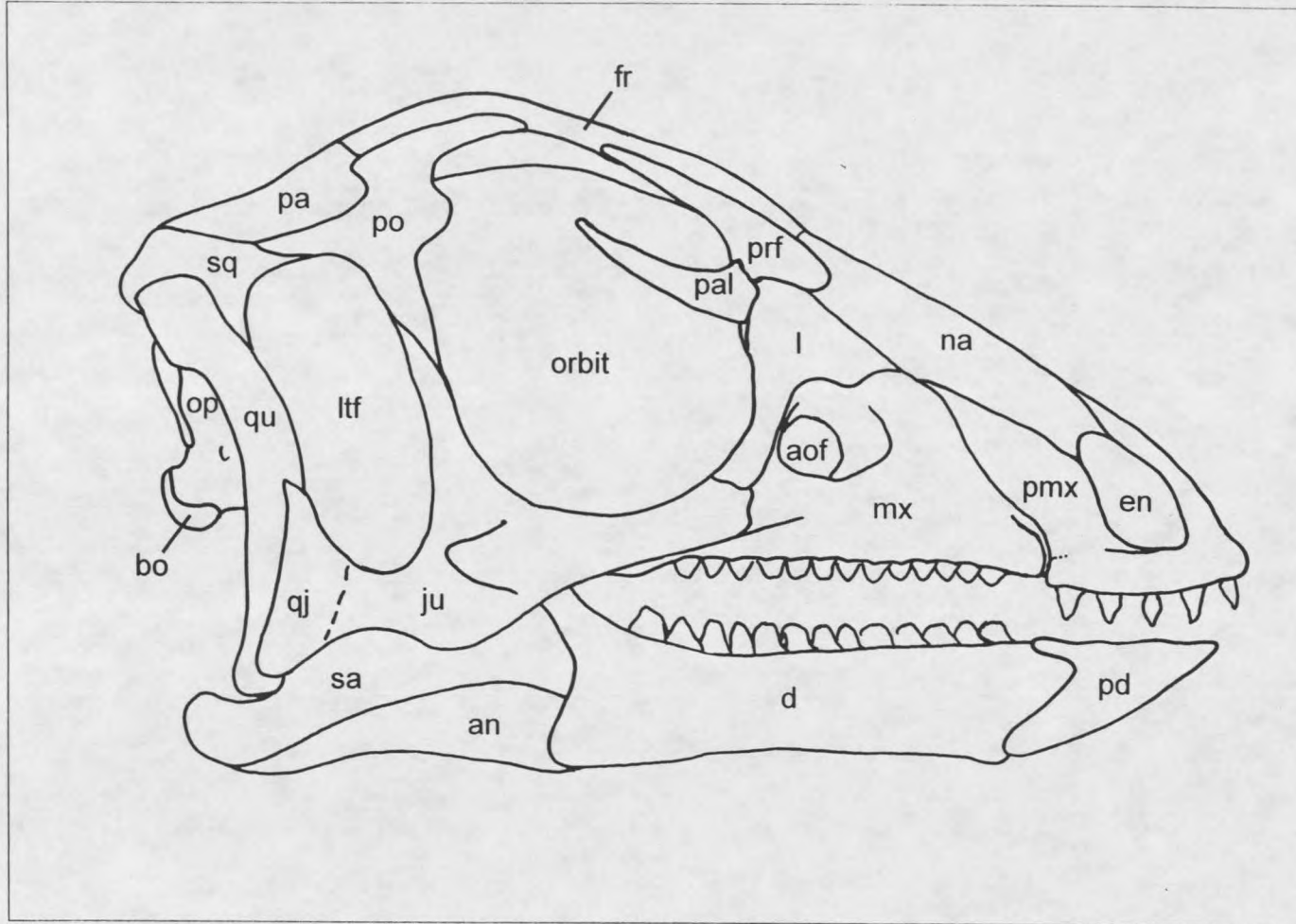


FIGURE 4. *Orodromeus makelai* skull reconstruction.
 Reconstructed left lateral view based on mature individual, MOR 436.
 Key to abbreviations is given in List of Nomenclature.

Premaxilla. Only two specimens with partial premaxillae are known. MOR 436 has a crushed, nearly complete pair of unfused premaxillae exposed in matrix. Only the right side is useful for description. Unlike most basal ornithopods, the lateral edge is everted or shelved, extending anteriorly to a narrow, bluntly rounded rostrum. Five premaxillary teeth are present on one side, the most anterior erupts from the rostral end, as in *Bugenasaura* (Galton, 1995). The anterodorsal process of the premaxilla is broken, with only the base preserved and measures 1/4 of the ventral premaxillary length. MOR 623 preserves only a posterior portion of the right premaxillary bone which bears two complete and one partial tooth crown. The teeth point ventrolabially. The posterior corner of the premaxilla ends in a rounded buttress that was backed by the anterolateral boss of the maxilla when articulated. Preserved portions of the palate are flat, terminating in a finished edge rostral to the last premaxillary tooth. The base of the maxillary process in MOR 623, rises from the posterior half of the premaxilla. Premaxillary tooth crowns possess a bulbous base, slightly concave lingual faces, and weak longitudinal striations across the highly convex labial side. Both mesial and distal carinae bear very small denticles, the distal carina being more developed.

Premaxillary teeth vary slightly in shape, but are all nearly the same size from rostral to rearward in MOR 436. These *Orodromeus* teeth compare favorably to those described for similarly sized ornithopods.

Maxilla. In the largest available specimen, MOR 473, the maxilla bears a prominent anterolateral boss before the anterior blade sweeps medially, then anteriorly to a pointed ramus. In the smaller holotype, the anterolateral boss is not as distinct (Figure 5). The flattened anteriorly-projecting ramus articulates with the opposing maxillary ramus along a sagittal suture and enters into the posterior end of the premaxilla above the palate, probably in conjunction with the vomers as in *Hypsilophodon* (Galton, 1974).

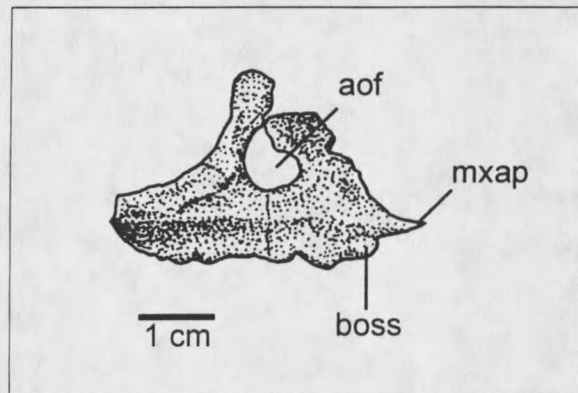


FIGURE 5. *Orodromeus* maxilla. Right maxilla in lateral view (MOR 294) Key to abbreviations is given in List of Nomenclature.

The ventral alveolar edge is straight and set more mesially in the posterior end. A small nutrient foramen is positioned dorsolateral to each alveolus. The jugal rides upon the posterior third of the maxilla above a medial horizontal shelf that bears faint, parasagittal striations, marking the palatine contact. In medial view, the maxilla is arched above the alveolar edge suggesting the soft palate was arched as well.

Above and slightly posterior to the anterolateral boss, the thin lateral sheet of the maxilla ascends and turns posteriorly to meet the anterior ramus of the lacrimal, defining the posterior border of the antorbital fossa. The somewhat triangular antorbital fossa is centered high within the mid-portion of the maxilla, bounded dorsally and posteriorly by the lacrimal, with a ventral edge extending

nearly as low as the ventral edge of the orbit. The inside wall of the antorbital fossa is a thin sheet of bone which had been damaged in the holotype, making the shape of the interior antorbital fenestra unclear, but it appears situated within the posteroventral portion of the fossa. Together, the medial and lateral walls of the maxilla define a dorsal groove within the body of the maxilla similar to that of *Zephyrosaurus*. The medial wall of the maxilla is poorly defined and damaged in observed specimens, but unlike most ornithopod taxa, the medial wall appears to have been short and thick. In *Dryosaurus* and *Bugenasaura*, the inner maxillary wall is more developed than the lateral, but both ascending walls are short.

Due to missing teeth and obscured or eroded alveoli, the tooth count of the holotype is uncertain. However, assuming teeth are evenly spaced throughout, the length of the dentary suggests the young holotype probably retained ten teeth (13 in the larger MOR 473). Few maxillary teeth are preserved in available specimens of *Orodromeus*. The crowns are triangular and laterally compressed (Figure 6). Maxillary crowns are nearly symmetrical with the apex situated only slightly anterior. They vary from slightly taller than wide, to wider than tall, with small denticles along each carina unsupported by ridges. Labially, the body of the crown is slightly concave above a moderately developed cingulum. Maxillary tooth roots are straight and swollen, with a distinct neck below the cingulum. As with those of the dentary, crowns are situated within the maxilla en echelon, with the anterior crown lapping outside the mesial edge of the one behind.

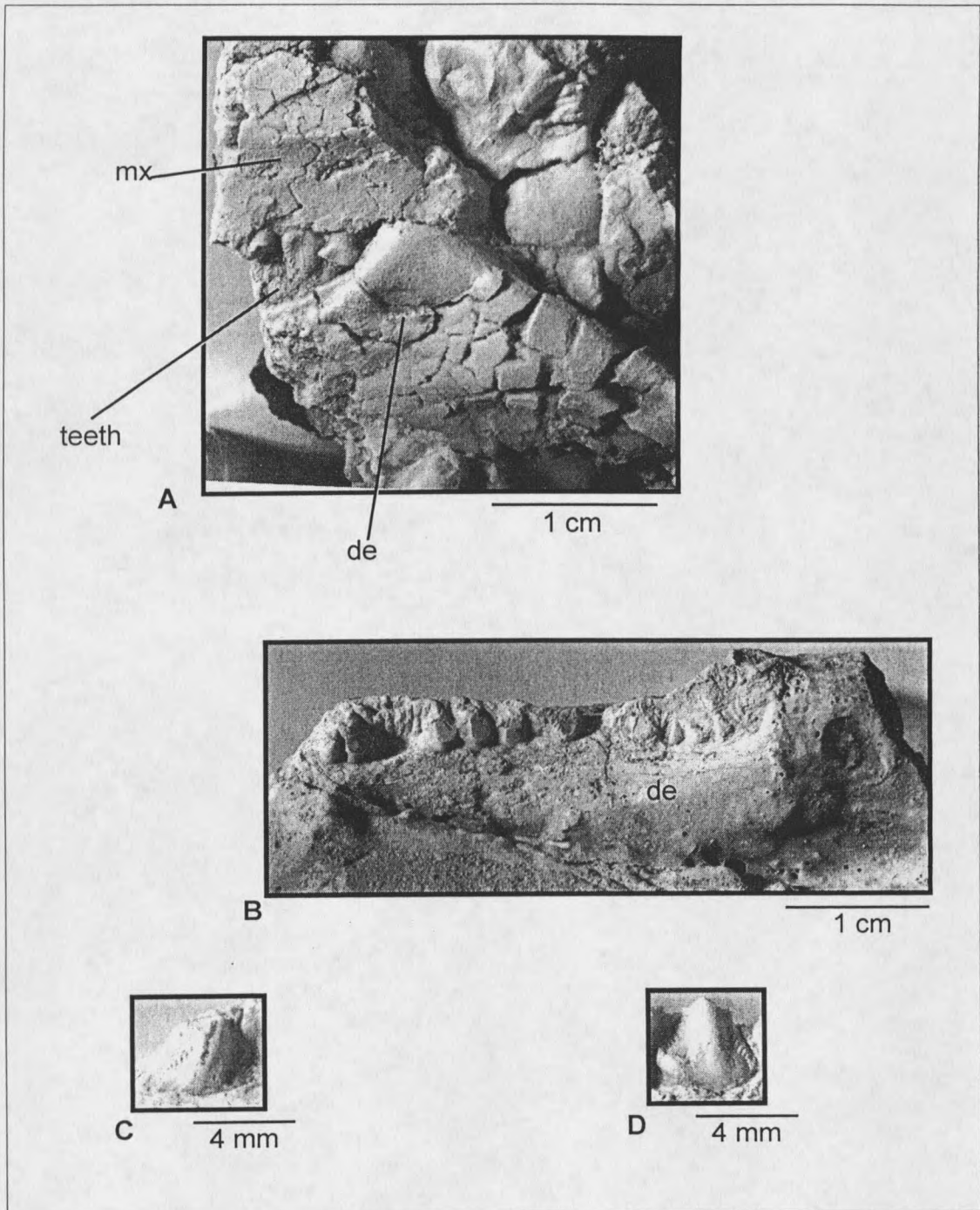


FIGURE 6. *Orodromeus* teeth.

A) Maxillary teeth in labial (lateral) view (MOR 613).

B) Dentary teeth in labial (lateral) view (MOR 248).

C) Dentary tooth in lingual view (PU 23247).

D) Dentary tooth in lingual view (PU 23247).

Key to abbreviations is given in List of Nomenclature.

Lacrimal. Only two partial lacrimals are available for this study: the ventral portion of the right lacrimal on the holotype MOR 294 and a partial left on of MOR 623. The incomplete lacrimal on the holotype demonstrates little, other than showing the ventral ramus prevents the jugal from participating with the antorbital fossa. The lacrimal-jugal contact is a thin butt joint on the anterodorsal corner of the jugal, lapping the maxilla posteriorly. The posterior margin of the lacrimal is sharp-edged, and together with the prefrontal, forms the anterior border of the orbit. Available lacrimals are poorly preserved anteriorly and dorsally; however, articular surfaces on the prefrontal indicate the lacrimal lapped both anterolaterally and ventrally, confining the dorsal extent of the lacrimal in a recess between the anterior and the ventral processes of the prefrontal. Neither nasals nor the dorsal processes of the premaxilla is preserved, making it impossible to determine the nature of the common lacrimal, nasal, and premaxillary contacts.

Supraorbital. The palpebral, or supraorbital, is a gently bowed spike with a medially faced anterior articular end for contact with the prefrontal (Figure 7). A broad, rugose region on the posterior edge of the prefrontal indicates a ligamentous union of the supraorbital and prefrontal. The anterior articular surface of the supraorbital bears a slender anterior projection that served to brace the supraorbital and prevented significant lateral rotation. The supraorbital is slightly wider transversely than it is vertically, with a sharp lateral edge. Ventromedially, it is irregularly textured for soft-tissue attachments. Posteriorly,

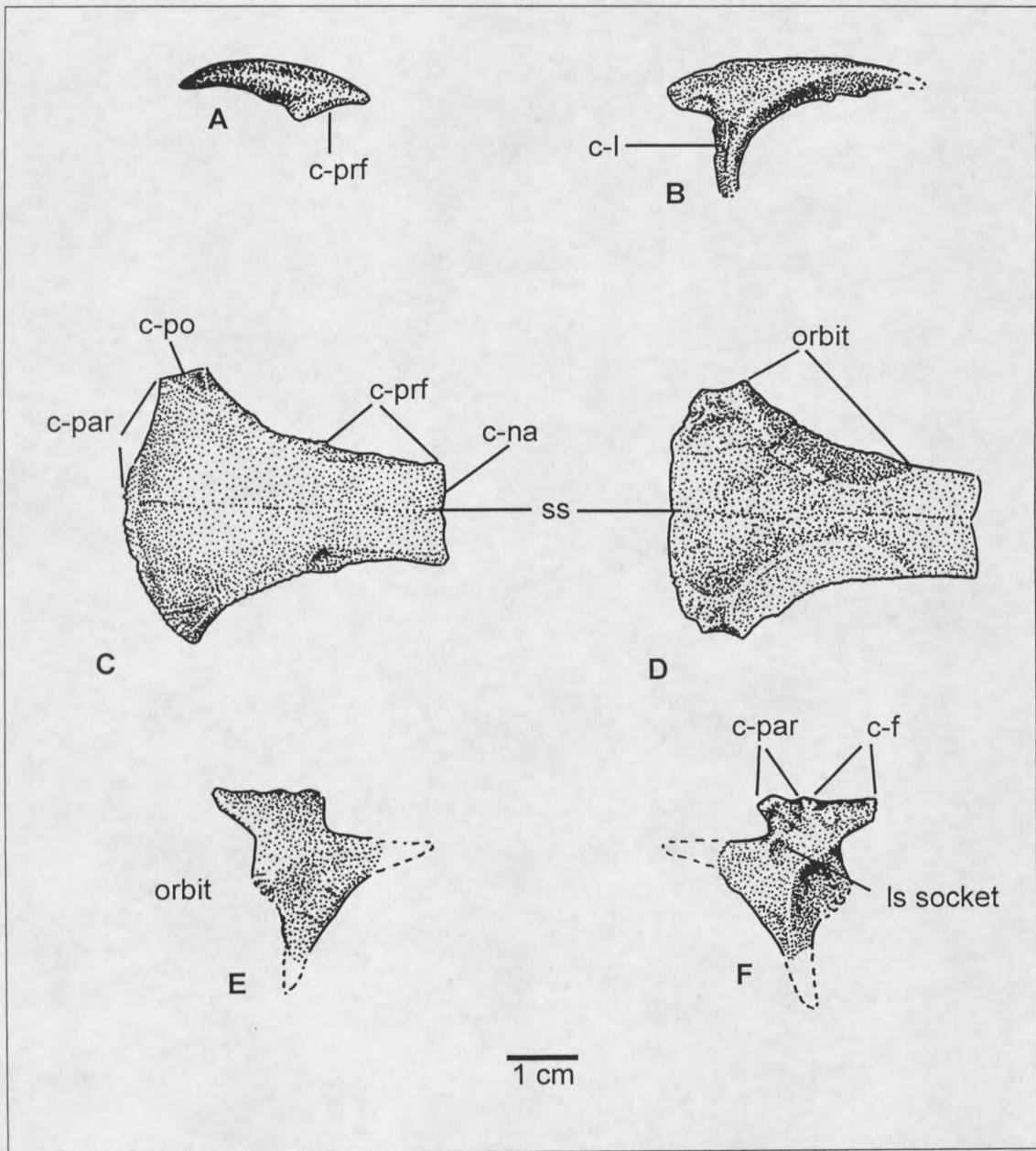


FIGURE 7. *Orodromeus* skull elements.

A) Left palpebral (supraorbital) in dorsal view (MOR unnumbered).

B) Left prefrontal in lateral view (MOR 995).

C) Paired frontals in dorsal view (MOR 995).

D) Paired frontals in ventral view showing frontal rim of orbit (MOR 995).

E) Left postorbital in lateral view (MOR 473).

F) Left postorbital in medial view (MOR 473).

Key to abbreviations is given in List of Nomenclature.

the supraorbital comes to a point, extending only about half-way into the orbit. Relative to the size of the orbit, the supraorbital is shorter in the younger holotype.

Prefrontal. The prefrontal is a T-shaped bone in lateral view (Figure 7), forming the anterodorsal border of the orbit and connecting the skull roof to the lateral face. The concave posterior surface bears a small foramen high into the orbital area. Posterodorsally, the prefrontal is formed into a sheet of bone with a long oblique contact with the anterolateral portion of the frontal. Rostrally, the suture narrows and is vertically oriented. The tongue-shaped rostral process of the prefrontal slopes ventrolaterally and is marked by longitudinal striations on its end, either for contact with the nasals or posterodorsal process of the premaxilla. Inferior to this anterior process is the lacrimal contact. A faint irregular rugosity posterior to the highest extent of the lacrimal likely held the supraorbital. Anteriorly, along the length of the ventral process, an oblique lap joint occurs, extending down the posteromedial edge of the lacrimal. Medially, the upper half of the prefrontal is transversely concave.

Frontal. The frontals are elongate plates of bone nearly 2.5 times longer than wide (Figure 7). The frontals unite along the sagittal plane, meeting more thinly in the posterior third by deep vertical striations, and anteriorly by longitudinal rugae. A deep, prominent, striated groove along the superior anterolateral edge of each frontal is the prefrontal contact. Rostrally, this contact

is more laterally positioned, resulting in a vertical contact near the anterior end.

The superior surface of the frontals is convex, being highest over the orbit. Posteriorly, the superior surface curves down to meet the parietals in an irregular transverse suture, turning slightly posteriorly at medial plane. This frontal-parietal suture is a short scarf joint, with the frontals slightly overlapping the parietals. A short dorsal groove occurs on the posterolateral corner of the frontal for the postorbital articulation. Conspicuous striations within the groove are posterolaterally oriented. Ventral to this groove and laterally directed, is a complex tongue-and-groove arrangement marking the ventral postorbital contact. Ventrally below this, a firm articular attachment occurs for the laterosphenoid. Common among some small ornithomimid dinosaurs, a synovial socket occurs at the underside of the parietal-frontal-postorbital triple-junction. However, no socket occurs within the frontals of *Orodromeus* for the head of the laterosphenoid.

The frontals, together with the parietals, form the dorsal roof of the braincase. Ventrally, the medial hour-glass shaped portion of the frontals is concave, wider and deeper posteriorly, and bordered on either side by a ridges formed by the ventrolateral concavities of the orbits.

Parietal. Only two specimens are preserved with parietals in the available material: a complete pair in holotype MOR 294 (although somewhat crushed), and the right parietal in MOR 473. The parietals are paired elements forming the posterodorsal roof of the braincase. Although they appear fused in the type

specimen, the elements in the larger MOR 473 are not fused, exposing their common broadly thick sagittal contact. Sereno (1991) observed separate parietals in *Lesothosaurus*, and suggested that this is a rare feature among ornithischians. Parietals occurring in an apparent fused condition in a juvenile of *Orodromeus*, and unfused in a more mature individual, indicates caution is warranted. Separate or unfused parietals may be a preservational anomaly, or, what might have been considered apparent fusion in other specimens, may be only superficial.

The superior surfaces of the parietals are lower than the frontals, sloping slightly posteriorly. The strongly concave lateral sides dip ventrolaterally about 30 degrees from horizontal and form the medial wall of the supratemporal fenestra. Among the few preserved parietals, the lateral sides meet dorsally to form a sharp sagittal crest. However, variation occurs among individuals of *Hypsilophodon*, the Proctor Lake ornithopod, and *Dryosaurus* in which the sagittal area is formed often by a narrow shelf. Variation in the dorsal apex of several supraoccipitals of *Orodromeus* suggest variation would occur in the parietals of this taxon as well. The ventrolateral edge of each parietal meets with the laterosphenoid and, posteriorly, with the supraoccipital.

Postorbital. The postorbital is a triradiate element (Figure 7) that separates the orbit, infratemporal, and supratemporal fenestrae. The frontal process is most dorsally expressed, situated within a wide interdigitate ventral groove of the skull roof, perpendicular to the transverse parietal-frontal suture.

Ventrally, and just excluded from the frontal, a smooth synovial socket for the head of the laterosphenoid occurs above and posterior to the orbit. From that point, the body of the postorbital curves lateroventrally and divides into tapering posterior squamosal and ventral jugal processes which lie in the same plane. The posterior wall of the orbit formed by the postorbital is concave with the lateral edge projecting anteriorly into the orbit. This portion is slightly striated on the edge. The orbit is expressed medially by a ridge on the under side of the frontals which continues down the inner side of the postorbital and down through the ventral process. This descending process thins and laps anteriorly (in MOR 473, laterally) onto the ascending process of the jugal, about halfway up the posterior side of the orbit. The posterior process of the postorbital forms more than half of the temporal bar, lapping the anterior process of the squamosal dorsolaterally.

Jugal. The jugal is decorated by a prominent posterolateral, somewhat dorso-obliquely oriented, boss (Figure 8). Jugal bosses vary in size and shape in *Orodromeus*: conical and striated, or somewhat flattened and keeled with striations limited to ventral and lateral

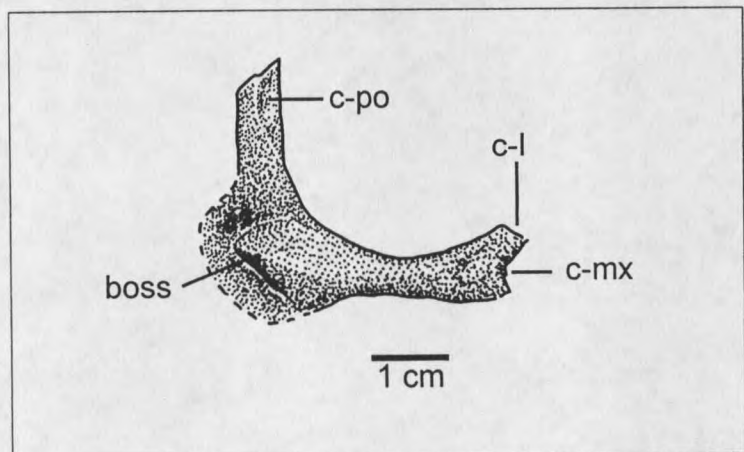


FIGURE 8. *Orodromeus* jugal. Right jugal in lateral view (MOR 473). Key to abbreviations in List of Nomenclature.

surfaces. The relatively bar-like maxillary process overlaps the posterodorsal end of the maxilla, ending in a butt joint with the lacrimal prior to reaching the antorbital fossa. Rostrally, the jugal thins transversely and flares slightly vertically to meet the posteroventral portion of the lacrimal. A palatine shelf extends medially on the anterior process, similarly seen in *Zephyrosaurus*, but oriented more anteriorly. The thin, nearly rod-like postorbital process reclines slightly posteriorly, lapping posteromedial to the jugal process of the postorbital. In the larger MOR 473, the postorbital laps along the lateral surface, into a groove of the jugal process. Anterior to the ascending postorbital process, the jugal forms the broadly curved, posteroventral corner of the orbit. Posteriorly, the jugal forms the anteroventral corner of the infratemporal fenestra, curving gently into a more acute angle.

The central region of the jugal is medially concave, with two nutrient foramina within the wall medial to the jugal bosses. The jugal thins into a posterior wing, fanning-out both ventromedially and posteromedially. The posteromedial portion of this wing is shallowly recessed just posterior to the ascending jugal process, similar to the position seen *Zephyrosaurus*, lapping extensively the lateral side of the quadratojugal.

Quadratojugal. The sheet-like quadratojugal is roughly triangular and somewhat laterally concave where it nestles within the jugal wing of the quadrate (Figure 3). A substantial anterior portion of the quadratojugal is hidden from lateral view by a shallow lap joint on the medial side of the jugal, just posterior to

the dorsal postorbital process. The quadratojugal forms nearly half of the ventral border of the post-temporal fenestra, gently curving for a short distance up the anterior edge of the quadrate, terminating well below the squamosal. The posteroventral corner of the quadratojugal ends near the base of the quadrate. Its height overlaps less than half the quadrate, forming a posterior shallow fossa between them, but no quadratojugal foramen exists.

Quadrate. The quadrate in *Orodromeus makelai* is a vertical, rostrally bowed, columnar element with two disproportionate bony plates emerging from its anterior edge. The lesser of the two bony plates is the lateral jugal wing which thins and projects rostrally in a similar arch defined by the posterior edge of the main body. This jugal wing begins dorsally, somewhat abruptly, a short distance below the head of the quadrate. The lower third of the quadratojugal contact is pronounced, ending just above the articular surface of the distal condyles. There is no paraquadratic foramen. The larger, medially oriented, pterygoid wing of the quadrate emerges a short distance below the dorsal end of the main body in a more subtle, tapering fashion than that of the jugal wing. In anterior view, the pterygoid wing tapers ventromedially to contact the quadrate ramus of the pterygoid which gives the wing a ventrally skewed profile. The ventral edge of the pterygoid wing is nearly horizontal and meets the shaft of the main body well above the distal condyles. The transversely expanded distal condyles meet the mandibular glenoid with a slight lateral incline. The smaller medial condyle falls directly in line with the columnar quadrate shaft and articulates with the articular,

while the larger lateral condyle articulates with the surangular. The two condyles are less differentiated in the older individual. Only the lower portion of the shaft of the main body is rostro-caudally compressed, with the rest of the shaft lateromedially compressed up through the quadrate head. The quadrate head is slightly recurved posteriorly, with a caudal buttress that is much more pronounced in the older individual. The synovial contact for the squamosal is smooth, rounded and slightly posteroventrally directed.

Squamosal. The squamosal forms the posterolateral bar of the supratemporal fenestra with thinning anterior and ventral processes (Figure 3). The posterior portion is dorsolaterally broad and rolls posteriorly over the quadrate head which fits snugly into the deep ventral socket. The ventral process of the squamosal descends along the anterior third of the quadrate, high above the quadratojugal. Anteriorly, the tapering process of the squamosal meets the posterior process of the postorbital ventromedially and obliquely, and extends half-way across the upper temporal bar. Posteriorly, the squamosal rides against the parietal wing, and ventrally against the lateral buttress of the supraoccipital.

Supraoccipital. The supraoccipital backs the skull, roofing the foramen magnum at its base and narrowing dorsally as it wedges between the posteriorly arched parietal wings (Figure 9). In MOR 294, the anterodorsal end of supraoccipital comes to a point. In MOR 473, the dorsal tip is somewhat planar, indicating the capping parietals may have possessed a dorsal shelf.

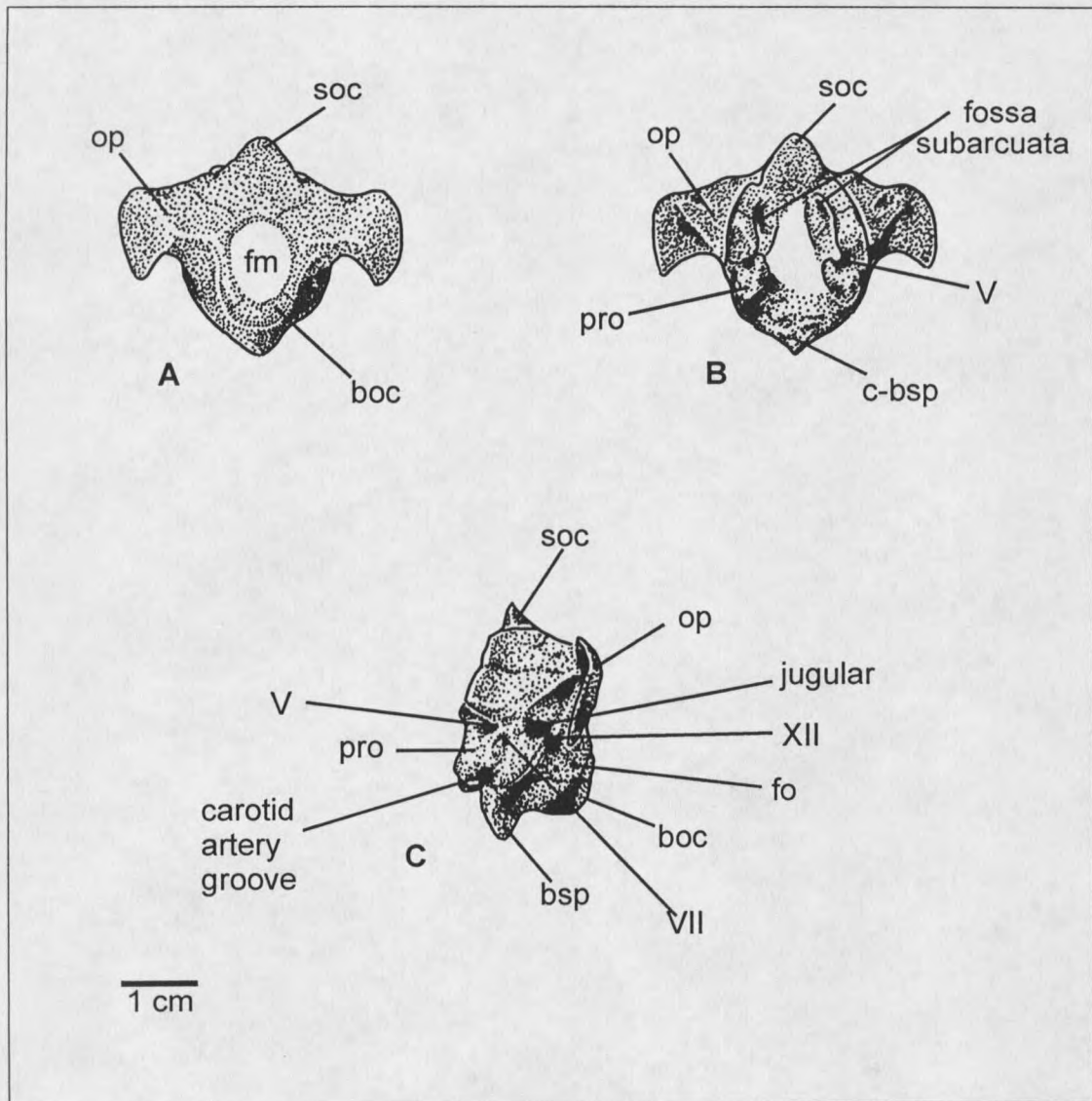


FIGURE 9. *Orodromeus* neurocranium.

A) Neurocranium in occipital view (MOR 403).

B) Neurocranium in anterior view (MOR 403).

C) Neurocranium in left lateral view (MOR 403).

Key to abbreviations is given in List of Nomenclature.

With a wide sutural contact with the opisthotics posteriorly, the base of the supraoccipital sweeps anteriorly under the parietal wings to contact the laterosphenoid. The supraoccipital joins with the prootics via a strong suture. This portion of the supraoccipital has been suggested by Sereno (1991) to

comprise a coossified epiotic for *Lesothosaurus diagnosticus*. As in all hypsilophodontid-grade ornithopods, the epiotic is not a separate bone in *Orodromeus*, even in very young individuals.

Posteriorly, the outer smooth surface of the supraoccipital lacks a sagittal crest.

At the most lateral basal extent, the supraoccipital forms a square buttress at the squamosal contact. This buttress is notched dorsally and is pierced by a vertical post temporal foramen for the *vena capitis dorsalis*. From this foramen, and just anterior to the lateral buttress, a groove extends ventroposteriorly toward the opisthotic.

Together with the underlying prootic, the supraoccipital is excavated within its medial wall by a high, deep fossa subarcuata, which housed the floccular lobes of the cerebellum (Galton, 1974) (Figure 9).

Opisthotic and exoccipitals. The opisthotics form the posterolateral walls of the braincase, framing the sides of the foramen magnum and expanding the occiput into broad paraoccipital processes (Figure 9). Each opisthotic extends posteriorly at the base, contributing to the dorsolateral corners of the occipital condyle. If exoccipitals are present, they form an indistinct fusion with the opisthotics, even in the smallest available specimens.

Ventrally, the opisthotics form a suture with the basioccipital, and anteriorly, with the prootics. These bones are articulated and appear fused in the small specimen MOR 403 and in the holotype MOR 294, but in the larger

MOR 473, the sutures are open. The opisthotics arch over the foramen magnum, but do not meet. Dorsomedially, they contact either side of the supraoccipitals via a wide butt joint suture. Curved, hatchet-shaped paraoccipital processes extend laterally and downward. Along the dorsal margin of these processes, a small post-temporal foramen extends anteroventrally, exiting the anterior side of the paraoccipital, just above (and in some, surrounded ventrally by) the prootic contact. Anteroventrally, a moderately deep ventrolateral fossa is partially roofed by the posterior process of the prootic. Two foramina transversely pierce the opisthotic pedicle, one situated slightly higher and posterior to the other. These foramina housed branches of the hypoglossal nerve (XII), becoming less separated as they exit laterally.

Together the opisthotics and supraoccipital form the greatest surface area on the occiput.

Prootic. The prootic forms the lateral wall of the braincase (Figure 9). It is taller than long and is extensively sutured posteriorly to the opisthotic, with the upper half addressed to a narrow, triangular suture on the anterodorsal side of the base of the paraoccipital process. Posteroventrally, the prootic borders two foramina with the opisthotic -- one at the base of the infra-paraoccipital lamina which corresponds to the jugular and cranial nerve XII, and the other, the *foramen ovalis* found just above the basioccipital articulation. Dorsally, the prootic contacts the supraorbital, internally forming the bottom half of a deep fossa (*fossa subarcuata*) that occur on the walls of the brain cavity (Figure 9).

Laterosphenoid. The laterosphenoid is a triangular, arched sheet of bone, forming the anterolateral wall of the braincase. It is ventrodorsally concave on the medial side, wider posteriorly and narrowing anterodorsally along the frontal-parietal-postorbital junction. Posteriorly, the laterosphenoid butts the anterior edge of prootic and anterior edge of the side wall of the supraoccipital (epiotic equivalent; Sereno, 1991). Dorsally it forms a continuous contact with the parietal and nearly comes to a point where the parietal meets the frontal and postorbital. From this point, the laterosphenoid head is somewhat separated and turns dorsolaterally to fit in the synovial socket of the postorbital. No foramina pierce the laterosphenoid, but a depression occurs anterior to the trigeminal nerve (V) of the prootic which it borders.

Basisphenoid. The basisphenoid forms a broad, immobile, transverse sutural joint with the anterior end of the basioccipital. As the anteroventral floor of the braincase, the basisphenoid angles up dramatically from the low floor formed of the basioccipital, at about 120 degrees in MOR 623 but shallower in all others.

Together with the prootic, the side of the basioccipital possesses a deep, constricted, lateral fossa that leads anteroventrally to the internal carotid foramen. Below and anterior to this, pterygoid processes extend from the anterior end of the main body, both lateroventrally and anteriorly, roughly 45 degrees from the medial plane. Facets for the pterygoid occur posteriorly and ventrolaterally on the feet of these processes. The body of the basisphenoid

without the parasphenoid process, measures slightly longer than the basioccipital, similarly seen in *Zephyrosaurus* and *Thescelosaurus* (Galton, 1989).

The parasphenoid appears as an anterior sagittal process of the basisphenoid, projecting rostrally below the orbit, ending about mid-skull. Laterally compressed, the parasphenoid expands somewhat ventrally toward its rostral end. A sharp, ventral keel extends along its length. The keel begins posteriorly within a groove between the pterygoid processes. Dorsally, a deep pituitary fossa begins anterior to the body of the basisphenoid and continues as a groove along the length of the parasphenoid, thinning rostrally.

Pterygoid, palatine, and vomer. The vomer is a long, laterally compressed tongue-shaped bone with the rostral end forming a narrow, flattened ventral shelf. This shelf joins the anterior ramus of the maxilla into the posterior end of the premaxilla, over the palate. Although the vomers are preserved out of position in the holotype, the relative length indicates they extended over the soft palate back to the palatines, just below the anterior edge of the orbit.

Behind and on either side of the vomers, the sheet-like palatines attach to the posteromedial portion of the maxilla and arch ventrally, possibly touching each other over the top of the vomers posteriorly. Dorsally, the palatines form a wide concavity for the anteroventral portion of the orbit, with the maxilla, jugal, and lacrimal laterally bounding the concavity.

Posterior to the palatines, the edge of pterygoids can be seen in the

matrix on the holotype detached from the basisphenoid.

Basioccipital. The basioccipital is a median element, that forms the posteroventral floor of the braincase and articulates with the vertebral column via a posteroventral occipital condyle. Dorsally, the groove of the foramen magnum comprises the central third of the occipital condyle width, and is marked at its opening by a distinctive short, square pit. Anterior to the pit, the floor of cranium widens and arches gently upward. On either side of the floor of the brain cavity deep, laterally directed sutural ridges mark the opisthotic contact. Anterolaterally, the basioccipital articulates with the prootic with oblique sutures. A low, median ridge on the floor of the braincase extends rostrally to the basisphenoid which is anchored to the anterior end of the basioccipital by an extensive, complex suture. Ventrally, the basioccipital bears a thin keel.

Dentary. The dentaries are laterally narrow bones that comprise the anterior two-thirds of the lower jaws (Figure 10). Each dentary turns medioventrally at the anterior end to meet at an obliquely inclined joint. Rostrally, the dentary is typical of primitive ornithischians, having a somewhat pointed

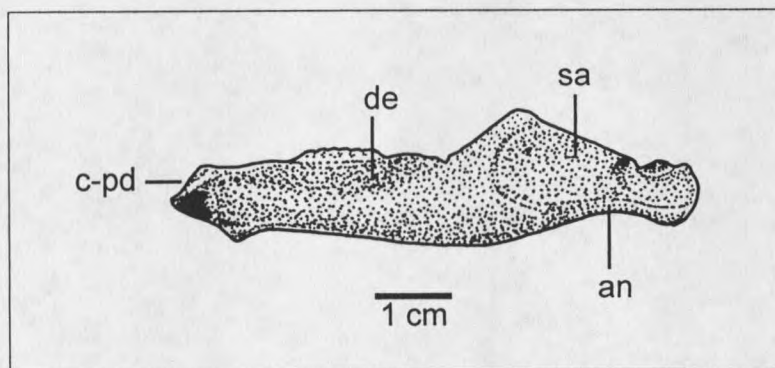


FIGURE 10. *Orodromeus* mandible without prementary. Left mandibular elements in lateral view -- although many teeth are broken or missing (MOR 294). Key to abbreviations is given in List on Nomenclature.

end which must have fitted, between the dorsal and ventral processes of the prementary. No prementaries have been found for *Orodromeus*. Anteroventrally, the prementary contact widens slightly posteriorly and measures nearly twice the length of the more steeply angled dorsal articulating surface. Along the entire anterior margin of the dentary, within the prementary articular surface, lies the Meckelian groove that extends ventrally and mesially, traversing dorsal to the medially turned tubercle that backs the ventral process of the prementary. This groove continues longitudinally on the medial side of the dentary, and widens and deepens posteriorly and is covered by the splenial. The lateral surface of the dentary is vertically convex and marked by an anteriorly directed foramen near its rostral tip, with two smaller foramina below and slightly posterior. A row of nutrient foramina occur within the lateral surface of the dentary, just ventral to the dorsal opening of each alveolus. The first few alveoli are small and begin immediately posterior to the prementary. Alveoli are circular and occur near the lateral edge rostrally, and become moderately inset along the posterior extent of the series. The ventral and dorsal margins of the dentary are relatively parallel for most of its length, ending posteriorly with a moderately high coronoid process. There are no teeth medial to the coronoid.

Although complete dentaries exist for *Orodromeus*, many of the alveoli are obliterated, making the determination of the number of teeth difficult. The best preserved specimen (MOR 248) is slightly larger than the young holotype and has nearly complete dentaries that provide an estimate of 14 alveoli for individuals that size. It seems likely an adult had more. Teeth touch neighboring

teeth only at their bases.

The roots of dentary teeth are straight and swollen, and slightly constricted below the crown. The crowns are triangular overall (Figure 6), laterally compressed, and are equally enameled on both sides. Teeth vary in size, with the larger teeth situated slightly posterior to mid-row. Each crown has a modestly bulbous cingulum and smooth lingual faces slightly concave on either side of a thick vertical center. The apex of each tooth is situated slightly anterior to the center of moderately steep mesial and distal carinae. The base of the distal carina of *Orodromeus* curves lingually above the swollen base, very similar to the denticulate cingulum found in the Upper Jurassic *Othnielia* and *Drinker* of North America, and in the maxillary teeth of the Lower Cretaceous *Phyllodon* of Spain. Ten to 12 short, weak denticles occur along each carina, more on larger teeth and considerably less on the small anterior teeth. *Orodromeus* dentary teeth are similar to fabrosaur teeth (Galton, 1983; Russell, 1984; Sullivan, 1987; Horner and Weishampel, 1988) in that teeth have steep, multiple wear surfaces. Teeth are typically set in an en echelon pattern.

Elements of the Posterior Jaw. The posterior 1/3 of the lower jaw gently slopes posteroventrally from the coronoid and coronoid process of the dentary. The bulk of this region consists of the sheet-like surangular which is pierced high on its lateral side by the anterior surangular foramen, and lower by the posterior foramen located just anterior to the hook-like boss in front of the glenoid fossa. Medially the surangular forms a broad fossa, flanked ventrally by the angular and

prearticular. Typical of ornithopod taxa, the glenoid fossa is formed by the surangular and articular, while being supported below by the angular. Unlike *Hypsilophodon*, the prearticular in *Orodromeus* extends to the posterior end of the small retroarticular process, bordering the glenoid fossa medially.

The Postcrania

The skeleton of *Orodromeus* is overall typical of small primitive ornithischians and basal ornithopods in having a light-weight build, long hindlimbs and relatively large feet -- considered necessary for a small, agile biped. The neck possesses a modest natural curve, holding the head away from, and higher than the body. The forelimbs are well developed in mature animals evidenced by large coracoids and a prominent scapular spine. The hands possess moderately short, but nimble digits capable of grasping. The back is narrow and is subtly arched dorsally. The pelvis consists of relatively long, slender elements with accessory support of the pubis directly to the sacrum. The femur is bowed anteriorly and much shorter than the tibia, characteristic of a femur held horizontally as in birds (Campbell & Marcus, 1992), making the leg swing primarily from the knee joint. The crus is long, with slender tibia, fibula and metatarsals. The digits of the pes are long with mobile joints and pointed unguis, capable of grasping or negotiating uneven terrain. The tail is slender and mobile.

Proatlas, Atlas & Axis. Only one proatlas (MOR 473) has been identified within the available specimens. The proatlas occurs as a pair of short, wing-

shaped bones, thicker in the middle and narrower at the posterior end, serving to extend the prezygapophyses of the atlas forward. These processes articulate with the occiput on the upper and outer edges of the foramen magnum, indicated by small notches on the opisthotic.

The neural arch of the atlas is likewise paired. Each neural arch has a double faceted base; one ventral and only slightly posterior, to fit against the atlas intercentrum, while the other faces anterodorsally and slightly medially, to articulate with the exoccipital. The neural arch rises dorsally from the lateral edge of the intercentrum and bends medially and rostrally to form a wing of the prezygapophysis. The posterodorsal corners of the neural arch are textured by ligament scars, but these rudimentary postzygapophyses do not extend posteriorly. Likewise, the prezygapophyses of the axis are weakly developed.

The atlas intercentrum is twice as wide transversely as it is long, and judging from the smooth facets, was surrounded by mobile joints. Anteriorly, the atlas intercentrum is concave with a sharp ventral margin, cupping the occipital condyle. Dorsally, rugose facets for the neural arches occur on either side of a concave center. Posterior to the center, there is a smooth concave facet for articulation with the odontoid process. This facet is incised medially by a groove which runs down the posterior end of the intercentrum. In posterior view, the atlas intercentrum has a low, smoothly rounded surface to fit against a steeply inclined axis intercentrum. On each end of this surface, are low posterolateral parapophyses for the atlantal ribs.

The odontoid process of the axis is an narrowing tongue of bone that

cradles the spinal cord to the occiput of the skull. Although articulated in the type specimen, the odontoid is not fused to the upper anterior face of the axis in any specimens. Ventrally, the odontoid is broad posteriorly with a smooth, low undercarriage that moved against the atlas intercentrum. Anteroventrally, a mobile articulation occurs with the occipital condyle by a smooth, rounded surface. Between these two convex anterior and posterior facets, a groove extends from the dorsolateral corner of the odontoid, ventrally and anteriorly, to return back up the opposite dorsolateral corner.

The axis intercentrum is a wedge that projects equally anteriorly and posteriorly, inserting into the anteroventral face of the axis -- the first of the more typical looking vertebrae of the series. The axis possesses an exaggerated neural arch that extends posterodorsally as a high-pitched roof over the third cervical vertebra. The postzygapophyses are well developed, and the prezygapophyses are modest. A well developed parapophysis is located at the anterolateral edge of the spool-shaped centrum. The centrum is longer than wide, and in some individuals, nearly twice the width. As in most of the cervical vertebrae, the axis centrum is taller than wide and ventrolaterally concave, producing a moderate ventral keel. A weak diapophysis occurs at the base of the neural arch, above and immediately posterior to the parapophysis. The posterior face tilts slightly rostrally.

Cervical Vertebrae. There are nine vertebrae in the neck of *Orodromeus* (Figures 11 & 12). Each centrum, from the axis on back, is strongly concave

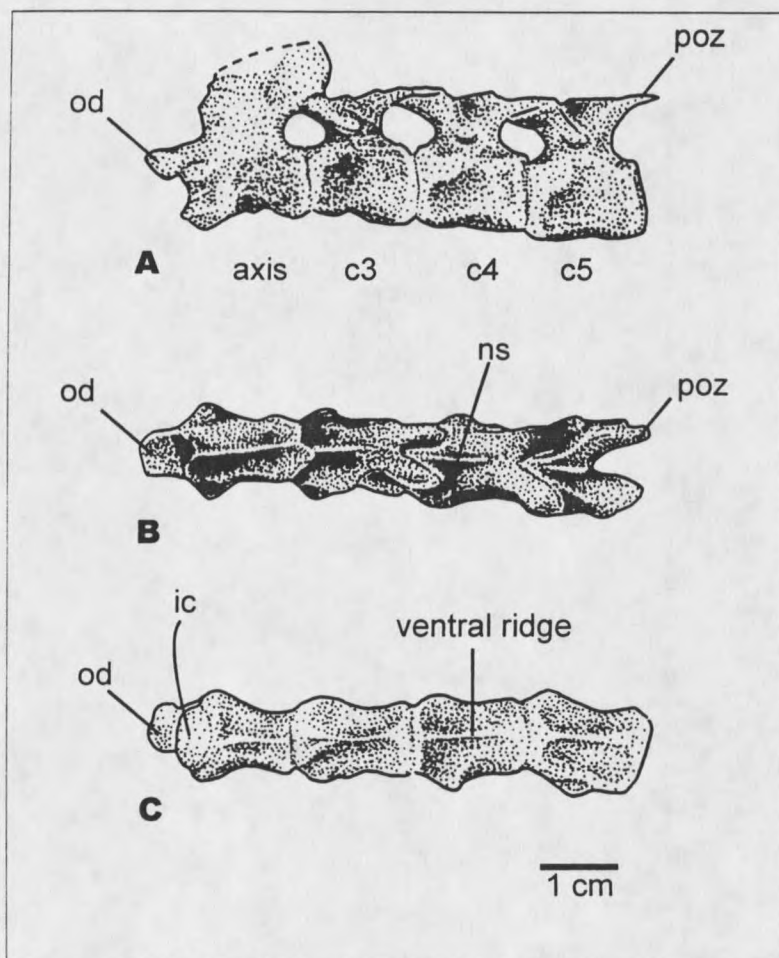


FIGURE 11. *Orodromeus* anterior cervical vertebrae.
A) Cervical vertebrae 2-5 in left lateral view (MOR 294).
B) Same vertebrae in dorsal view.
C) Same vertebrae in ventral view. Note the ventral ridge with concavities on either side.
 Key to abbreviations is given in the List of Nomenclature.

ventrolaterally with a sharp ventral keel. The anterior faces of the centra are wider than high and heart-shaped, while posteriorly, the centra are slightly higher than wide and D-shaped (flat end up). The axis through the fourth cervical vertebrae are slightly longer and taller than the posterior four vertebrae, the middle being transitional.

Starting at the base of the neural arch of the axis, slightly anterior to mid-length, the diapophyses progressively rise and lengthen laterally through the column. In the ninth cervical, the diapophysis is aligned vertically, and a slightly lateral, to the parapophysis.

On the axis, the parapophysis is on the anterolateral edge of the centrum. In the next two cervical vertebrae, three and four, the parapophyses occur at the anterior dorsal corner of the centra. In cervical vertebrae five and six, the

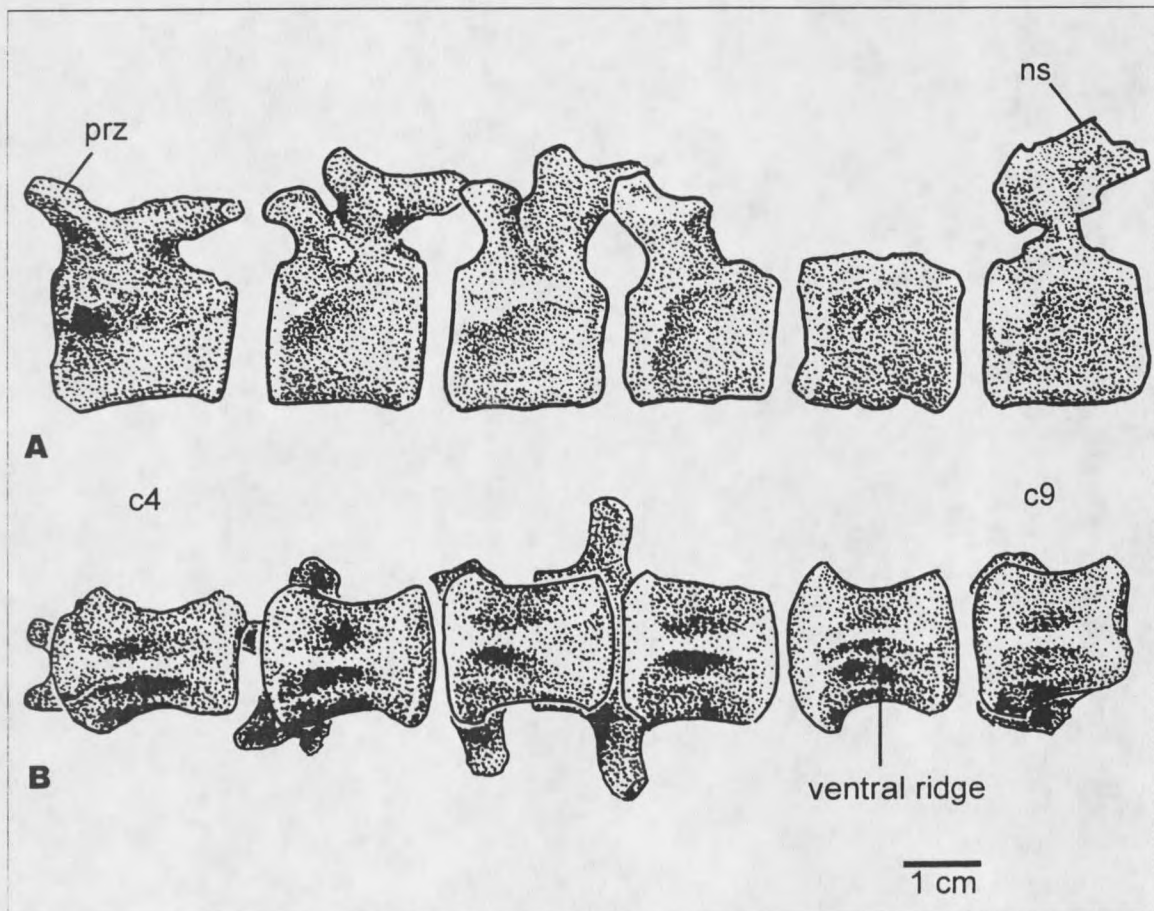


FIGURE 12. *Orodromeus* mid- and posterior cervical vertebrae of mature animal. A) Cervical vertebrae 4-9 in left lateral view (MOR 473). B) Same vertebrae in ventral view. Key to abbreviations is given in List of Nomenclature.

parapophyses are situated slightly posterior of the anterior edge and consist of both the centrum and the anteroventral corner of the base of the neuropophyses. The last three cervical vertebrae have parapophyses extending from the anterior edge again, incorporating even more of the basal corner of the neuropophysis.

In post-axial cervical vertebrae, the small, low spines rise from the high posterior portion of the neural arch just anterior to the diverging postzygapophyses. The sharp anterior edge of spine extends down to the top of the high neural canal, while the sharp posterior edge terminates prior to the separation of the postzygapophyses. The spines rise, as do the zygapophyses, gradually in succeeding vertebrae. The prezygapophyses are much shorter than the postzygapophyses, being positioned above the anterior end of the centra. The zygapophyses become progressively larger, more widely spaced, and more inclined down the cervical column. The infra-zygapophyseal lamina, both pre- and post-, arise from the base of the neural arch.

Each neural arch contacts the centrum on essentially a horizontal plane, with both the anterior and posterior peduncles participating in the articular faces of the centrum. In the ninth cervical centrum, the ventral length is longer than the dorsal, angling the terminal faces slightly. In cervical vertebrae seven and eight, the angling faces are less apparent. In the type specimen, as preserved, the articulated cervical series is strongly curved in this area. Cervical vertebrae 3, 4 and 5 slope slightly anteriorly.

Few cervical ribs are preserved. In the anterior cervical ribs, the tuberculum extends anterodorsally creating an acute angle between the

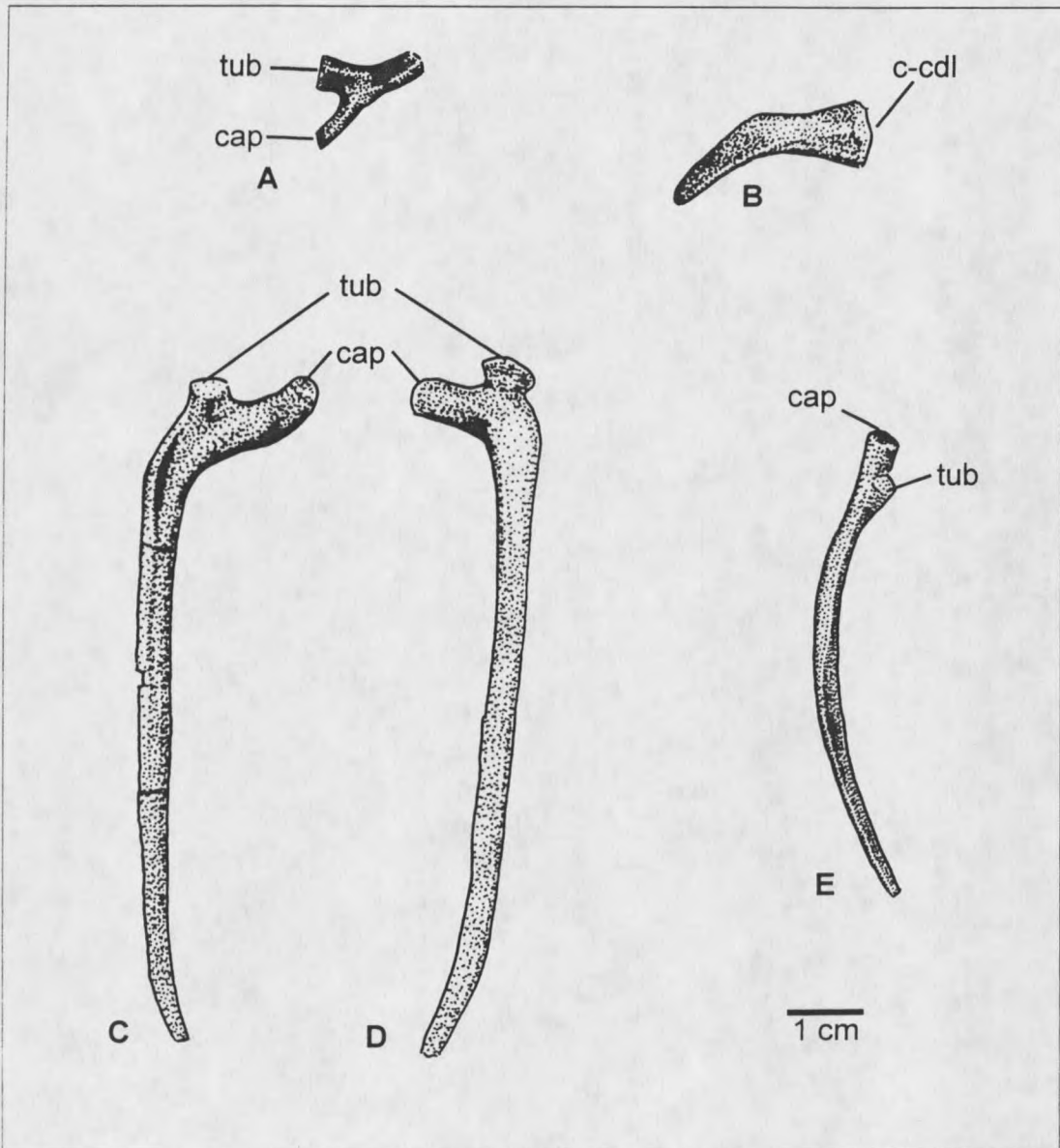


FIGURE 13. *Orodromeus* cervical, dorsal and caudal ribs.
A) Cervical rib in lateral view, distal end missing (MOR 623).
B) Left rib of first caudal vertebra in dorsal view (MOR 623).
C) Left anterior dorsal rib in anterior view (MOR 623).
D) Left anterior dorsal rib in posterior view (MOR 623).
E) Left posterior dorsal rib in posterior view (MOR 623).
 Key to abbreviations is given in List of Nomenclature.

tuberculum and the longer capitulum (Figure 13). The tip of the capitulum is small, whereas the short tuberculum forms a broader articulation with the diapophysis. When articulated, the ribs sweep out and back. Rib lengths have yet to be determined, as no complete cervical ribs are preserved.

Dorsal Vertebrae. A complete series of 15 dorsal vertebrae are present in MOR 473, MOR 294, and MOR 623 (Figures 14 & 15). The anterior dorsal vertebrae differ from the posterior cervical vertebrae in that centra of the latter are not as sharply keeled, the parapophyses are high on the side of the neural arch and tucked under the transverse processes, and both the anterior and posterior faces of the centra are equadimensional. Although longer, the first six centra are the most lightly built of the dorsal vertebrae, slightly taller than wide (more so in MOR 623), ventrally keeled, and ventrolaterally concave.

The next six dorsal centra are shorter, tall as wide, with weakly concave ventrolateral sides that produce ill-defined ventral keels.

The last three centra are transversely rounded centrally with no keel. Dorsal vertebrae thirteen and fourteen are as short as the few previous to them, but wider than tall. The largest, dorsal fifteen, is equadimensional in height, width and length (see Figure 16).

The long transverse processes of the anterior dorsal vertebrae angle dorsolaterally. At about the third or fourth dorsal, a transition occurs where the transverse processes extend horizontal with the parapophysis situated anterior to the diapophysis, rather than ventral to it. Posteriorly through the column,

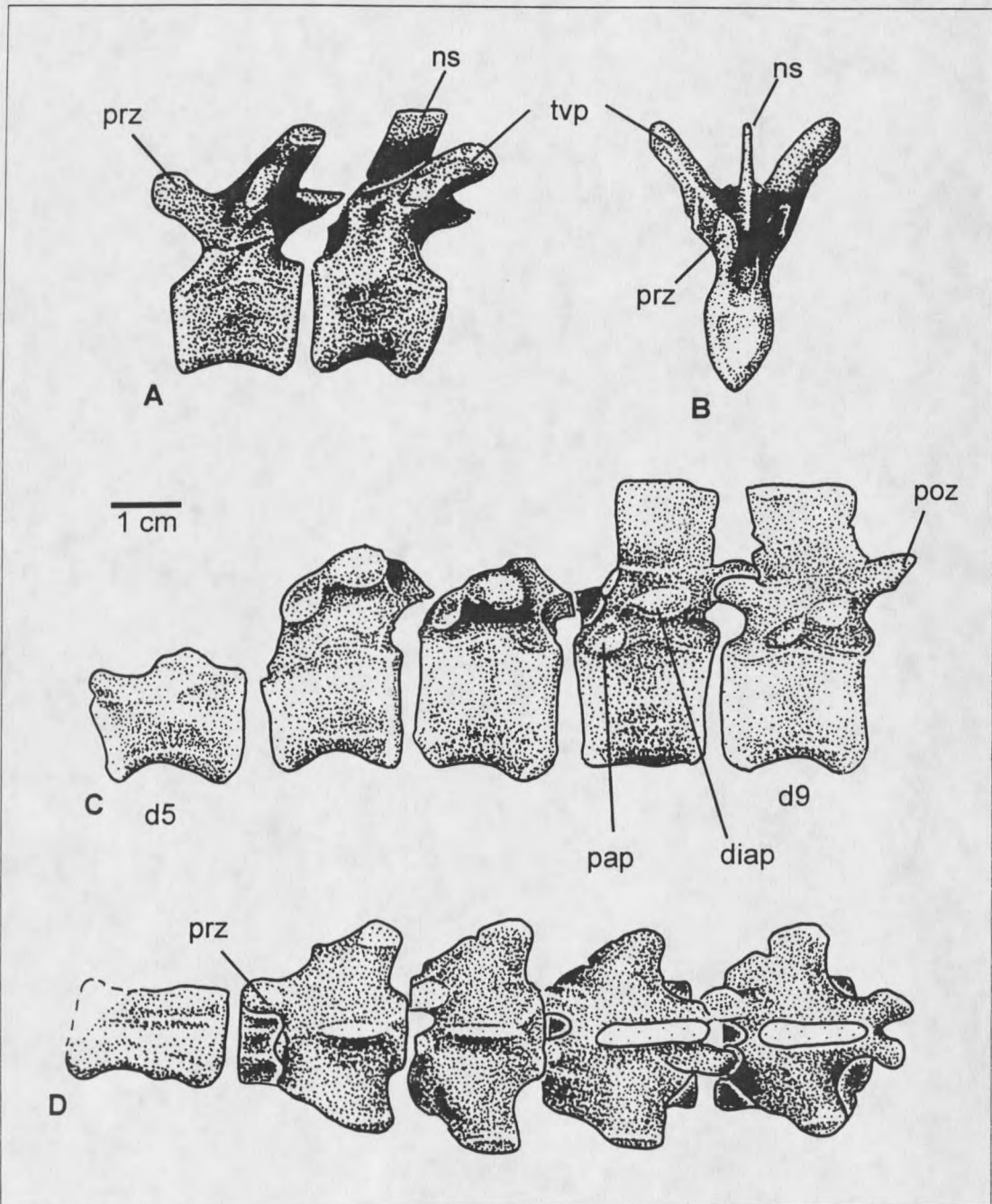


FIGURE 14. *Orodromeus* anterior and mid-dorsal vertebrae.

A) Anterior dorsal vertebrae 2 and 3, or 3 and 4 in left lateral view (MOR 623).

B) Anterior-most vertebra in A in anterior view (MOR 623).

C) Dorsal vertebrae 5-9 in left lateral view (MOR 473).

D) Dorsal vertebrae 5-9 in dorsal view (MOR 473).

Key to abbreviations is given in List of Nomenclature.

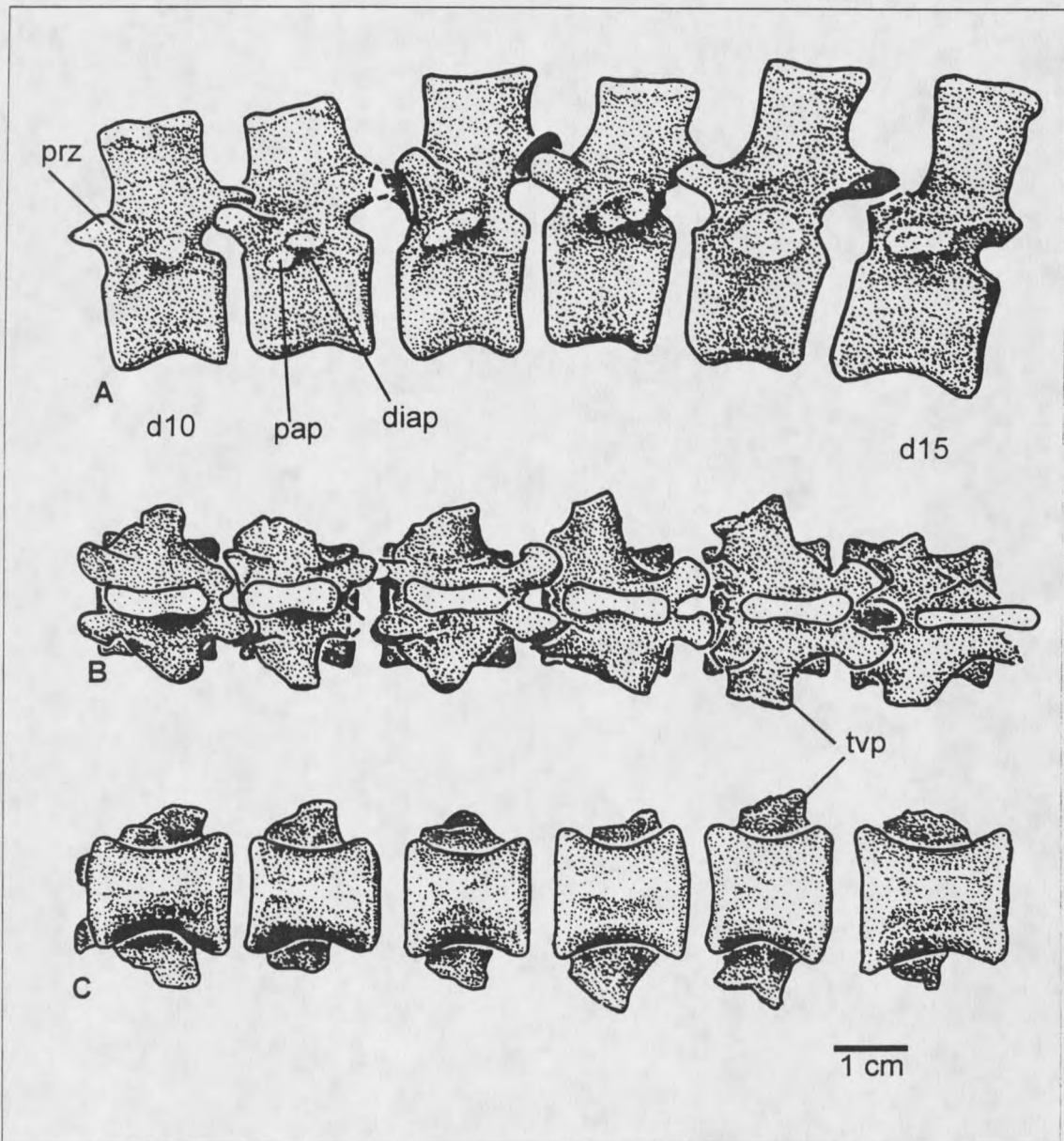


FIGURE 15. *Orodromeus* posterior dorsal vertebrae.

A) Posterior dorsal vertebrae 10-15 in left lateral view (MOR 473).

B) Posterior dorsal vertebrae 10-15 in dorsal view (MOR 473).

C) Posterior dorsal vertebrae 10-15 in ventral view (MOR 473).

Key to abbreviations is given in List of Nomenclature.

transverse processes arise lower on the neural arch and shorten until the parapophysis and diapophysis become one facet on the last two dorsal

vertebrae. These rib attachments remain centered over the centrum, except in dorsal vertebra fifteen where the single rib attachment is situated anterior of center to clear the anterior process of the ilium.

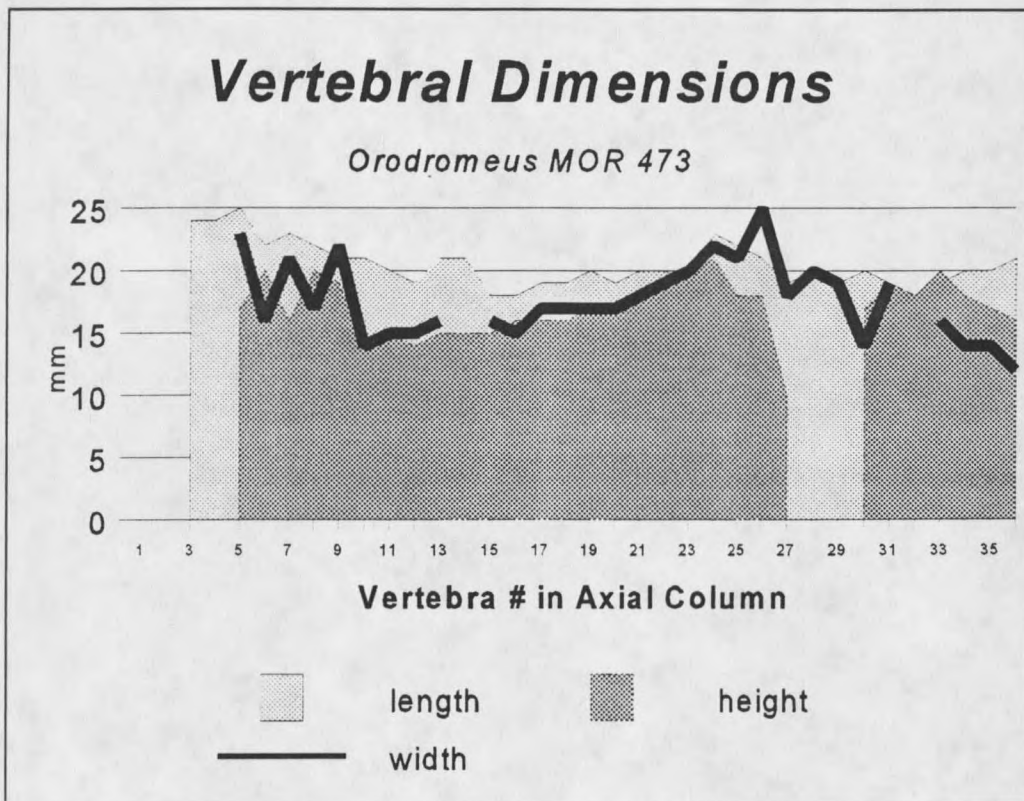


FIGURE 16. Measurements of vertebral centra through axial column of *Orodromeus*, MOR 473. Centra 1-9 cervical vertebrae, 10-24 dorsal vertebrae, 25-29 sacral vertebrae, and remainder caudal vertebrae.

The zygapophyses are large and widely separated in anterior dorsal vertebrae. By dorsal vertebrae 6 and 7 the zygapophyses are closer, smaller, and steeply inclined up and away from midline. The base of the transverse processes are wide, forming a broad shelf. In anterior dorsal vertebrae, this shelf slopes downward anteriorly and outside the prezygapophyses. Posteriorly,

the transverse processes are positioned lower on the neural arch and the parapophyses rise, the shelf widens but the slope still curves down anteriorly unlike that seen in *Zephyrosaurus*. The relative position of the zygapophyses is progressively lower from the first dorsal vertebra through to the fourth, then rises slightly higher in the fifth. The zygapophyses continue low until about the tenth dorsal vertebra, rising progressively again through the last. The postzygapophyses extend slightly further than the prezygapophyses.

Anteriorly in the series, the neural spines are tall, transversely thin and as narrow as the transverse processes. Each spine is situated, and reclines, somewhat posteriorly. In the latter half of the dorsal series, the neural spines have squared corners and are dorsally flattened, creating an uneven lateral brim. Each spine is centered over the centrum, and in the last dorsal vertebra, measures nearly as long antero-posteriorly as the centrum.

All dorsal centra have intervertebral muscle scars along the outer edge of the ends and on the ends of the ventral keels. Even on centra lacking keels, the ventral ends are rugose. The neurocentral sutures extend the full length of the centra throughout the dorsal vertebral series.

Sacral Vertebrae. *Orodromeus* has six sacral vertebrae. The first sacral centrum is the largest in every dimension, having a broad, nearly flattened ventral surface. The other sacrals are narrow, but all are ventrally flat, the last being transitional to a more rounded ventral surface as in the first caudal centrum. In the holotype, MOR 294, the sacrals appear fused into a single unit

(Figure 17). However, sacral vertebrae are separate in the largest specimen available, MOR 473, so the fusion in the smaller specimens may be superficial. Ends of the centra are U-shaped with a deep neural canal.

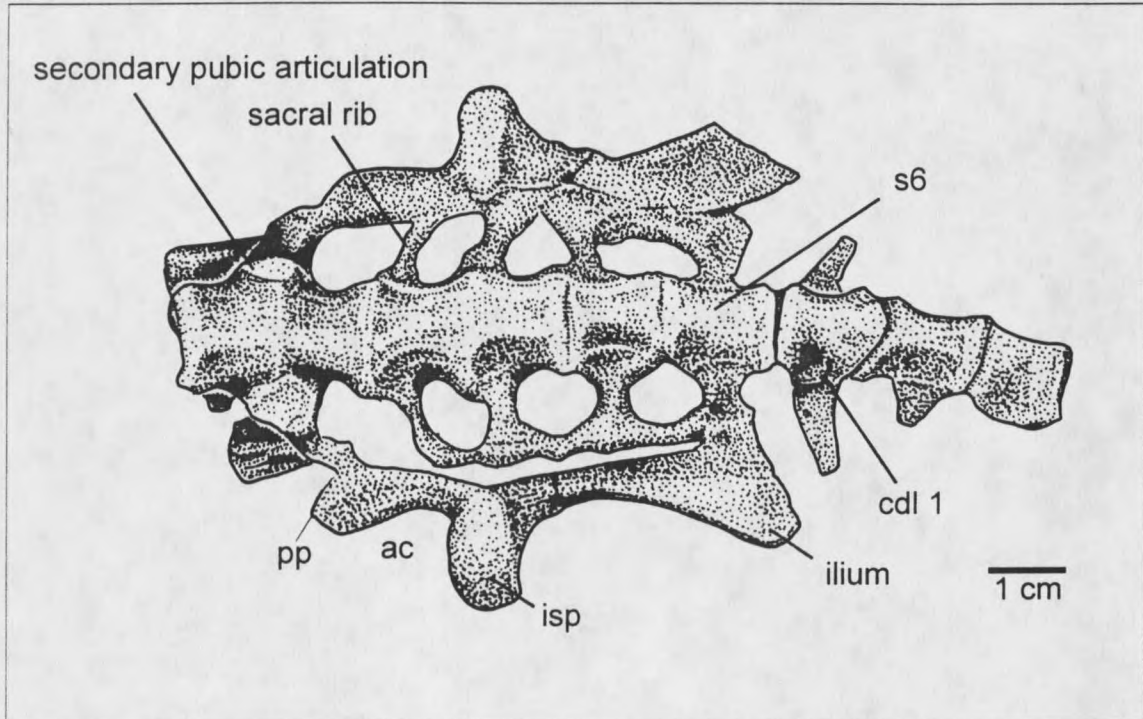


FIGURE 17. *Orodromeus* sacrum. Sacrum, ilia, and first caudal vertebrae in ventral view (MOR 294). Key to abbreviations is given in List of Nomenclature.

The irregular surface of the anterior face of the first sacral (or sacrodorsal) indicates a firm attachment to the last dorsal. The transverse process is short and contacts the anterior process of the ilium. The first and second sacral centra are noticeably wide where they meet, sharing a prominent ventrolateral socket below an intervertebral sacral rib. This socket is the articulation for the medial protuberance of the main body of the pubis. The sacral rib above this

joint served to support both the pubis and pubic peduncle of the ilium.

The second sacral rib arises laterally from the anterior base of the neuropophysis on the third sacral and supports the ilium above the acetabulum.

The robust third sacral rib braces the medial side of the ischiatic peduncle of the ilium. It arises laterally from the anterior edge of the base of the neuropophysis of the fourth sacral. Here, the base of the neural arch is much lower on the centrum than posteriorly.

The last two longer sacral ribs rise from the neurocentral suture in the remaining sacral vertebrae, migrating more posteriorly. Both ribs flare anteroposteriorly to contact the thin, brevis shelf of the ilium. The extension of these ribs, together with the modest brevis shelf, expand the posterior portion of the pelvis.

The sacral spines are transversely very thin, but broadened anteroposteriorly, nearly coalescing with one another in MOR 623. The top of the spines do not extend above the top of the ilium when articulated and are not dorsally flattened as seen in the dorsal vertebrae. In the young holotype, MOR 294, tendons are preserved along the sides of the spines throughout the length of the sacrum.

Caudal Vertebrae. Caudal vertebrae occur in about 30 specimens, but no complete caudal series, nor good articulated sections exist. And although tendons occur in the sacral series, no *Orodromeus* specimens preserve any ossified caudal tendons.

Only the holotype (MOR 294) and MOR 623 have good anterior caudal vertebrae. In these, the caudal vertebral ribs attach at the neurocentral suture (Figure 18) and are not fused. The first caudal rib is quite variable between specimens, some lie within the horizontal plane, others directed dorsolaterally, while others sweep more posteriorly. Anterior ribs behind the first, angle slightly dorsolaterally, and are twice as long as the centra are wide.

The first caudal centrum is equidimensional, but after the second caudal vertebrae, centra are noticeably taller, with height and width decreasing distally along the tail. Ventrally, anterior caudal vertebrae possess a weakly depressed groove. Dorsally, the neural arches cover the length of the centrum, sinking deeper onto the centrum anteriorly in the anterior-most caudal vertebrae. The first chevron occurs on the posterior end of the first caudal.

The first caudal vertebral spine reclines only slightly posteriorly and is situated posterior on the neural arch. Its sharp anterior edge does not continue down to the top of the neural canal. The posterior edge of the spine is broad near the base above the zygapophyses, and narrows dorsally to a sharp edge. The laterally thin and blade-like spines become progressively more reclined in succeeding vertebrae.

Both the pre- and post- zygapophyses extend just beyond the end of the centra, and even in anterior caudal vertebrae, are not large. Zygapophyses get progressively smaller posteriorly in distal vertebrae and angle 25 degrees from horizontal.

The mid-caudal centra are only slightly taller than wide and elongate

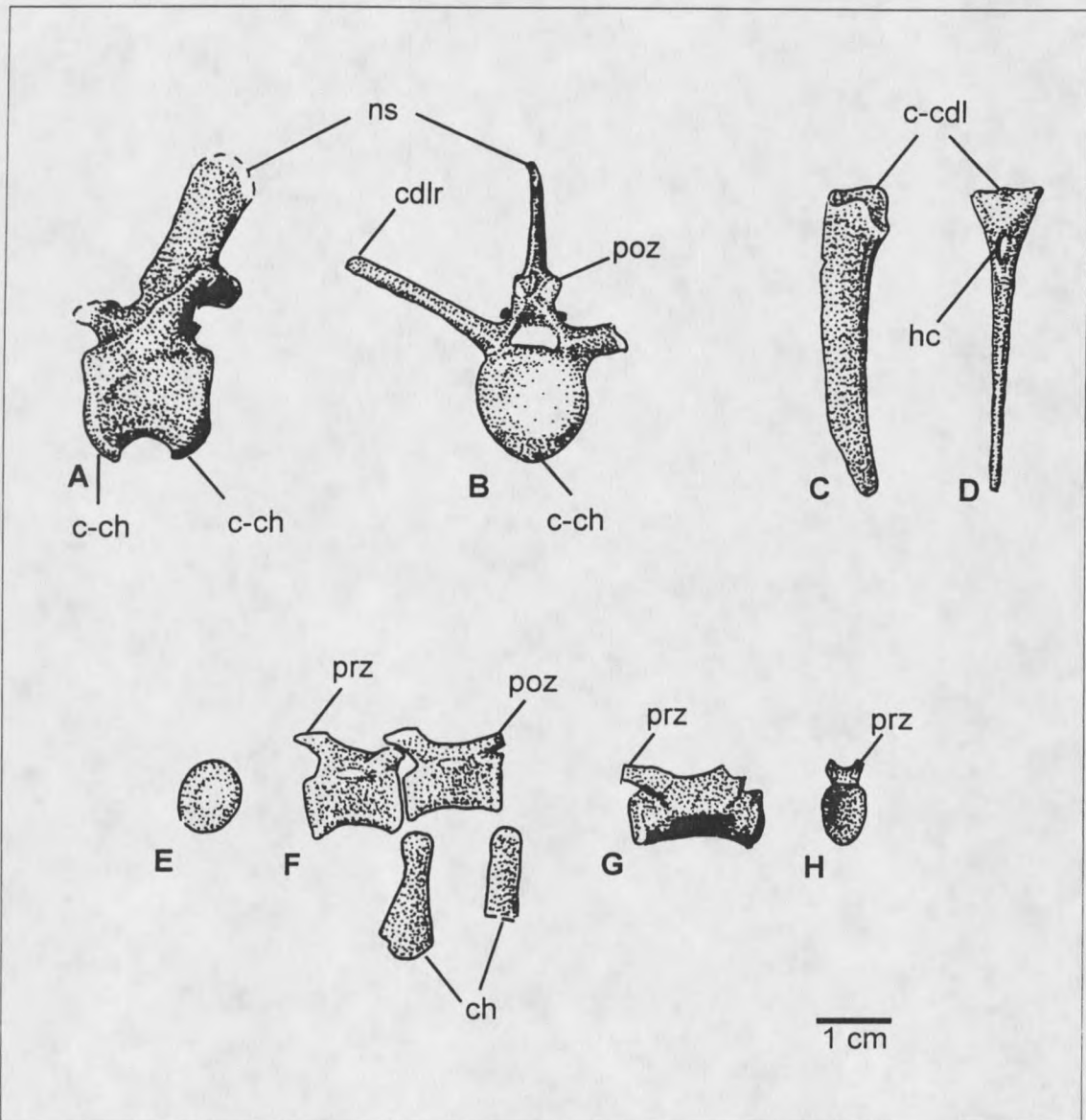


FIGURE 18. *Orodromeus* caudal vertebrae and chevrons.

A) Anterior caudal vertebra in left lateral view (MOR 623).

B) Anterior caudal vertebra in posterior view (MOR 623).

C) Anterior chevron in left lateral view (MOR 623).

D) Anterior chevron in posterior view (MOR 623).

E) Proximal articular surface of the anterior-most mid-series caudal centrum shown in F (MOR 650).

F) Mid-series caudal vertebrae with chevrons, all in left lateral view (MOR 650).

G) Posterior caudal vertebra in left lateral view (MOR 650).

H) Posterior caudal vertebra in anterior view (MOR 650).

Key to abbreviations is given in List of Nomenclature.

(Figure 18). Some individuals possess narrower mid-caudal centra with a deeper ventral groove. Posterior chevron facets are larger than anterior. The caudal rib consists of a boss arising from the upper edge of the centrum side and is set slightly posteriorly. The neural arch is low. Zygapophyses are small and nearly vertical articular facets that extend barely beyond the centrum. Neural arches are shorter and centered on the centra.

The distal caudal vertebrae retain a fairly consistent length, but appear elongate because the decreased height and width. As with the mid-caudal vertebrae, neural arches are shorter than the centra. The low neural arches lack spines. The minute zygapophyses are nearly vertical. No caudal rib exists, but for a full-length ridge along the side of the centra. Width and height are nearly equal, making The ends of the centra are nearly round in outline. The venter is weakly grooved.

Scapula. The scapula is described with the blade in horizontal position for the purpose of clarity. The scapula is a slender, bladiform element that curves medially at the expanded anterior end (Figure 19). Laterally, the anterior end is broadly concave above the glenoid, and roofed by a prominent scapular spine. The blade is fairly straight, expanding gradually posteriorly. The distal end is thin, with an irregular surface, suggesting a cartilaginous extension was present in life. The superior border of the broad scapular shaft bears a sharp edge. The ventral edge of the neck is thick and rounded, becoming sharper posteriorly along the scapular blade. A prominent scapular spine begins at the dorsal edge

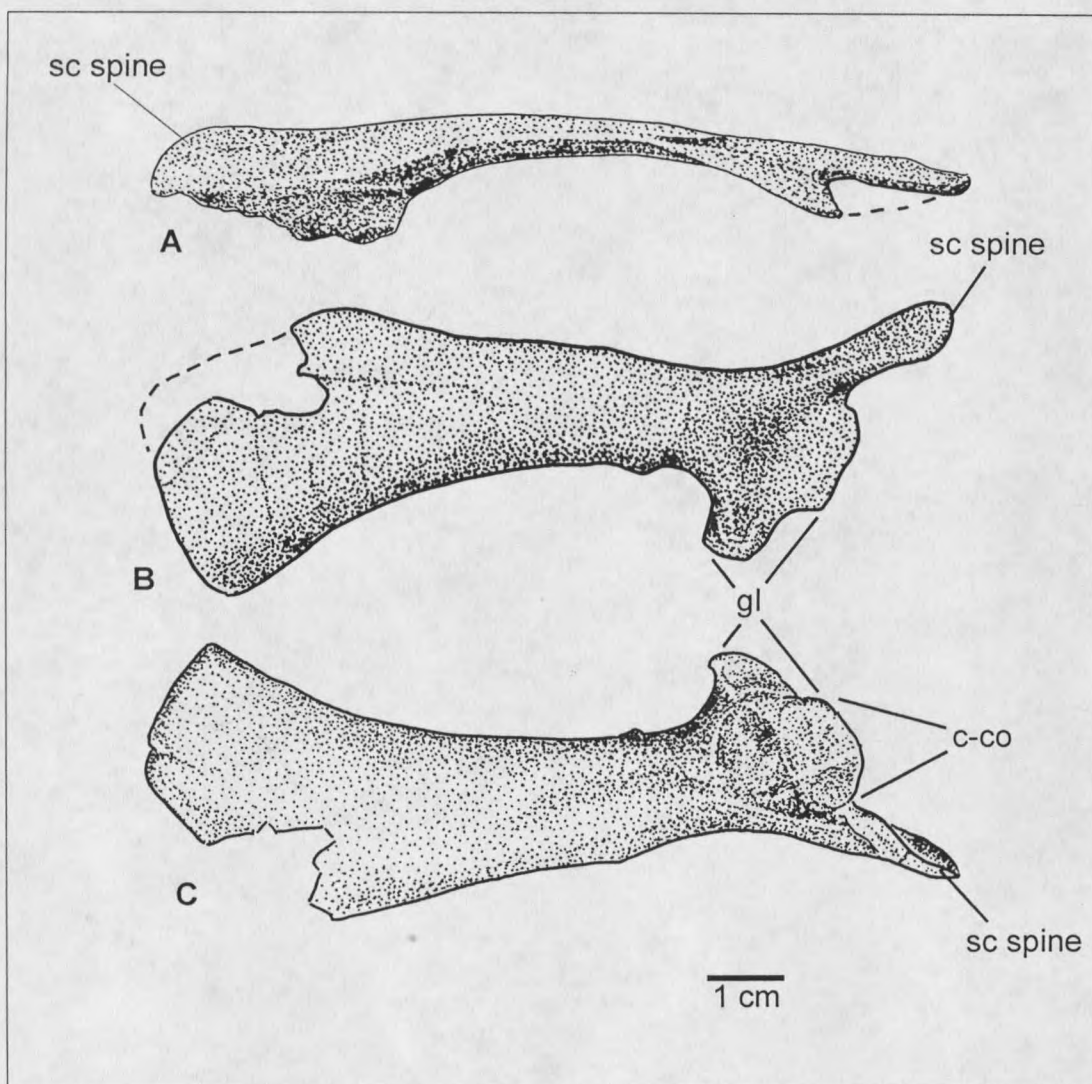


FIGURE 19. *Orodromeus* scapula.

A) Right scapula in dorsal view (MOR 623).

B) Right scapula in lateral view (MOR 623).

C) Right scapula in inverted medial view (MOR 623).

Key to abbreviations is given in List of Nomenclature.

of the shaft, and becomes sharper anteriorly. The scapular spine is a wide, flattened roof projecting over the posterodorsal edge of the coracoid.

Anteriorly, the articular surface for the coracoid is rugose, with radiating ridges and valleys for a tight interdigitate suture. Neither are fused however, even in the largest specimen, MOR 473. The thickest part of the scapula occurs

backing the glenoid. The glenoid is broad and smooth, angling 35-40 degrees posteriorly from the coracoid\scapula articulation.

Coracoid. The large coracoid is a relatively flat, thin bone (Figure 20), bordered posteriorly by a thick scapular articular surface, and posteroventrally by

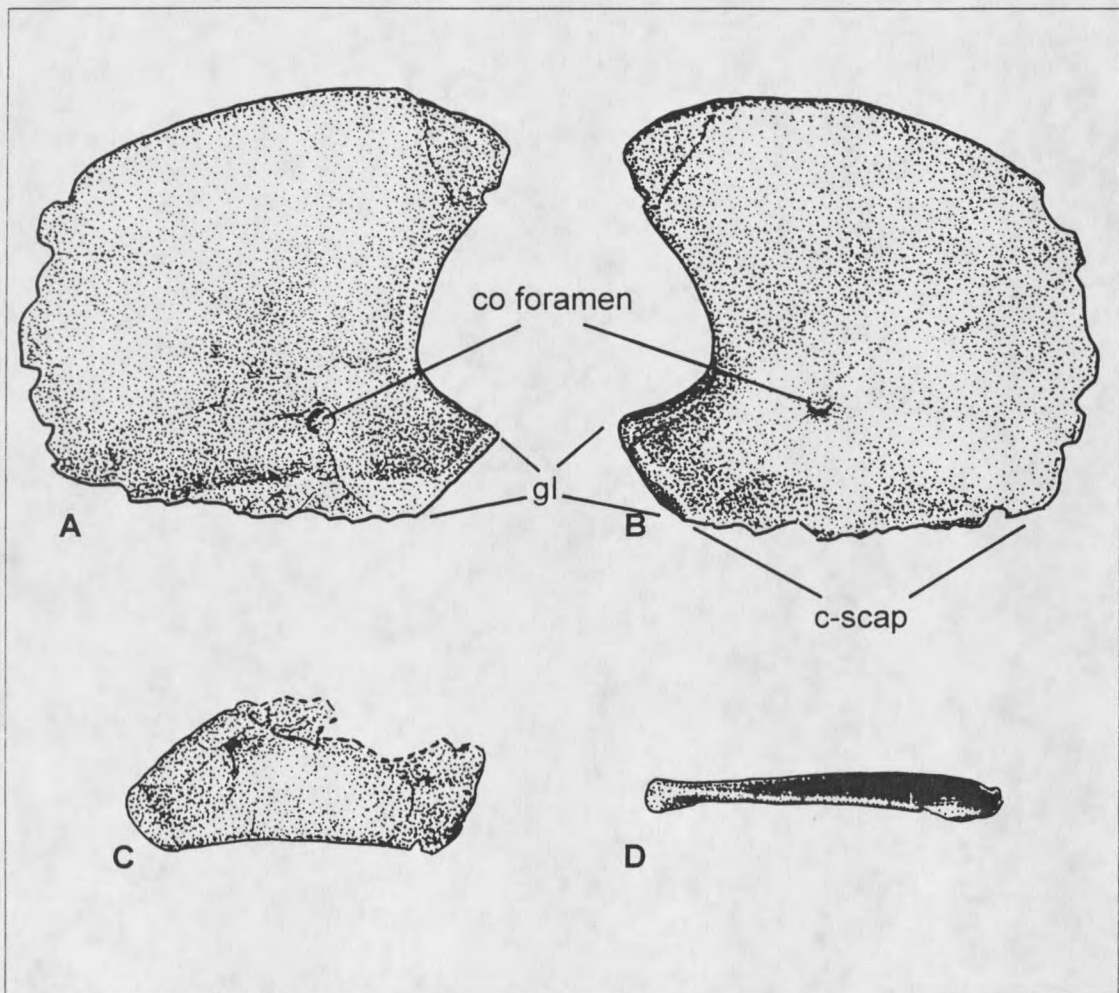


FIGURE 20. *Orodromeus* coracoid and sternal.

A) Left coracoid in lateral view (MOR 994).

B) Left coracoid in medial view (MOR 994).

C) Right sternal in ventral view (MOR 623).

D) Right sternal in lateral view (MOR 623).

Key to abbreviations is given in List of Nomenclature.

an equally large, smooth glenoid. The coracoid glenoid cavity is similar in size and shape to the other half of the glenoid formed by the scapula. Both measure 40 degrees from the scapula-coracoid articular surface, forming a 100 degree cup to house the humerus head. The glenoid cavity, when directed ventrally, orients the coracoid to angle out anterolaterally, creating an expanded pectoral region. In the young holotype (MOR 248), the coracoid is equally dimensional in height and width, whereas in the larger individual, the coracoid is broader than long and relatively flatter. Medially, the broad coracoid is subtly concave. The lower margin of the coracoid is arched along a ventral sulcus leading to a moderate anterior hook. The coracoid foramen extends straight through the coracoid, well anterior to the scapula, with a posterior recess on the lateral side, exiting medially with a depressed dorsal rim.

Sternal. *Orodromeus* sternals are of typical shape for primitive ornithopods (Figure 20). The flat plate-like element is distinctively longer than wide, with rounded, thicker medial edges. Laterally, the edges are sharper and straighter.

Humerus. The humerus in *Orodromeus makelai* does not differ significantly from *Hypsilophodon* and is typical of small ornithopods. In lateral view, the humerus is slightly sigmoidal, bending at the prominent deltopectoral crest, with the upper expanded portion extending medially and posteriorly (Figure 21). The humerus is widest at the proximal end with a centered, slightly raised

