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

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 phytogeny. The revision of the Hypsilophodontidae resulted in a dissolution of the group into a pectinate grade of dinosaurs with a concommitment 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.

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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   John R. Horner (Signature)   4/23/99 (Date)

Approved for the Department of Biology

Dr. Ernest R. Vyse   E R Vyse (Signature)   4/23/99 (Date)

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Dr. Bruce R. McLeod   Bruce R. McLeod (Signature)   5-3-99 (Date)

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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.

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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: supraocciptal
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 concommitment 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.

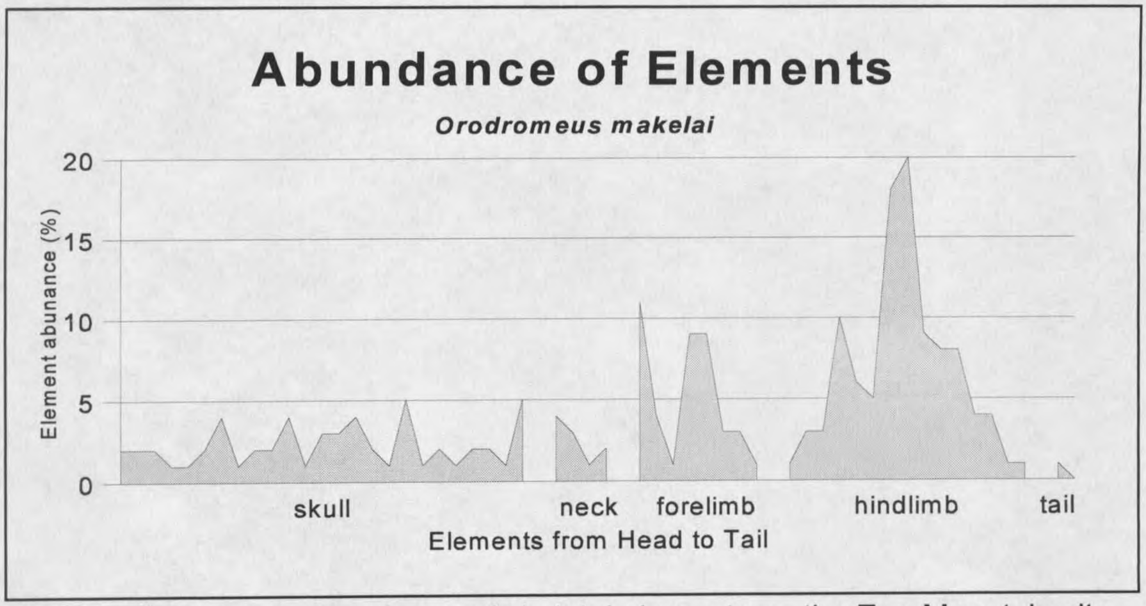

FIGURE 1. Relative abundance of skeletal elements on the Egg Mountain site of the Two Medicine Formation. Highest peak represents femora and tibiae as most abundant, with scapulae and ilia occurring in about 10% of the specimens.

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.

<u>Stratigraphic Context</u>

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 $^{40}Ar/^{39}Ar$ 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 ornithopod (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

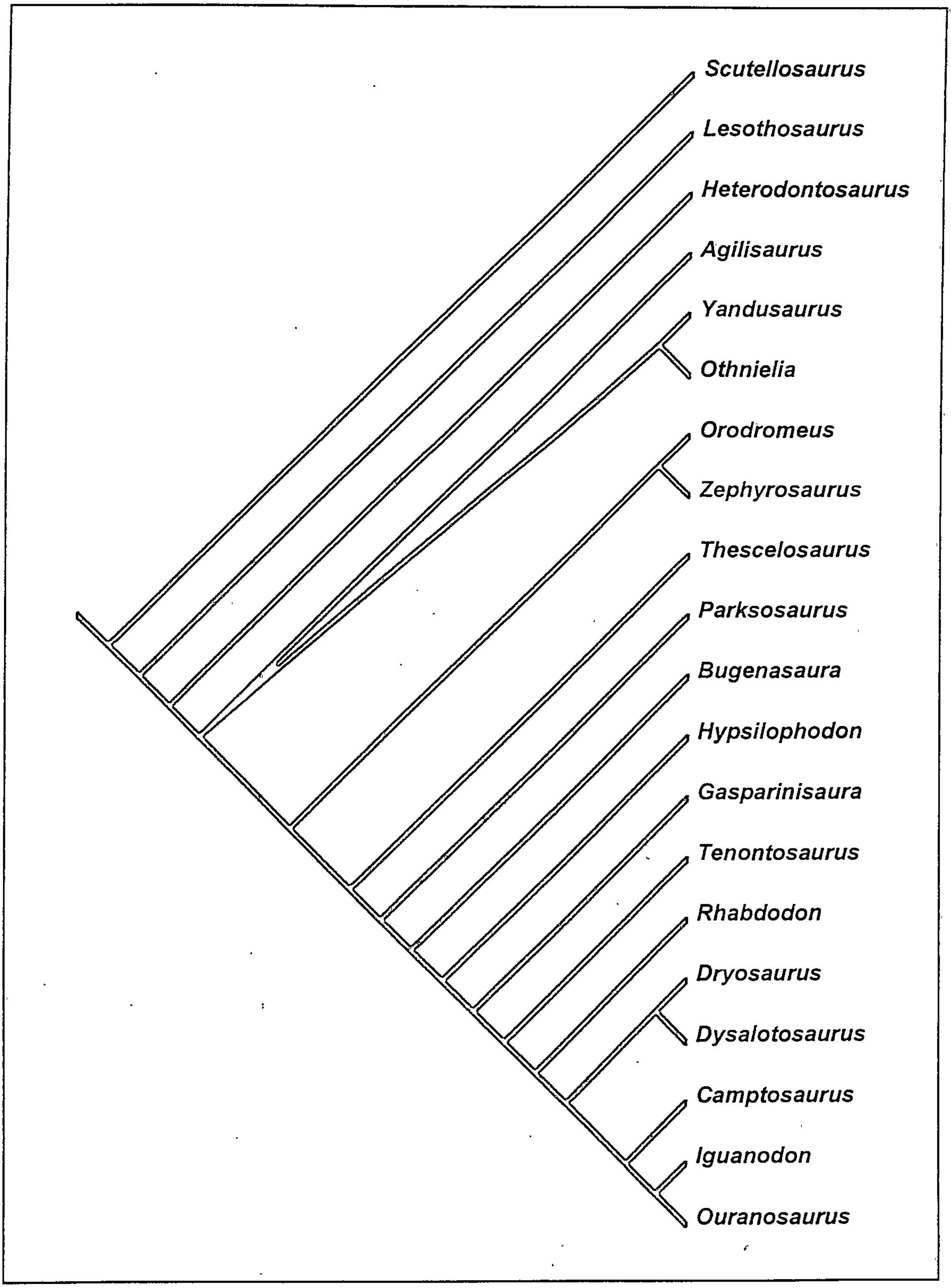

FIGURE 2. Cladogram of the phylogeny of basal ornithopods based on this study.

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 neotoneus, 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 ontogentic stage is by documenting histological development. Even though *exact* skeletalchronology 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.

OORODROMEUS 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 predentary, 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

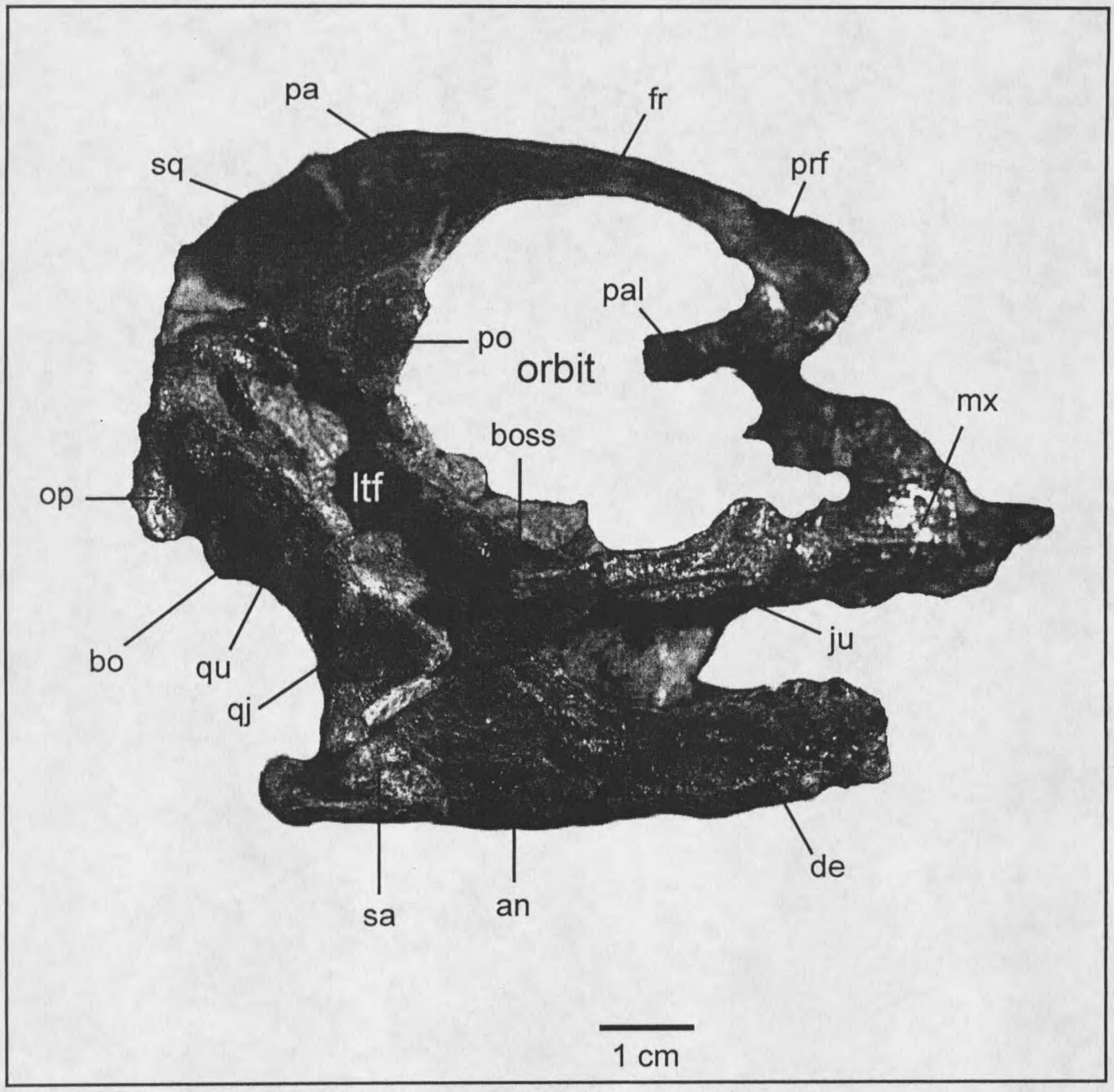

FIGURE 3. Skull of *Orodromeus makelai* type specimen.
Skull of juvenile in right lateral view (MOR 294). Rostrum is missing.
Key to abbreviations is given in List of Nomenclature.

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.