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A reinterpretation of the small Captorhinid Reptile Captorhinikos Parvus Olson as a new genus, reanalysis of its cranial anatomy, and a phylogenetic analysis of the basal reptilian family Captorhinidae

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ITS CRANIAL ANATOMY, AND A PHYLOGENETIC ANALYSIS OF THE

BASAL REPTILIAN FAMILY CAPTORHINIDAE

A Project

Presented to the

Faculty of

California State University,

San Bernardino

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science

in

Biology:

Paleontology

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by

Gavan McBride Albright

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6 June 2003
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ABSTRACT

The cranial anatomy of the basal captorhinid reptile *Captorhinikos parvus* (Reptilia, Captorhinidae), is reinterpreted here based on analysis of a group of new specimens recovered subsequent to it's original diagnosis as well as further analysis of the original specimens utilized in E.C. Olson's (1970) original characterization of the species. Structural features inconsistent with the generic description of *Captorhinikos* suggest the redefinition of *C. parvus* as a new genus, *Rhodotheratus parvus*. *Rhodotheratus* is represented by: adult material and characterized by it's small size when compared to most other captorhinid species; possession of multiple rows of non-ogival maxillary and mandibular marginal teeth; lack of a supratemporal bone; and the maxillary articulation with palate contacting both palatine and vomer

Phylogenetic analyses of basal members and selected derived members of the Captorhinidae support the characterization of *Rhodotheratus* as a distinct taxon and indicated that it is closely related to the South African form *Saurorictus*.

and colleagues at Crafton Hills College for dragging the author kicking and screaming back into graduate school in the first place, and for their patience and understanding with the author over the course of the project. Finally, the author wishes to thank Charles Darwin, without who's ground-breaking research the field of Paleontology wouldn't exist as it does, and Juan Valdez, for helping the author through many late nights and early mornings worth of work.

TABLE OF CONTENTS

LIST OF FIGURES

ix

CHAPTER ONE

INTRODUCTION

Background

The development of the Amniota within terrestrial vertebrates was marked by the emergence of an important suite of adaptations. Collectively, these adaptations are considered to be an example of a key adaptation (Martin and Sumida, 1997). Amniota is traditionally defined by the presence of an egg with extra-embryonic membranes that facilitate its ability to withstand desiccation and mechanical insult (Stewart, 1997). The evolution of organisms that were reproductively independent from the water allowed for more effective exploitation of the terrestrial environment, and preceded a great radiation of new forms (Martin and Sumida, 1997). In addition to the developing embryo itself, an amniotic egg includes several extra-embryonic membranes, including, minimally, an amnion, a chorion, and an allontois (Sumida, 1997). In some forms, a shell membrane is also present. These traits most likely developed individually over an extended period of geologic time.

Evidence of soft tissue morphology, particularly developmental features, is rare to nonexistent in the fossil record. Fortunately, a suite of skeletal characters accompanies this transition. Cranial features that are currently considered unambiguous characters of the amniote clade include: the loss of the intertemporal bone, the presence of supraoccipital ossification, lack of contact between a parietal lappet and the squamosal, the presence of a single splenial in the lower jaw, and inclusion of the frontal bone in the margin of the orbit (Sumida et al., 1992; Laurin and Reisz, 1995, 1997). Table 1 provides a complete listing of skeletal characteristics that are currently considered to define the clade Amniota.

Some of the earliest organisms commonly accepted as true amniotes include those belonging to the Synapsida (the lineage ultimately leading to mammals), the poorly defined Parareptilia (currently including Paraeiasauroidea, Millerosauroidea, and Procolophonia) (Gauthier et al. 1988; Laurin and Reisz, 1995) within Reptilia, and the more extensively studied "captorhinomorpha" within the Eureptilia. Figure 1 summarizes a relationship among the taxa spanning the amphibian to amniote transition, as well as some of the first radiations of basal amniotes.

2

"Captorhinomorpha" is a paraphyletic grouping
encompassing the Captorhinidae and the Protorothyrididae,
and most recent analyses (e.g. Lombard and Sumida, 1992;
Berman et al., 1997) suggest that Synapsida, Parareptilia,
Captorhinidae, and Protorothyrididae, plus Diapsida
describe a series of successively more derived amniote
clades. Given these possible relationships, the
Parareptilia and Captorhinidae represent the best
candidates for a model of basal reptilian structure.
Gauthier et al. (1988) and Berman et al. (2000) note that
members of the Parareptilia are only partially known.
Thus, the Captorhinidae emerge as a pivotal group in
understanding basal reptilian structure and relationships.

Reptilia is perhaps best known for the Diapsida, one
of the most diverse and persistent of vertebrate groups
(Heaton and Reisz, 1986; Dodick and Modesto, 1995; Laurin
and Reisz, 1995), including extant lizards and snakes,
dinosaurs, and their hierarchical subset, Aves.
Captorhinidae represents one of the earliest clearly
defined clades within the Reptilia. To date, captorhinid
remains have been recovered from Permian deposits (between
290 - 250 million years before present) in Africa, India,
Europe (the former Soviet Union), North America (the United

States) (Olson, 1962a; Dilkes and Reisz, 1986; Sumida,

1989; Ivachenko, 1990; Jalil and Dutuit, 1996; Gow, 2000),

and possibly Tasmania (Romer, 1973). Captorhinidae,

believed to be the more primitive of the two

"captorhinomorph" families (Reisz and Baird, 1983; Ricqlés

and Bolt, 1983; Heaton and Reisz, 1985; Sumida, 1990;

1997), includes 14 genera: *Romeria**, *Protocaptorhinus**,

Rhiodenticulatus*, *Captorhinus**, *Labidosaurus**, *Riabininus*,

Labidisaurikos*, *Rothianiscus**, *Captorhinikos**,

Hecatogomphius, *Kahneria**, *Moradisaurus*, *Acrodontia*, and

Saurorictus[1] (Olson, 1962a; Ricqlès, 1984; Dilkes and Reisz,

1986; Ivachenko, 1990; Dodick and Modesto, 1995; Laurin and

Reisz, 1995; Jalil and Dutuit, 1996; Modesto and Smith,

2001).

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[1] * = Species for which fossil material has been found in North America

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370        350        330        310       290       270       250
      360        340        320       300       280       260       240
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Dev. | Miss. | Penn. | Permian | Triassic

———— Anthracosauroidia

———— Seymouriamorpha

———— Westlothiana

1

———— Diadectomorpha

2

———— Synapsida

———— Paraeiasauroidia

3

———— Millerosauroidia

———— Procolophonia

———— Captorhinidae

4

———— Protorothyrididae

5

———— Araeoscelidia
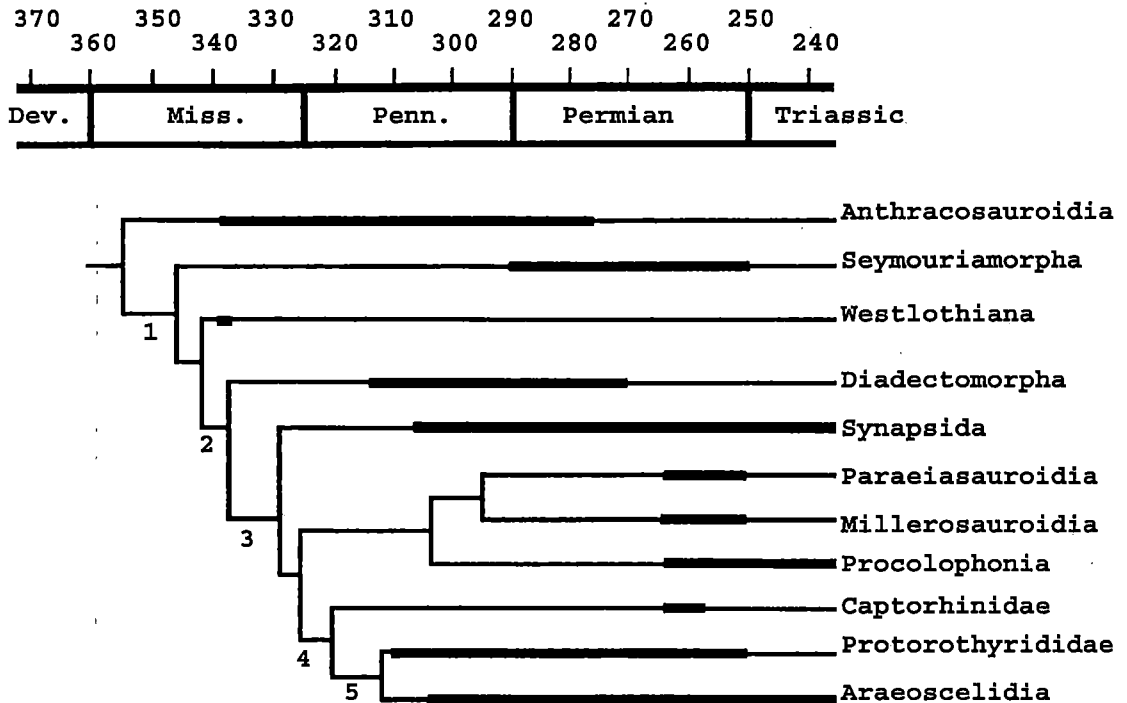
Figure 1. Detailed cladogram showing the temporal framework of the captorhinidae and related taxa. 1) Batrachosauria; 2) Cotylosauria; 3) Amniota; 4) Sauropsida; 5) Eureptilia. Dev. = Devonian; Miss. = Mississippian; Penn. = Pennsylvanian (After Lombard and Sumida, 1992).

Overview of Cranial Anatomy
in the Captorhinidae

Cranial anatomy in captorhinid reptiles has generally been characterized as being "heavily and stoutly" constructed, irrespective of taxon size. For this reason, and because the skull yields a large number of systematic characters, most published reports have focused on interpretation of cranial material (Seltin, 1959; Heaton, 1979). Members of this group display a highly conserved cranial design (Dilkes and Reisz, 1986; Olson, 1962b), resulting in a diagnostic group of captorhinid cranial characteristics. Such features include: a low, flat dorsal surface profile forming nearly a 90 degree angle with the posterior border of the skull; a posteroventrally angled premaxilla; lateral maxillary flexure, or "swelling" of the cheek region; distinctively textured dermal bone surfaces (possibly a characteristic for the diffusion of stress and increasing the skull's resistance to fracture [Coldiron, 1974]); and the loss of the tabular bone (Ricqlès and Bolt, 1983; Heaton and Reisz, 1985; Dodick and Modesto, 1995).

A frequently proposed evolutionary trend within the family Captorhinidae is a general increase in overall (and hence, skull) size in more derived members of the group.

In most cases a concomitant increase in the number of maxillary and mandibular tooth rows accompanies the increase in skull size. This is accompanied by an increase in "cheek-flaring." Reisz and Baird (1983), Ricqlès and Bolt (1983), and Dilkes and Reisz (1986), have suggested that this was probably associated with the increase in number of tooth rows as species within the family become more derived. This hypothesis presumes that the increase in tooth row number is a single, well-defined trend. Skull size in captorhinids spans an order of magnitude, from specimens assigned to *Captorhinikos parvus*, the primary taxon considered in this review, with an average skull size of approximately 23 - 26 mm (Olson, 1970), to the largest, *Moradisaurus grandis*, with an average skull length up to 45 cm (Taquet, 1969; Heaton and Reisz, 1980; Ricqlès and Bolt, 1983). *Labidosaurikos meachami* with an average skull length of 28 cm (Dodick and Modesto, 1995), 6 maxillary and 5 mandibular tooth rows, and *Moradisaurus*, with approximately 12 tooth rows, provide excellent examples of large captorhinids with multiple tooth rows. Twelve tooth rows in *Moradisaurus* are the most of all known captorhinid species (DeRicqlés and Bolt, 1983).

The Genus *Captorhinikos*

Within the Captorhinidae, the genus *Captorhinikos* was originally erected by Olson (1954) to include two species; *C. valensis* and *C. chozaensis*, named, respectively, for the Lower Permian Vale and Choza Formations of north-central Texas. Olson's (1954) cranial description of the genus is as follows:

> Lower jaw with four regular rows of bulbous, sub-conical post-canine teeth. Outer and inner rows not extending full length of post-canine series and not overlapping so that there are but three effective rows at any level. Enlarged "canine" tooth above and below. Maxillary dentition with five rows of bulbous, sub-conical teeth, forming a crescentic tooth plate; teeth increasing in size from anterior and posterior ends of plate to center and rows most widely spaces at center. Skull heart shaped in outline.

In his subsequent review of the family Captorhinidae, Seltin (1959) noted fundamental differences between *Captorhinikos chozaensis* and *C. valensis* and confirmed their taxonomic validity and placement within the genus (based only on similarities in the number of tooth rows and

8

general dental patterns). He made no changes to Olson's diagnosis of the genus.

With the description of *C. parvus* by Olson (1970), a third species was assigned to the genus *Captorhinikos*. Information on the relative relationships of the more derived "captorhinikomorphs" and the other members of the family is extremely limited. Berman and Reisz (1986) proposed a possible relationship for six basal genera within the Captorhinidae (*Romeria, Protocaptorhinus, Rhiodenticulatus, Labidosaurus,* and *Eocaptorhinus/Captorhinus*) based upon a suite of shared derived characters. However, the focus of their study was on *Rhiodenticulatus* and basal members of the Captorhinidae; the more derived genera, including *Captorhinikos*, were not included in their analysis of relationships. Gaffney and McKenna (1979) proposed a phylogenetic relationship that encompassed the majority of the accepted members of the Captorhinidae at the time of publication, but did not describe the relationships between the more derived genera making up the last branch of their cladogram, which lumped together *Kahneria, Hecatogomphius, Rothia, Moradisaurus, Labidosaurikos,* and *Captorhinikos*. Ricqlès (1984) proposed at least one phylogenetic hypothesis for the position of

Captorhinikos within this group. However, Dodick and Modesto (1995) now question the validity of its placement, though they did not provide an alternative hypothesis.

Captorhinikos parvus was originally described by Olson (1970). Notably, certain elements of the specific diagnosis contradict the generic diagnosis (see above) that Olson provided twenty years earlier (Olson, 1954).

A small, but mature captorhinid with a skull length ranging from about 23 to 26 mm. Skull broad, with maximum width about two-thirds that of the skull length. Upper dentition with four premaxillary teeth, 13 to 15 marginal maxillary teeth. And two inner rows on maxillary, the outer with five and inner with three teeth respectively. Premaxillary teeth long, but not recurved. Second and third maxillary teeth robust and long.

Lower jaw with second and third teeth elongated. Fifth tooth inset slightly and continuing as part of inner of two rows of teeth in posterior part of tooth row. Labial row of four or five teeth beginning back of level of

fifth tooth. Coronoid process of lower jaw

strong, and post-coronoid ramus long and slender.

Significant differences between the original generic

diagnosis and that of *Captorhinikos parvus* include: only

three maxillary tooth rows (as opposed to five in the

original diagnosis), only two mandibular tooth rows (as

opposed to four), and a distinct caniniform region (as

opposed a single tooth with teeth increasing in size from

anterior and posterior ends of toothplate). *C. parvus* has

not been restudied since Olson's initial 1970 description.

In his initial description, Olson (1970) reviewed a body of

specimens, all of which were recovered from a locality in

the Hennessey Formation, Cleveland County, Oklahoma (Figure

2). The cranial material was so fragmentary that Olson

(1970) turned to the appendicular skeleton and the degree

of limb-bone ossification to support his contention that *C.*

parvus was a small adult. Subsequent to his initial

description, Olson collected additional specimens, which he

also ascribed to *C. parvus*, from what he initially

interpreted as another Hennessey Formation locality near

Norman, Oklahoma (Figure 2). These specimens, cataloged
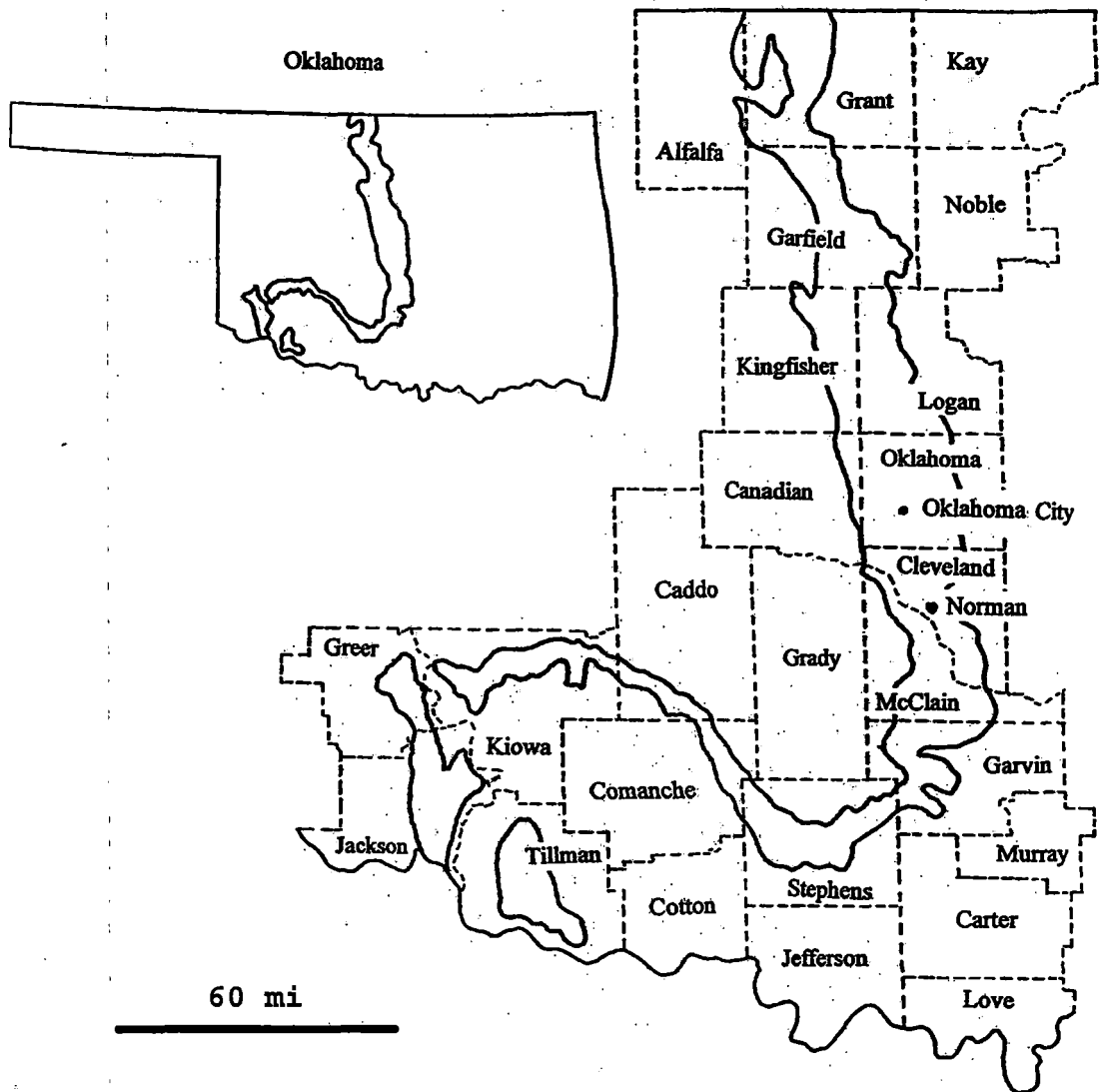
Figure 2. Map of Oklahoma displaying the extent of exposure of the Hennessey Formation, an approximately S-shaped band running between the northern and southern borders of Oklahoma (from Olson, 1967).

into the UCLA vertebrate paleontology collection, were not completely prepared or described before his death. Significantly, these more recently collected specimens include much more complete and better-preserved cranial material than those originally available to Olson in 1970.

Geologic and Geographic
Context

All of the specimens germane to this study (see materials) were recovered from the Lower Permian Hennessey Formation of Oklahoma. Hennessey Formation exposure extends across central and southwestern Oklahoma (Figure 2). The Hennessey Formation is a complex unit consisting primarily of red and multicolored shale and sandstone, with small amounts of siltstone and mudstone. Most of the specimens described here were recovered from the red shale deposits (Olson, 1967).

The holotype of *Captorhinikos parvus* as well as all of the specimens assigned to the species by Olson in his initial study (See Table 2 for a complete list of specimens and descriptions) were recovered from a locality approximately 1.5 miles southeast of the University of Oklahoma at Norman (SW ¼, NW ¼, sec. 13, T. 8 N., R. 2 W), in Cleveland County, Oklahoma, approximately 70 feet above

13

the base of the Hennessey Formation (Olson, 1970).

Initially, it appeared that all of the more recently

recovered specimens reviewed in this reinterpretation were

recovered from a similar, but separate site also in the

region of Norman. Re-evaluation of the locality

information listed in Olson's 1967, 1970 and 1971 studies,

as well as Olson and Vaughn (1970), and comparison with the

locality information of the new specimens, however,

revealed that all of the specimens ascribed to *C. parvus*

originated from the same locality as those described in the

initial study.

Most of the published stratigraphic analyses of the

south-central and south-western United States focus on New

Mexico and north-central Texas (Hentz, 1988; 1989; Eberth

and Berman, 1993; Sumida et. al., 1996), resulting in a

reasonable consensus among paleontologists regarding the

correlations between the various Permo-Pennsylvanian rock

units within those states. Traditional methods of dividing

the terrestrial Lower Permian deposits of north-central

Texas have recently been revised by Hentz (1988). Hook

(1989) has provided a useful key to the appropriate

formational nomenclature. Unfortunately, there is not such

agreement regarding the rock formations of corresponding

14

age in Oklahoma. Perhaps surprisingly, even in the case of

Texas, there is little correlative data with Oklahoma

(Hook, 1989). Although a detailed analysis of the

Hennessey Formation rock units of central Oklahoma is

beyond the scope of this study, their accurate temporal

assignment is, however, important. There have been several

attempts to correlate rock units in Oklahoma with the

better-known Texas rock units. Currently, the best

comparative studies of these regions are those of Olson

(1967), and Olson and Vaughn (1970). They suggested a

correlation between the Hennessey Formation exposures of

central and north-central Oklahoma and the upper portion of

Hook's (1989) "undivided" Clear Fork Group (formerly the

Choza Formation) of north-central Texas based on

similarities in rock units and fossil assemblages (Figure

3). Olson and Chudinov later (1991) reaffirmed this

correlation in a manuscript, which, unfortunately, remained

unpublished. If the correlation of the Hennessey Formation

with the upper section of the Clear Fork Groupis correct,

this establishes the Hennessey Formation as Middle Lower

Permian, Upper Leonardian in age (Jones and Hentz, 1988)

	Series	Four Corners (S.E. Utah)	North-central New Mexico	North-central Texas	Central Oklahoma	Dunkard Basin
L O W E R P E R M I A N	Guadalupian			Pease River Group		
	Leonardian		San Andreas / Glorieta Ss.	Clear Fork Group - Undivided (Formerly Choza, Vale, and Arroyo Formations)	Hennessey / Hennessey-Garber Transition / Garber	
	Wolfcampian	DeChelly Sandstone	YESO — San Ysidro Member / Meseta Blanca	Wichita Group		Dunkard Group
		Organ Rock Shale	Cutler Formation			
		Cedar Mesa Sandstone		Bowie Group		
		Halgaito Formation				
C A R B.	Virgilian To Desmoian	Hermosa Group	Madera Formation			Monogahela Group

Figure 3. Correlations of the Lower Permian rock formations and groups of North America (Adapted from Olson and Vaughn, 1970; Jones and Hentz, 1988; Hook, 1989; Sumida, et. al., 1996).

and an approximate date of 270-275 million years before present.

By looking at the depositional characteristics of sediments as well as faunal assemblages, Olson and others (Olson and Vaughn, 1970; Olson, 1977; Olson and Mead, 1982) determined the climatic patterns for the Clear Fork Group of Texas and its equivalents in Oklahoma during the Permo-Carboniferous time segment. This was a period of transition in central North America. The climate was moving from a non-seasonal one with high humidity and year-round rainfall to a drier one, characterized by a high degree of seasonality with regard to rainfall. During this drier climate, lakes and other bodies of water were subject to regular annual restrictions. Olson (1977) has noted a shift in vertebrate faunal assemblages of Permo-Carboniferous red bed communities concurrent with this climatic shift. With the increasing seasonal aridity, conditions became less favorable for amphibians, which needed regular moisture to avoid desiccation, instead selecting for organisms that could withstand first temporary, and finally permanent separation from the water. Captorhinomorphs were some of the first organisms to exploit these new conditions, and are common in sediments

17

of lakes and ponds in this region of alternating wet and dry periods (Olson, 1977).

CHAPTER TWO

METHODOLOGY

Materials

The following lists identify all of the specimens
attributed to *Captorhinikos parvus* Olson (to date) reviewed
in this study.

Previously undescribed specimens (16):

UCLA-VP 2894: (Partial) skull with lower

jaw.

UCLA-VP 2898: Partial skull.

UCLA-VP 2900: Badly crushed skull.

UCLA-VP 2908: Skull.

UCLA-VP 2910: Skull.

UCLA-VP 2912: Skull.

UCLA-VP 2915: Skull (with braincase).

UCLA-VP 2918: Partial skull.

UCLA-VP 2922: Partially crushed skull.

UCLA-VP 2933: Partial skull with limb bone.

UCLA-VP 3023: Three skulls; (a) crushed

skull, (b) partial skull, (c)

skull with partial lower jaw.

UCLA-VP 3024: (a) and (b) Two skulls, both

(badly) crushed with lower

jaw.

UCLA-VP 3025: Partial crushed skull.

Specimens included in Olson's (1970) initial
characterization of *C. parvus* but which have been more
fully prepared, and re-examined as part of this study (7):

FMNH UR 1255: Skull (with braincase).

FMNH UR 1256: Skull (with braincase).

FMNH UR 1257: Partially crushed skull (with

braincase).

FMNH UR 1258: Partial Skull.

FMNH UR 1272: Right lower jaw.

FMNH UR 1273: Partial right lower jaw.

FMNH UR 1278: Partial left lower jaw.

Methods

The vertebrate paleontology lab in the Department of
Biology at California State University San Bernardino
obtained the listed UCLA-VP (University of California at
Los Angeles, Vertebrate Paleontology) specimens assigned to
Captorhinikos parvus (see Materials) on extended loan from

the UCLA vertebrate paleontology collection. FMNH (Field Museum of Natural History, Chicago, IL) specimens previously described by Olson (1970) were examined at the Field Museum of Natural History in Chicago. Observed FMNH specimens were photographed for later interpretation and study, and a limited selection of specimens (listed above) were loaned to the CSUSB Vertebrate Paleontology lab for further preparation and reanalysis.

Most of the more recently recovered specimens had already been prepared, but not completely. Mechanical preparation, consisting primarily of matrix removal and specimen stabilization, was performed on both groups of specimens before they were described and illustrated. NIH Image-J (Image J, 2002) image analysis software was utilized to make reliable measurements, considering the extremely small size and delicate nature of all observed specimens (Listed above). Illustration of specimens conformed to common standards of paleontological description: (1) Color, and black & white photography, as well as surface scanning of the specimens using a flatbed scanner; and (2) stippled, black and white, pen and ink line drawings with the lighting from the upper left position.

Specimens assigned to *Captorhinikos parvus* are amongst the smallest assigned to the Captorhinidae and yet, display multiple tooth rows. This represents a significant deviation from the proposed trend of increased size accompanying increased numbers of tooth rows in the family. Furthermore, Olson's (1970) own description of *C. parvus'* diagnostic characters is inconsistent with many of the features he used to characterize the genus to which he assigned it. Thus, the validity of *C. parvus'* placement within *Captorhinikos* is called into question. Data from newly studied specimens, as well as information acquired through additional preparation of Olson's original specimens now allow a more thorough consideration of the question of: cranial morphology of the species, degree of maturity represented by the specimens, and ultimately the phylogenetic disposition of the species. The last of these questions can only be assessed subsequent to the other two.

The morphological question is two-fold: (1) is *Captorhinikos parvus* a distinct, valid taxon or a member of a previously described taxon, and (2) has it been described from adult or juvenile material? Three possible hypotheses emerge: (1) *C. parvus* may be a valid adult taxon; (2) it may be a distinct taxon, but one based on juvenile

material; (3) it may be a juvenile representative of a previously described taxon. Features used to assess the degree of maturity of observed specimens include: (1) degree of cranial sutural interdigitation complexity (decreased complexity implies juvenility; extreme immaturity can be marked by incompletely closed sutures or presence of fontanels) (Rieppel, 1992), (2) degree of dermal sculpturing (less pronounced texture implies juvenility), (3) relationship between orbit and skull size (greater orbit size relative to overall skull size implies juvenility), and (4) tooth row development morphology (based upon criteria described by Ricqlés and Bolt, 1983).

If *Captorhinikos parvus* is indeed a valid taxon, careful anatomical analysis should assist in refining an understanding of the interrelationships of it and other members of the Captorhinidae. Phylogenetic analysis was performed using PAUP* 4.0b (Swofford, 2002) to analyze a data matrix (Table 4) of 43 morphological skull characters (Albright et al., 2002). The anatomical descriptions that form the basis of this data set are presented in chapter three. Appendix B summarizes all characters and character-states used in this analysis.

Using the morphological characters, the taxonomic validity of each of the captorhinid taxa were examined to determine the phylogenetic relationship between them. Cladistic methodology demands that any valid taxon be diagnosable with one or more apomorphic (unique, derived) characters or, lacking that, a unique combination of primitive and derived characters. Phylogenetic systematics, or "cladistics," states that the interrelationships of taxa must be based not on overall similarity, but on the presence of shared, derived characters. In other words, shared primitive features (symplesiomorphies) may give information about structure, but not about relatedness or phylogenetic position. A clear understanding of cladistic methodology is critical to any study that could be important to understanding the radiation or basal members of an important grouping. As the Captorhinidae are important to the understanding of basal Amniota, cladistic methodology was utilized throughout this study.

Abbreviations

Institutional abbreviations used in text: FMNH, Field Museum of Natural History, Chicago, Illinois; CM, Carnegie Museum of Natural History; UCLA-VP, University of California at Los Angeles, Vertebrate Paleontology. From 1988-1990, the UCLA VP collections were subsumed into the collections of the University of California Museum of Paleontology (UCMP) and the Carnegie Museum of Natural History (CM). The specimens in this study were acquired immediately before that transfer, and therefore do not yet have corresponding CM accession numbers.

Anatomical abbreviations used in figures: a, angular; ant ridge, anterior ridge; ar, articular; bo, basioccipital; br, basicranial recess (pterygoid); bs, basisphenoid; c, coronoid cb, cornua branchalia; col, columella (stapes); cult. pr., cultriform process (parasphenoid); d, dentary; ect, ectopterygoid; eo, exoccipital; f, frontal; ftpl, footplate (stapes); j, jugal; l, lacrimal; m, maxilla; max pr, maxillary process; max fa, maxillary facet (palatine/vomer); n, nasal; o, occipital; op, opisthotic; p, parietal; pa, prearticular; pl, palatine; pas, parasphenoid; pf, postfrontal; pin for, pineal foramen; pm, premaxilla; po, postorbital; pp,

postparietal; pr, palatine ramus (pterygoid); prf, prefrontal; pt, pterygoid; ptp, pterygoid process (quadrate);q, quadrate; qj, quadratojugal; qr, quadrate ramus (pterygoid); qu, quadratojugal; sa, surangular; sm, septomaxilla; sp, splenial; sq, squamosal; s, stapes; st for, stapedial foramen; tf, transverse flange (pterygoid); v, vomer.

CHAPTER THREE

SYSTEMATIC PALEONTOLOGY

Systematic Paleontology

Given that the morphology of the specimens examined

here and the phylogenetic analysis of those specimens

(discussed in chapter 4) warrant the description of a new

genus, the following the following formal characterization

is presented.

Reptilia - Laurenti, 1768

Eureptilia - Olson, 1947

Captorhinidae - Case, 1911

Rhodotheratus – New Genus, 2003

Rhodotheratus parvus - New Combination

Etymology

Rhodon - Greek, meaning rose (flower)

Therates - Greek, meaning to hunt. The dentitional

characteristics of *Rhodotheratus parvus* indicate that,

despite its small size, it was a carnivore, probably

feeding on small insects.

Parvus - Latin, meaning small. The original species

name was retained for E. C. Olson's original diagnosis of

this organism as a small, adult captorhinid.

Type Species

Rhodotheratus parvus

New Holotype

UCLA VP 2910 - With the reassignment of all specimens originally assigned by Olson (1970) to *Captorhinikos parvus* to the new genus *Rhodotheratus*, a new holotype specimen has been assigned for *Rhodotheratus parvus*. UCLA VP 2910, a nearly complete skull that most clearly displays the new areas and structures which structures described and illustrated for the first time in the following pages.

Horizon and locality

Lower Permian Hennessey Formation, approximately 21.3 m above the base. SW ¼, NW ¼, sec. 13, T. 8 N., R. 2 W., Cleveland County, Oklahoma (approximately 1½ miles southeast of University of Oklahoma, Norman).

Diagnosis

Small-sized captorhinid reptile with, skull length approximately 23-29 mm (average length approximately 25 mm). Maximum skull width relatively broad, approximately two-thirds skull length. Skull shape triangular, as opposed to "heart-shaped," as in other multiple-tooth-rowed species. Lack of supratemporal bone. Maxillary articulation with the palate contacts both the palatine and

vomer. Quadrate non-symmetrical dumbbell shape with the larger of the two condyles medial, with a long-axis orientation offset approximately 40-45 degrees from the short axis (perpendicular to the rostro-caudal axis). Diamond-shaped section of the posterior parasphenoid separated from the remaining anterior portion by thin sutures. Coronoid process of lower jaw strongly developed, and post-coronoid ramus long and slender. Upper dentition consists of four premaxillary teeth and three maxillary tooth rows. Twelve to fourteen marginal maxillary teeth and two inner tooth rows on maxillary, the outer with five and inner with three to four teeth. Dentary dentition with two tooth rows. Second and third teeth of outer lower tooth row mesio-distally elongated. Sixth tooth inset slightly and continuing as part of inner of the two rows of teeth in posterior part of tooth row. Labial row of four or five teeth beginning at level of fifth or sixth tooth of labial row. All teeth are non-recurved and lack labial fluting.

Description

General

The skull of *Rhodotheratus parvus* displays all of the
characteristic captorhinid features: a low, flat profile,
dermal sculpturing, cheek flaring, down-turned premaxilla,
and loss of the tabular bone. Dermal sculpturing covers
the entire dorsal surface of the skull and is quite
prominent on most specimens, though some of the specimens
used by Olson (1970) in his initial description were
prepared to a degree that resulted in destruction of some
or all of the sculpture. Heaton (1979) noted that such
over-preparation can impact significantly character-state
interpretations, particularly those based on sutural
patterns. Thus, the new specimens described here become
extremely important to a confident interpretation of
anatomical and phylogenetic data for *Rhodotheratus*. Cheek
flaring and down-turned premaxilla, though present, are not
present to the degree that is seen in other, larger
captorhinid species.

More detailed evaluation, both of previously described
and new specimens demand modification of Olson's original
reconstruction. The general outline of the skull of
Rhodotheratus (dorsal view), is "triangular," as opposed to

"heart-shaped," as in the members of the family with greater numbers of maxillary tooth rows. Olson (1970) described the skull table as having bilateral embayments along the posterior borders of the squamosals. However, newly examined specimens indicate that the caudal border of the skull roof has a straight margin. The ventral border of the skull, save for the slight downward hooking of the premaxilla, is relatively straight in lateral view with slight undulations. As with *Captorhinus laticeps* (1979), the lateral surface of the muzzle of *Rhodotheratus* is vertical or nearly so. The dentition is non-ogival.

Table 3 provides a complete list of all skull elements visible in each specimen.
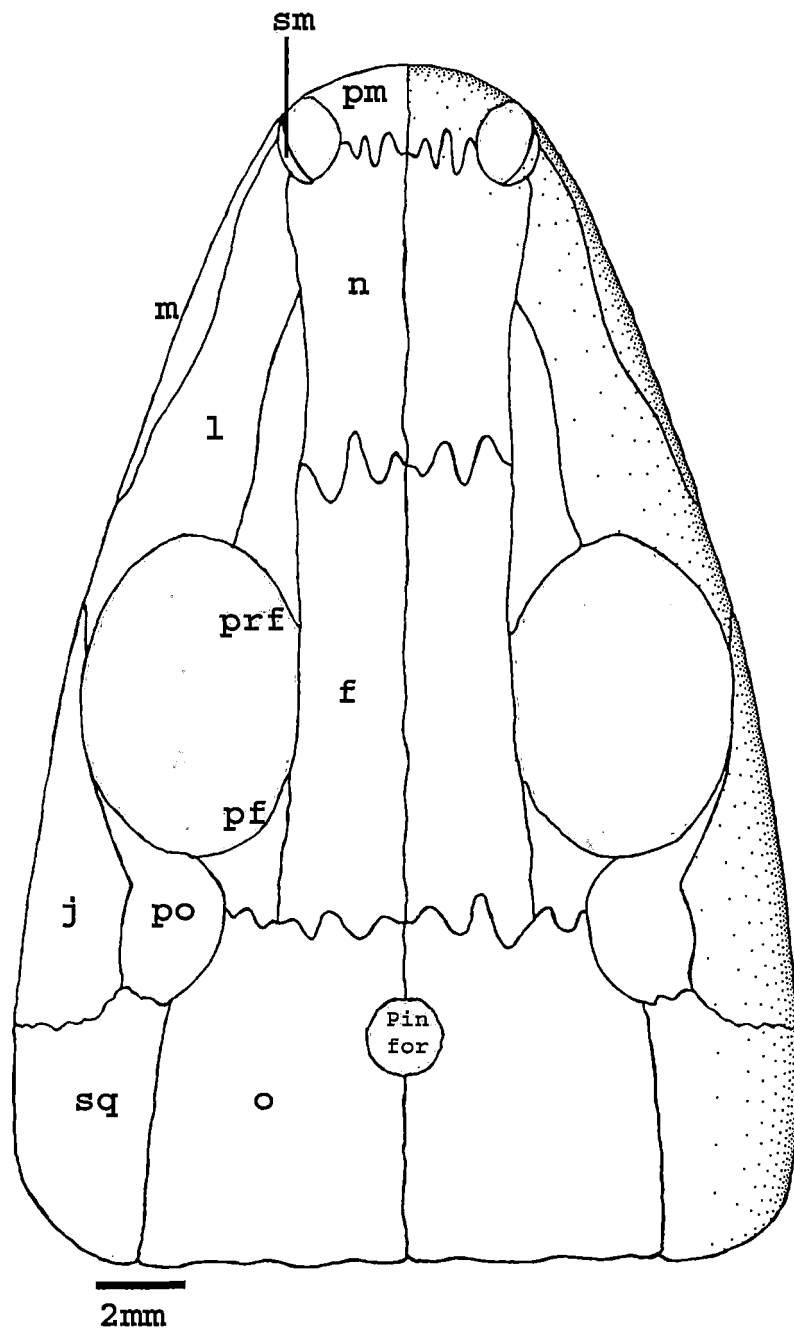
Figure 4A. *Rhodotheratus parvus*, Reconstruction of Skull in Dorsal View.
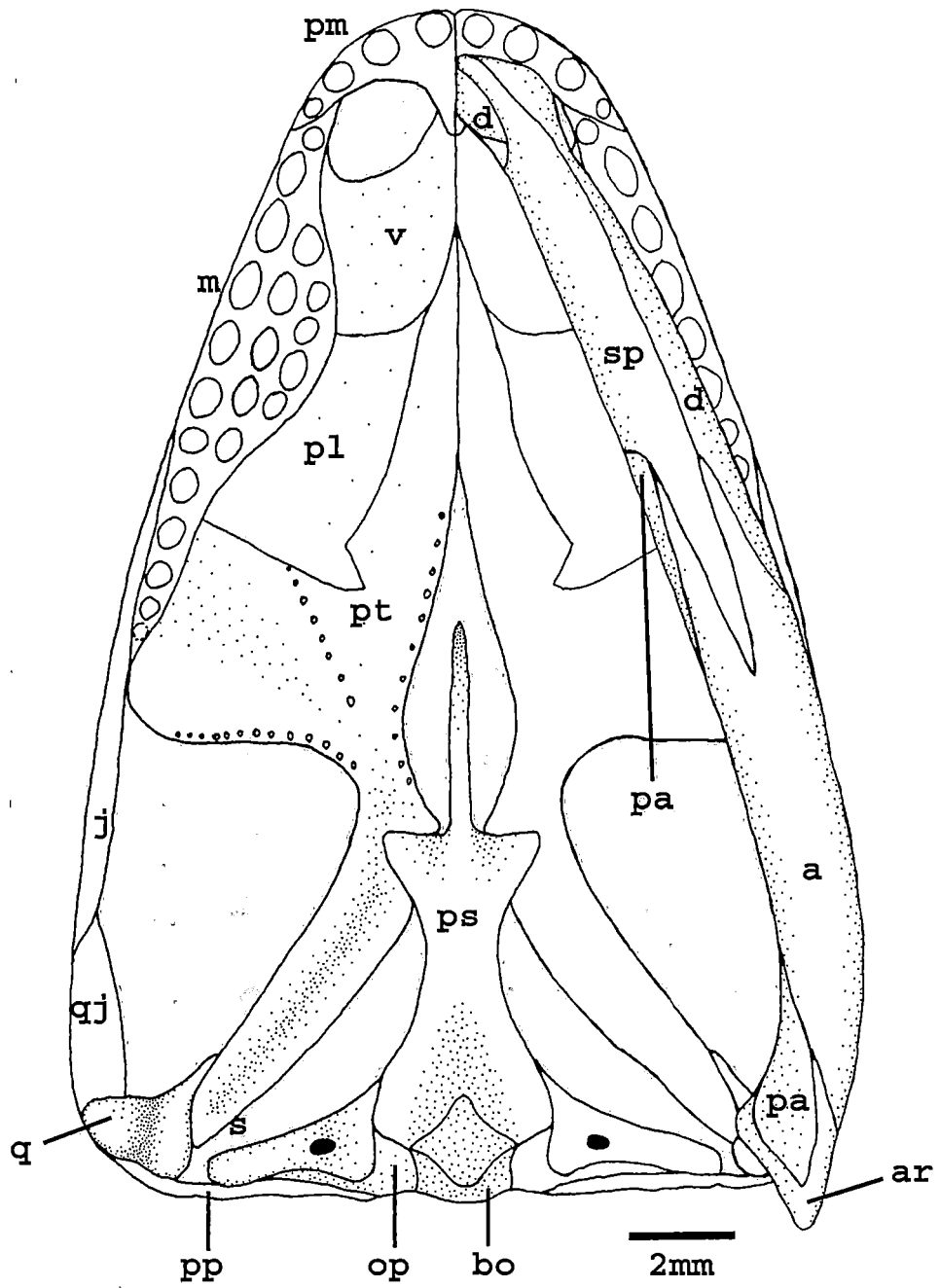
Figure 4B. *Rhodotheratus parvus*, Reconstruction of Skull in Ventral View.
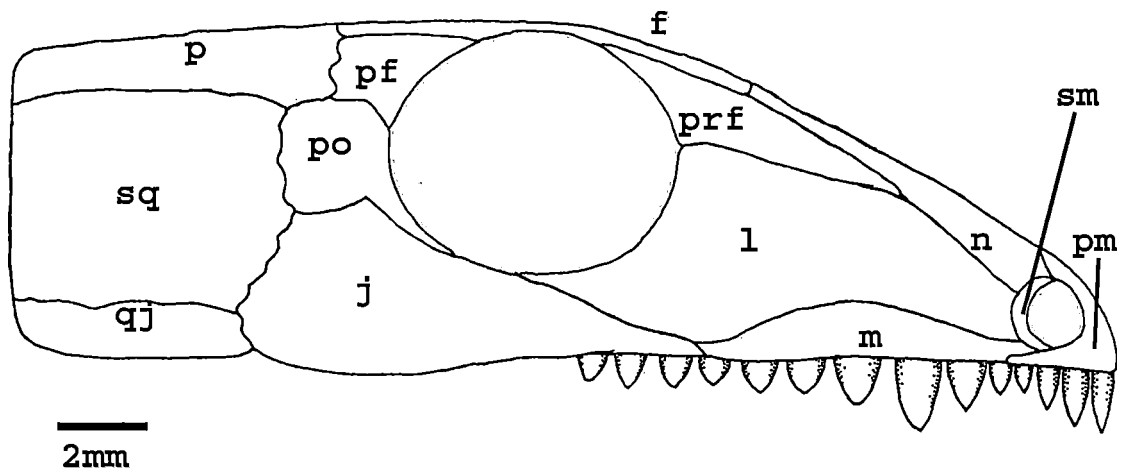
Figure 4C. *Rhodotheratus parvus*, Reconstruction of Skull in Right Lateral View.
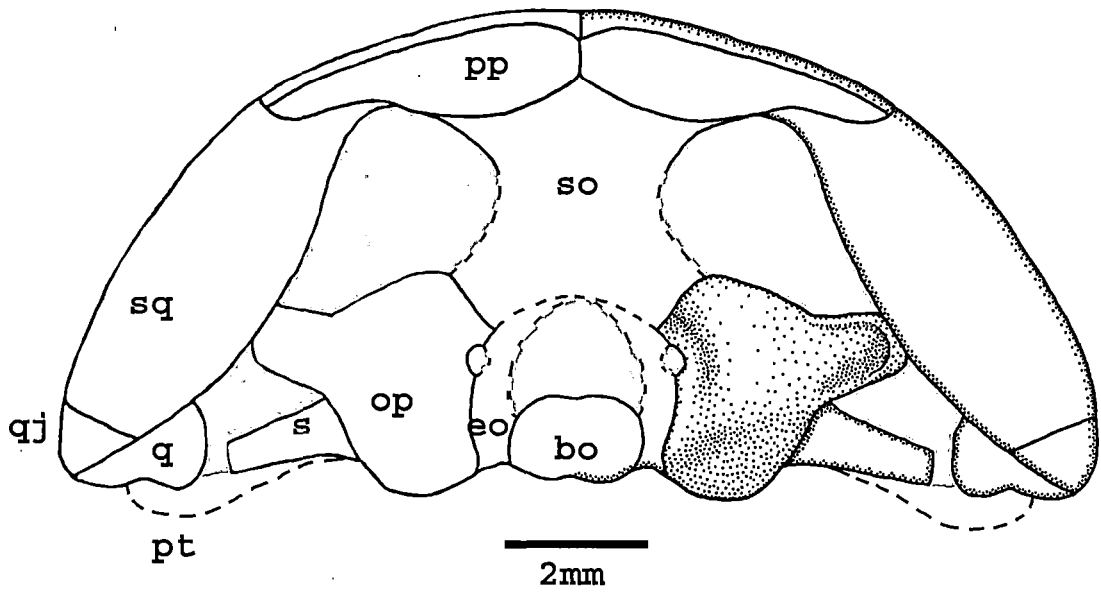
Figure 4D. *Rhodotheratus parvus*, Reconstruction of Skull in Occipital View.
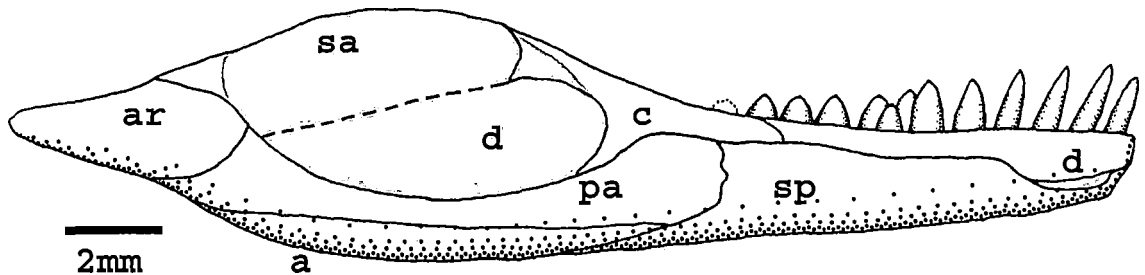
Figure 5A. *Rhodotheratus parvus*, Reconstruction of Left Mandible in Lingual View.
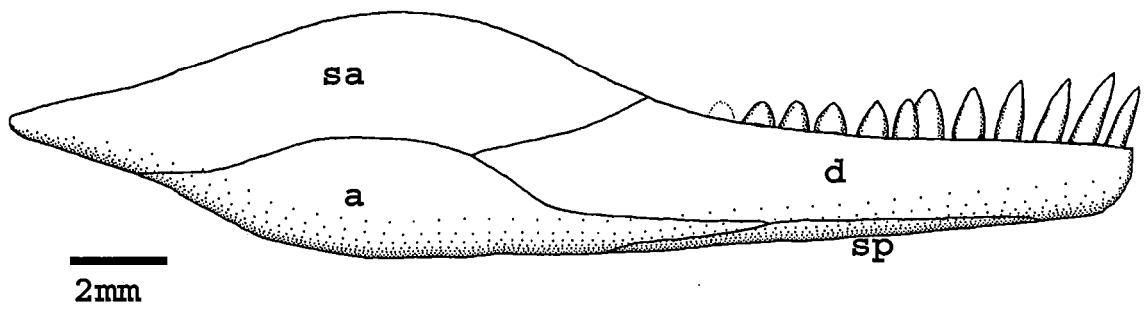
Figure 5B. *Rhodotheratus parvus*, Reconstruction of
Right Mandible in Lateral View.

Dermal Skull Roof

Premaxilla. The premaxilla is a tri-radiate structure consisting of nasal, maxillary, and vomerine rami. The maxillary ramus (measured from the anterior border of the external narial opening) tapers distally, and carries the two distal-most premaxillary teeth (Figures 4,6,7). Only the dorsal-most portion of the nasal ramus is visible in a strictly dorsal view, and it contacts the nasal bone posterodorsally along a highly interdigitated suture. The vomerine ramus extends posteriorly to contact the anterior tip of the vomer along the mid-sagittal suture of the palate. The premaxilla has an average height of 2.2 mm, average total anterior-posterior length (lateral view) of 2.4 mm, and encompasses the anterior and anteroventral borders of external narial opening. Light sculpturing is present on the external surfaces, and it is angled only slightly postero-ventrally to the horizontal plane (Figure 7).

Four conical, premaxillary teeth are present. They are much longer (from base to tip) than wide and taper to a sharp point. The first tooth is the largest and close to mesial edge of the bone. The remaining teeth decrease in size distolaterally.
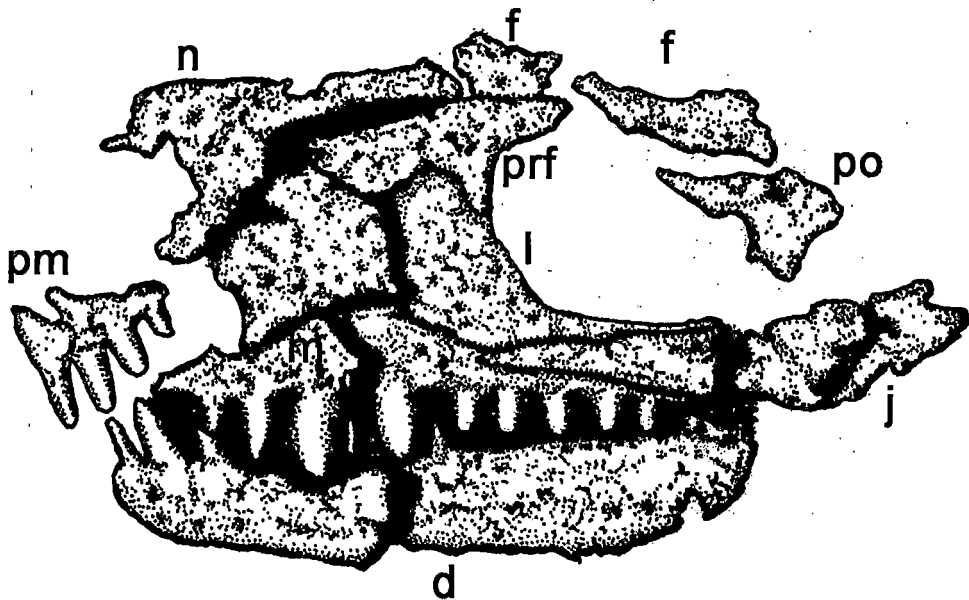
Figure 6. UCLA VP 2922. *Rhodotheratus parvus*, Skull
in Left Lateral View.

Maxilla. The maxilla is the primary tooth-bearing element of the skull, and is a long, narrow bone, average total length approximately 11.2 mm (Figures 4,6,7,10). The rostral end of the maxilla is drawn out, to form a thin premaxillary process that overlaps the posterior maxillary process of the premaxilla. The anterodorsal border of premaxillary process forms the posteroventral border of external narial opening. Passing posteriorly, the dorsal edge of the maxilla increases in height and then decreases to form a convex "humplike" region with its maximum height (average 1.4 mm) above a caniniform tooth approximately one-third of the way down the length of the bone. The anterior two thirds of the maxilla contacts the lachrymal dorsally, whereas the posterior third underlies the jugal. Rostrally, a distinct mesial widening of the maxilla contacts the vomer and palatine to accommodate the three maxillary tooth rows. The facet on the palate marking its connection with the maxilla straddles the suture connecting the vomer and palatine. There is only light sculpturing on the lateral dermal surface of the maxilla.

Septomaxilla. The septomaxilla, visible only in FMNH

UR 1255, is a scroll-shaped bone whose outer edge forms the

mouth of the narial opening. The diameter of the opening

decreases medially, forming a funnel shaped canal.

Lachrymal. The lachrymal is a large, irregularly

shaped bone comprising most of the lateral aspect of the

snout on each side of the skull, extending from the

posterior margin of external narial opening to the anterior

and anteroventral margin of the orbit (Figures 4,6,7,8,10).

The lachrymal contacts the nasal anterodorsally, the

prefrontal posterodorsally, maxilla ventrally, and jugal

posteriorly. Posteroventrally, an acuminate, suborbital

process extends to approximately the midpoint of the orbit.

The dorsal border is concave upward in the region of the

suture with the prefrontal, and the height of the bone

decreases to accommodate the anterior process of the

prefrontal before increasing slightly again to contact the

lateral border of the nasal bone. The posterodorsal border

is drawn out into a slightly projecting antorbital process,

though it is not as long as the posterior process. Two

vertically aligned foramina are visible on the bone's

posterior orbital surface. These correspond roughly to the

positions of the lachrymal puncta of *Captorhinus laticeps* (Heaton, 1979).
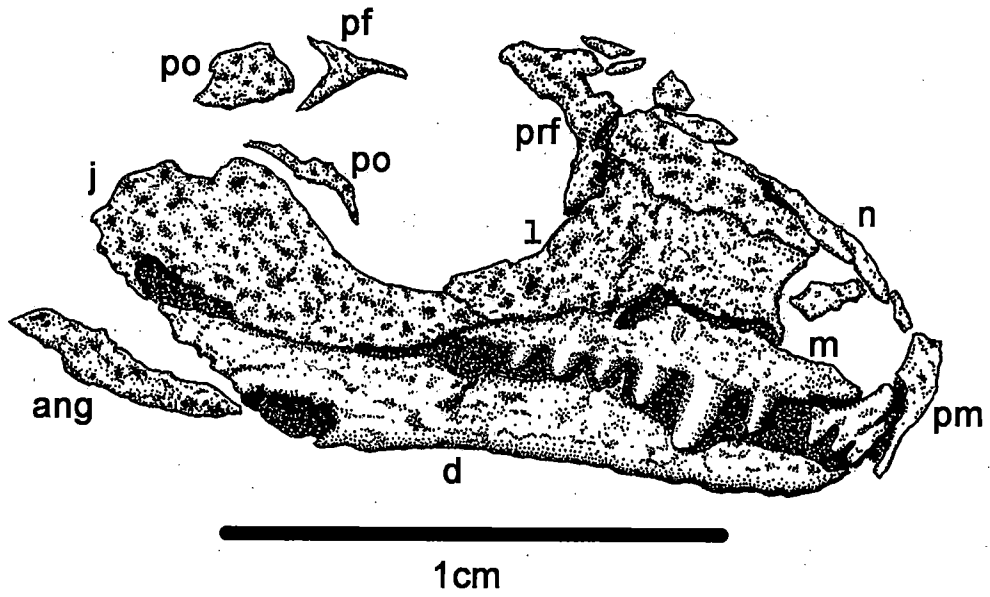
Figure 7. UCLA VP 3023B. *Rhodotheratus parvus*, Skull in Right Lateral View.

Nasal. The paired nasals make up the dorsal aspect of the snout, articulating fully with each other along a relatively straight mid-saggital suture. They are subrectangular in shape with some lateral anterior swelling. They average 5.9 mm, and 2.5 mm in length and maximum width respectively. Rostrally, the anterior border articulates with the premaxilla, and the lateral protion of the bone's anterior edge forms the dorsal border of the external narial opening (average diameter 2.4 mm). Posterior to the nasal opening, the antero-lateral border of the nasal contacts the lachrymal, and the posterolateral edge contacts the medial edge of the prefrontal's anterior process. Each nasal is dorsally convex, giving it a gently arched aspect. The anterior and posterior sutures with the premaxilla and frontal bones are highly interdigitated.
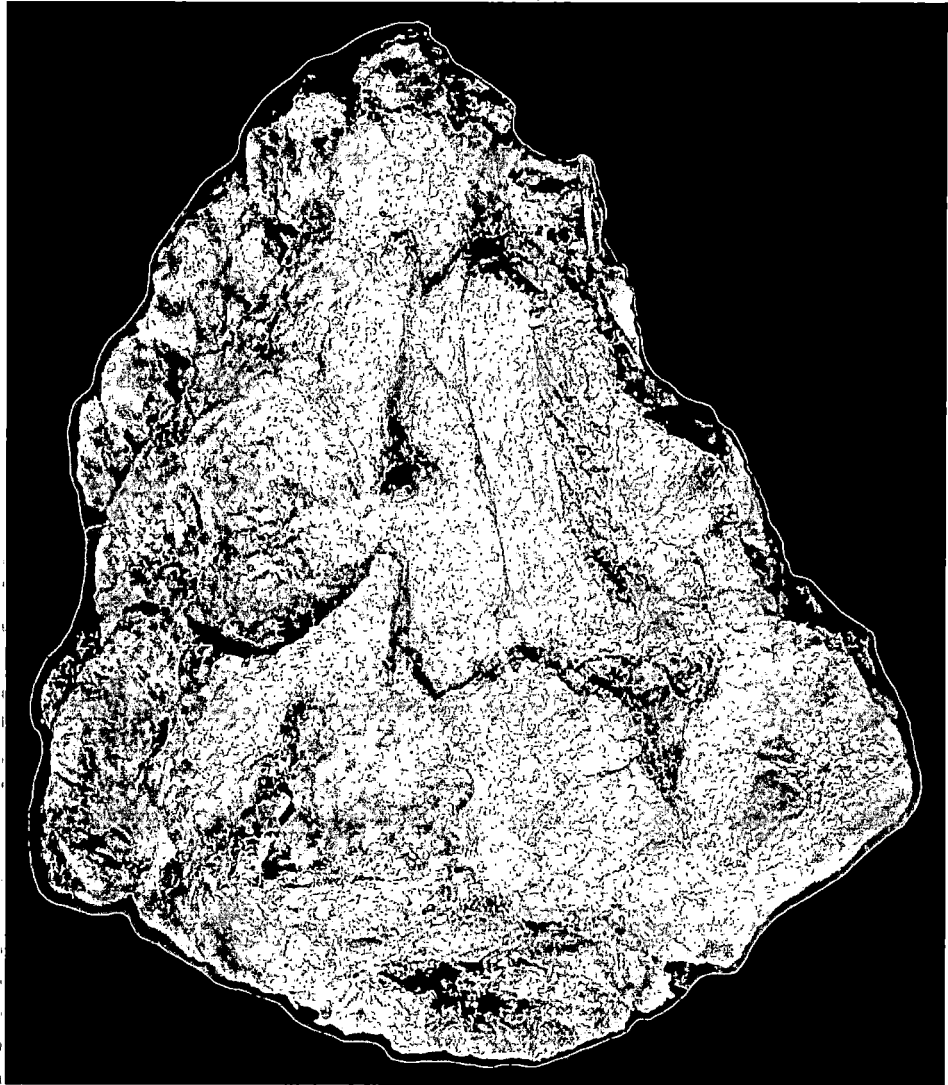
Figure 8A. UCLA VP 3023A. *Rhodotheratus parvus*, Skull
in Dorsal View.
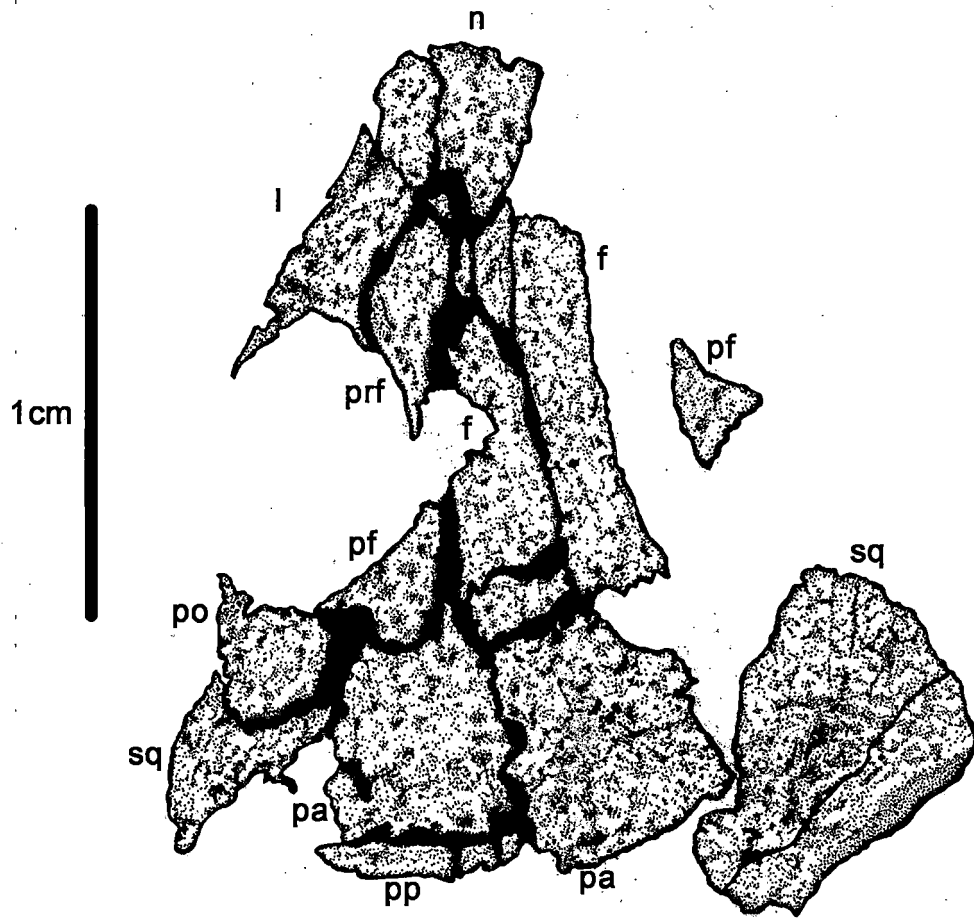
Figure 8B. UCLA VP 3023A. *Rhodotheratus parvus*, Skull in Dorsal View.

Prefrontal. Heaton (1979) noted the internal sutural complexities involved in the articulations between the prefrontal, lachrymal and nasal bones of (Eo)*Captorhinus laticeps*. Constraints imposed by the extremely small size of *Rhodotheratus* preclude a detailed comparison of such articulations here, but an approximation of positional relationships is nonetheless determinable. The prefrontal in *Rhodotheratus* is a triradiate bone with an average length of 5.7 mm and average height at the anterior orbital margin of 2.1 mm (Figures 4,6,7,8,10). Its posteroventrolateral edge forms the anterodorsal border of the orbit. As with *C. laticeps* a ventral process forms the anterior border of the orbit medial to the lachrymal (Heaton 1979). The lateral edge of this ventral process forms a suture with the medial edge of the lachrymal. A prominent anterior process averages 2.9 mm as measured from anterior edge of orbit and extends forward from the orbit to articulate ventrolaterally with the lachrymal, anteromedially with the nasal, and posteroventrally with the frontal. This anterior process is directed laterally, giving it a rounded, ventrally concave ventrolateral border. There is also a shorter, sharply acuminate posterior process.

Frontal. The deeply sculptured frontals are anterior-posteriorly elongate, subrectangular elements that average 8.9 mm in length and 2.1 mm width. There is also a slight lateral widening along the posterior border of the frontals. They contact each other medially along a straight suture, the nasals anteriorly along a highly interdigitated suture, the prefrontals anterolaterally along a predominately straight suture, the postfrontals posterolaterally also along a straight suture, and parietals posteriorly. The posterior suture with parietal bone is oriented perpendicular to the midline of the skull and deeply interdigitated (Figures 4,9). As in other basal amniotes, they form the most dorsal margin of the orbit between the pre and post-frontal bones. In addition, a prominent, keel projects ventrally along the lateral edge of the ventral surface.

Parietal. The parietals of *Rhodotheratus* are flat, quadrangular elements (average length 6.66 mm; average width approximately 5.2 mm) occupying the posteromedial portion of the dermal roof. The parietals contact each other medially, in a straight suture continuous with those of the postparietals, frontals, nasals and premaxillae. The pineal foramen averages 1.5 mm in anterior-posterior

diameter, and is located slightly anterior to midpoint of inter-parietal suture. The parietals contact the frontals anteromedially, postfrontals anterolaterally, postorbitals anterolaterally (lateral to postfrontals), postorbitals anterolaterally, and squamosals posterolaterally. The fronto-parietal sutures are deeply interdigitated. The frontal bones overlie significantly, the parietal bones at the suture. This was the only case in which the internal sutural relationships could be determined between bones for *Rhodotheratus*. No supratempotal bone exists, and therefore, there is no supratemporal notch. As with the other dermal skull elements, significant dermal sculpturing occurs on the dorsal surface of these bones (Figure 9).

Although given a new generic designation, Olson's (1970) diagnosis of the loss of the supratemporals in this taxon is upheld. All specimens for which the posterolateral ends of the parietals are preserved show no indications of the presence of this bone. Curiously, the only other captorhinid species in which this condition is observed is *Saurorictus australis*, from the Upper Permian of South Africa (Modesto & Smith, 2001), also an extremely small captorhinid species. Modesto & Smith (2001) described *S. australis* as having an approximate skull

48

length of 22 mm. Although this is smaller than the average

skull length of *Rhodotheratus*, some of the individual

specimens have skull lengths within 1 mm of that of

Saurorictus.
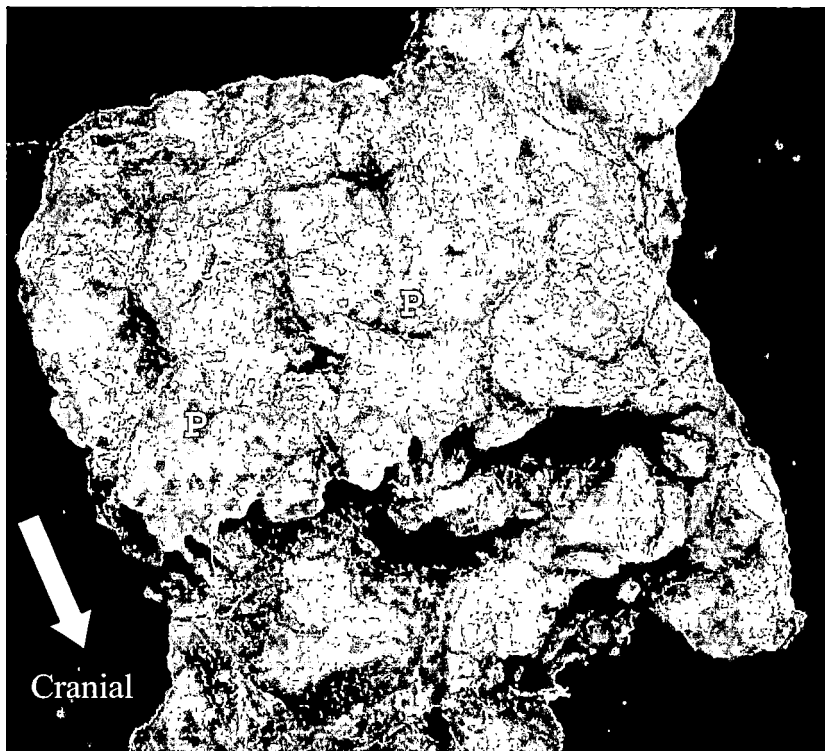
Figure 9. UCLA VP 3024A. *Rhodotheratus parvus*,
Parietal Bones in Posterodorsal View (Note the highly
interdigitated fronto-parietal suture).

Postparietal. Posterior to the parietals, the skull

table drops off at an angle nearly 90° to the plane of the

skull table at the postparietal bones. Though dermally

derived during development and therefore part of the dermal

roof, the postparietals in *Rhodotheratus* are vertically

oriented with a caudally directed exposure on the occipital

surface of the skull. They are paired elements that

contact each other along the full extent of their straight,

median suture. They are subrectangular in shape, with

average heights and widths of 0.9 mm and 4.0 mm

respectively.

Postfrontal. The postfrontals are triangularly shaped

bones making up the posterodorsal border of each orbit.

The anterior and ventral apices taper into the orbit,

forming narrowly angled processes. The postfrontals are

bordered dorsomedially by the posterolateral border of the

frontal bones, ventrolaterally by the postorbitals, and

posteriorly by the anterolateral border of the parietals.

They demonstrate pronounced sculpturing on the external

surfaces.

Postorbital. Making up the posterior to

posteroventral portions of orbital margin as well as some

of the "cheek space" caudal to it, the postorbital bones

are comprised of two sections; a relatively longer (average

length 1.2 mm), anteroventrally projecting anterior process

that overlies the jugals along the posteroventral portion

of the orbital margin, and a subrectangular, more posterior

component with an average anterior-posterior length of 4.1

mm, and an average height of 3.0 mm). Ventrally, the

suture between the postorbital and jugal is concave. The

postorbitals contact and underly the postfrontals

anterodorsally, the squamosals posteriorly and

posteroventrally, and the parietals posterodorsally. The

postorbital-jugal suture is essentially straight, with some

undulation posteriorly in some specimens. The postorbital-

postfrontal suture is straight, whereas the postorbital-

parietal and postorbital-squamosal sutures undulate to a

small degree. The postorbitals exhibit significant surface

sculpturing.

Olson's (1970) description of this element depicted it

with a greatly reduced posterior component, but this study

suggests that his description was probably based upon a

fragmented specimen (FMNH UR 1255). This revised

description brings the shape of the postorbital in

Rhodotheratus more in line with the general shape of the

bone observed in other captorhinid reptiles.

Jugal. The jugals are sub-triangular elements that make up the posteroventral border of the orbit. The vertically oriented jugal bones parallel the long axis of the skull, with an average length of 10 mm. An acuminate anterior process extends an average of 3 mm beyond the contact with the orbit, where it is bordered ventrally by the maxilla and dorsally by the lacrimal. The height increases posterior to orbital margin forming a fan shaped posterior plate, averaging approximately 4 mm in height. The jugal is bordered superiorly by the postorbital, posterodorsally by the squamosal, and posteroventrally by the quadratojugal (Figures 4,10).
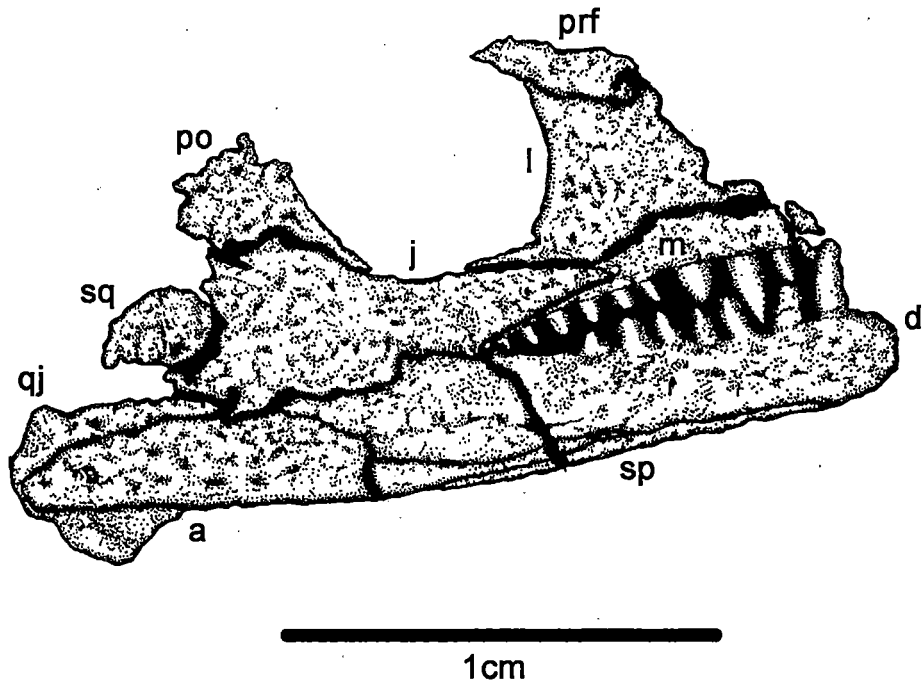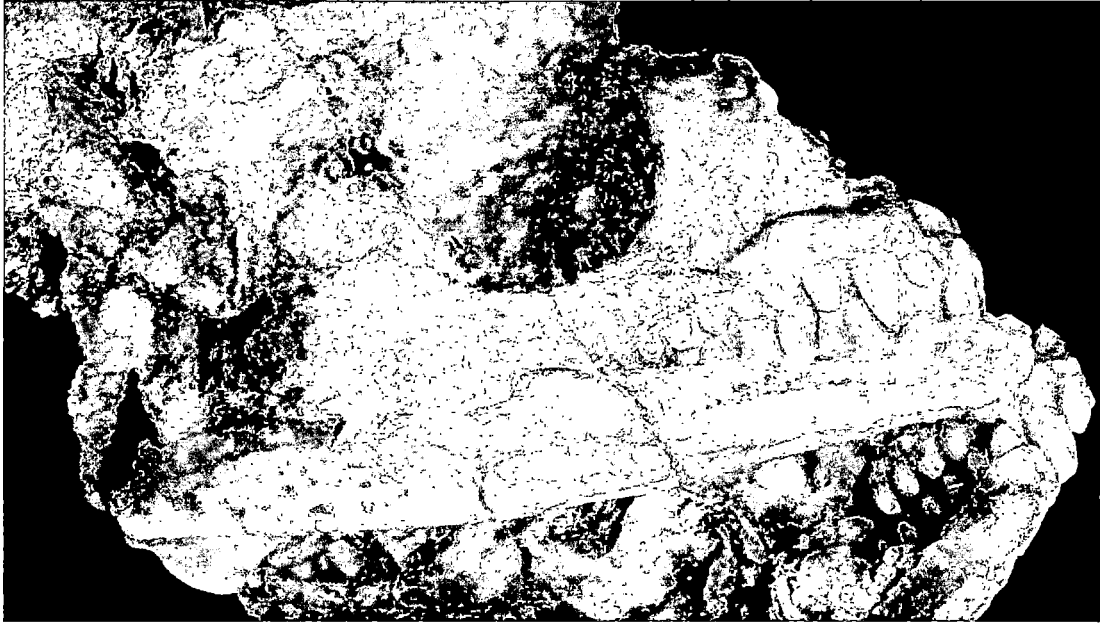
Figure 10. UCLA VP 2894. *Rhodotheratus parvus*, Skull in Right Lateral View.

Squamosal. The paired squamosals are subrectangular,

and make up the posterolateral portion of the cheek dorsal

to the quadratojugals. A prominent occipital flange

projects medially along the plane of the occiput. There is

significant dermal sculpturing along the dorsal surface,

but not along that of the occipital flange. The medial

edge of the squamosal has been chipped and slightly damaged

in the specimens available for study, but the outline

suggests that the medial aspect of the dorsal margin of the

post-temporal fenestra is concave. This, combined with the

convex ventrolateral border of the squamosal gives the

posteroventral margin of the squamosal a sigmoid shape

overall.

Quadratojugal. The quadratojugal bones are laterally,

subrectangular in shape and contact the jugal anteriorly

and the squamosal dorsally along a relatively straight

suture. Posteriorly, they follow the contour of the

squamosal forming a medially projecting posterior occipital

flange flush with the medial flange of the squamosal. As

with the squamosals, there is significant dermal

sculpturing along the lateral surface, though none on the

posterior flange.

Palate

Vomer. The vomers are the anterior-most of the palatal bones. Medially, the left and right vomers articulate along the anterior two thirds of the mid-longitudinal palatal suture before each makes contact with the vomerine ramus of the premaxilla on that side of the palate. Posteriorly, they articulate with the anterior edge of the palatine bone along a jagged suture. Posteromedially, these bones articulate with the anterolateral edge of the tip of the palatine ramus of the pterygoid bone along a straight suture.

Palatine. The paired palatines are relatively large, quadrangular bones inserted into the angle formed by the palatine ramus and the transverse flange of the pterygoid. The palatines articulate anteriorly with the vomer along a jagged suture and anterolaterally with the maxilla. A well-developed semicircular facet marks the connection of the maxilla to the palate. The posterior portion of the facet is made up by the palatine, and the anterior portion is comprised of the vomer.

Pterygoid. The pterygoids are the largest components to the palate of *Rhodotheratus* and are consist of three primary portions: (1) a slender anteromedial palatine

ramus, (2) a laterally projecting subrectangular transverse flange, and (3) a long posterolaterally projecting quadrate ramus.

The anterior rami (average length 9.6 mm) are gently tapered as they extend rostrally, their medial edges forming the lateral borders of the narrow interpterygoid vacuity. Anterior to the interpterygoid vacuity, the two rami come together to form the posterior third of a long, mid-longitudinal suture, which bisects the anterior palate. Olson (1970) incorrectly described the two palatine rami as being fused anteriorly. Further preparation of Olson's original study specimens shows clearly, the paired condition of two, separate pterygoid bones. The only specimen (UCLA VP 2910) displaying an intact interpterygoid vacuity reveals an anterior-posterior length of 7.0 mm. Proceeding from the posterior margin rostrally, the interpterygoid vacuity widens rapidly, coming to a maximum width of 1.2 mm within the first third of its length. Anterior to this point, the vacuity tapers gently, forming a sharp terminus. Posterior to the palatine ramus, the transverse pterygoid flange expands laterally into a flat, subrectangular sheet of bone. The posterior margin of the

transverse flange forms a sharp, straight edge

perpendicular to the anterior-posterior axis of the skull.

Figure 11A. FMNH UR 1256. *Rhodotheratus parvus*, Skull in Ventral View.
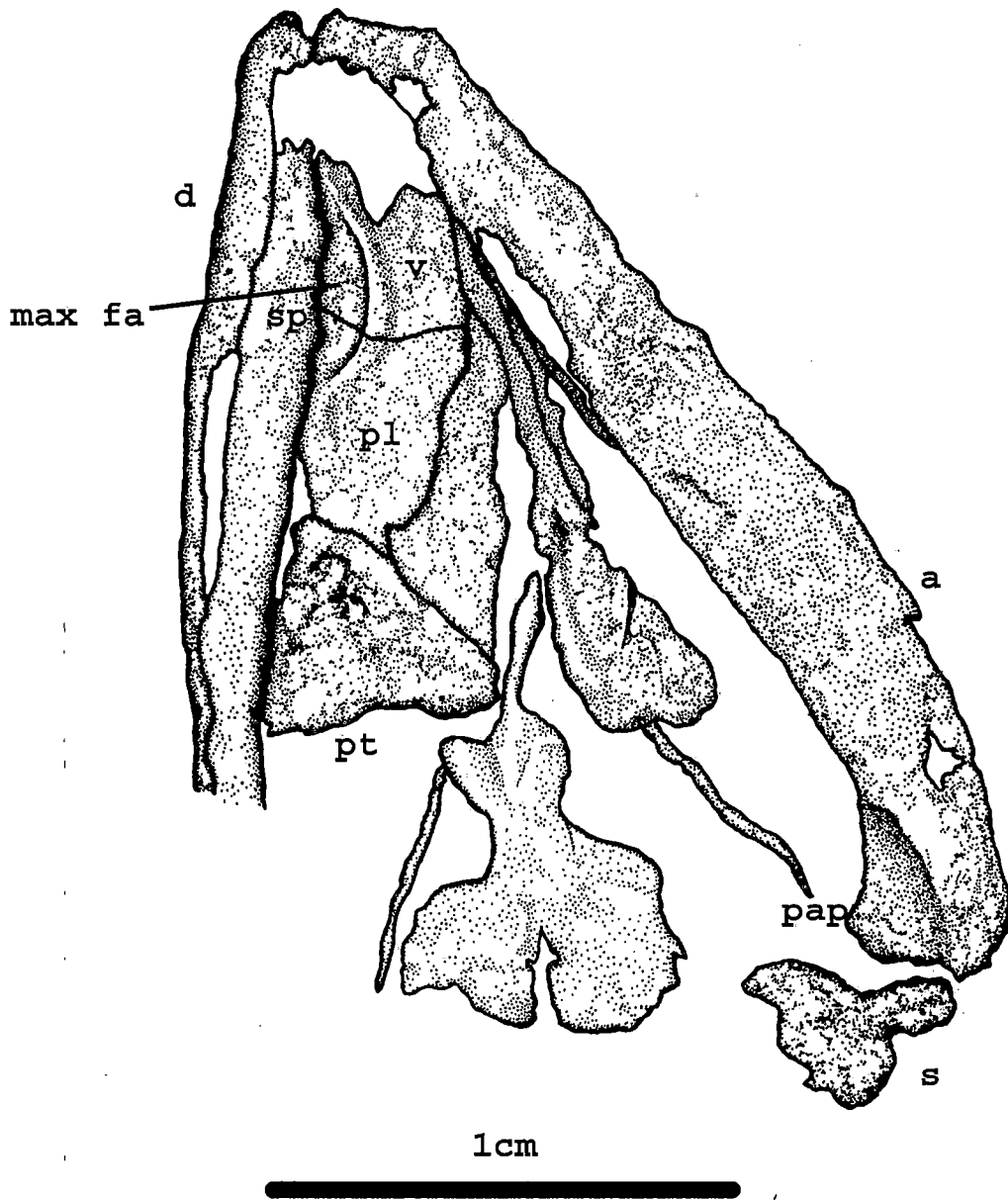
Figure 11B. FMNH UR 1256. *Rhodotheratus parvus*, Skull in Ventral View.

Posterior to the pterygoid flange, the quadrate ramus of

the pterygoid (average length 6.7 mm) projects

posterolaterally at an approximately 45-degree angle to the

anterior-posterior axis. The quadrate ramus is also a

subrectangular process, though much longer than it is wide,

and is slightly concave in ventral view along its long

axis. The distolateral surface of the quadrate ramus curls

vertically to articulate with the medial edge of the

anteromedially projecting process of the quadrate.

Medial to the connection between the transverse flange

and the quadrate ramus, the basicranial recess is a small,

medially oriented facet, within which, the basipterygoid

tubera of the basisphenoid articulate with the palate.

Additionally, three rows of palatal teeth are present on

the pterygoids: (1) a single row on medial border of

anterior process, (2) a group at posterior and

posterolateral regions of lateral flange, and (3) a small

group along anterolateral border of lateral flange (Figure

4,12).
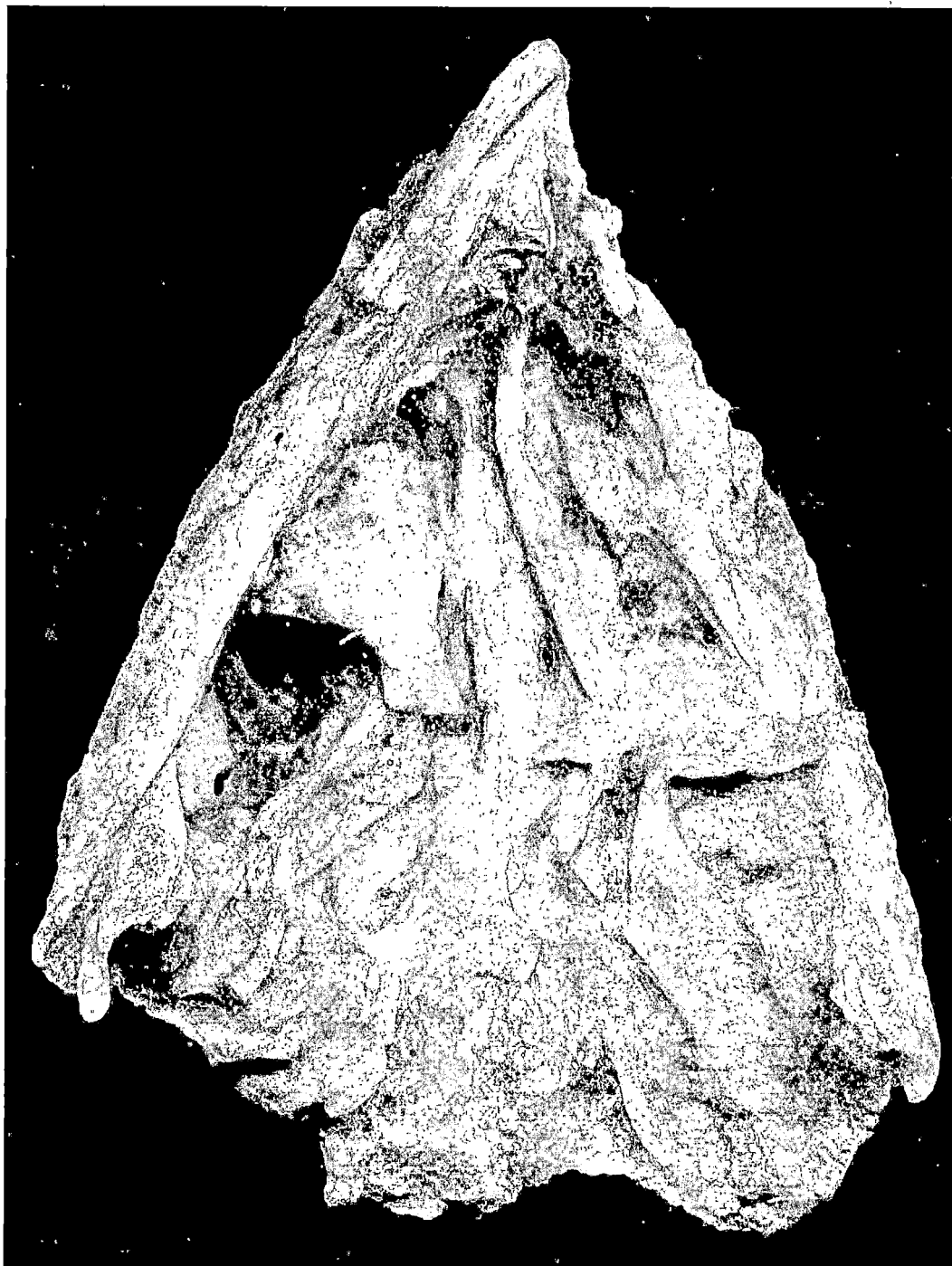
Figure 12A. UCLA VP 2910. *Rhodotheratus parvus*, Skull
in Ventral View.
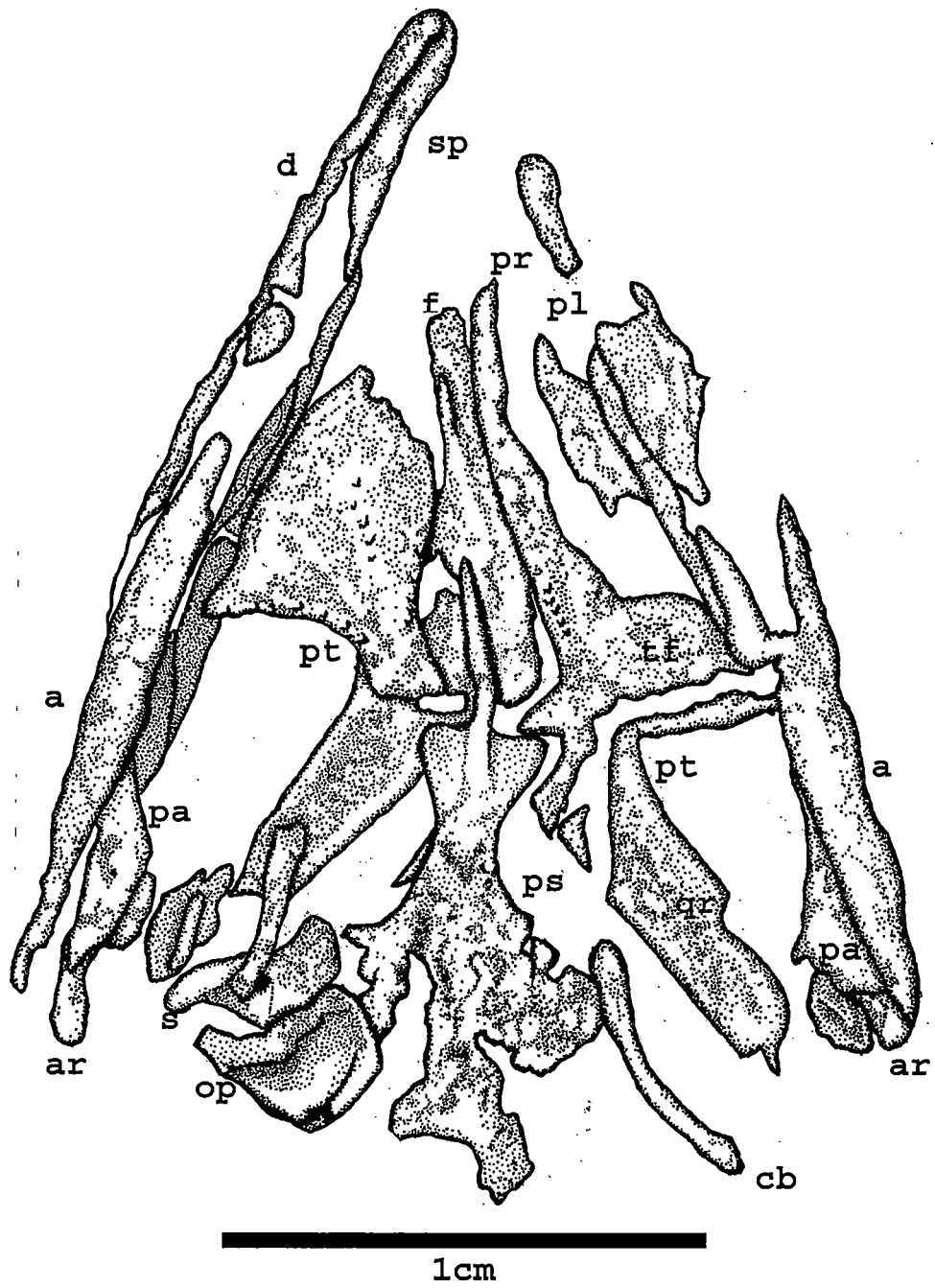
Figure 12B. UCLA VP 2910. *Rhodotheratus parvus*, Skull in Ventral View.

Epipterygoid. Heaton (1979) identified the epipterygoids of *Captorhinus laticeps* (= "Eocaptorhinus") on the dorsal surface of the pterygoid with no visible ventral contribution to the palate. This is also the case with *Rhodotheratus*. None of the specimens examined in this study afford a dorsal view of (that region of) the palate, but in all cases where a confident ventral view is afforded, there is no visible evidence of an epipterygoid. Some fragments of bone were observed in some of the specimens in which the palate has been fractured and/or displaced which could belong to the epipterygoids, but a confident identification for *Rhodotheratus* is not possible at this time.

Quadrate. In ventral view, the quadrate has an approximately "dumbbell" shaped outline formed by a larger, medial and slightly smaller, lateral condyle (Figure 13). The quadrate of *Rhodotheratus* differs from reconstructions of other captorhinids, in that the long axis of the articular surface is not oriented at a 90-degree, transverse angle to the long axis of the skull. Instead, the quadrate is positioned such that the long axis is at an approximately 40-45-degree angle to the transverse plane. The medial and lateral condyles form the basis for the

articular surface of the quadrate, which is somewhat

saddle-shaped. In additionally, there is a vertically

oriented, anteromedially projecting process, for

articulation with the quadrate ramus of the pterygoid
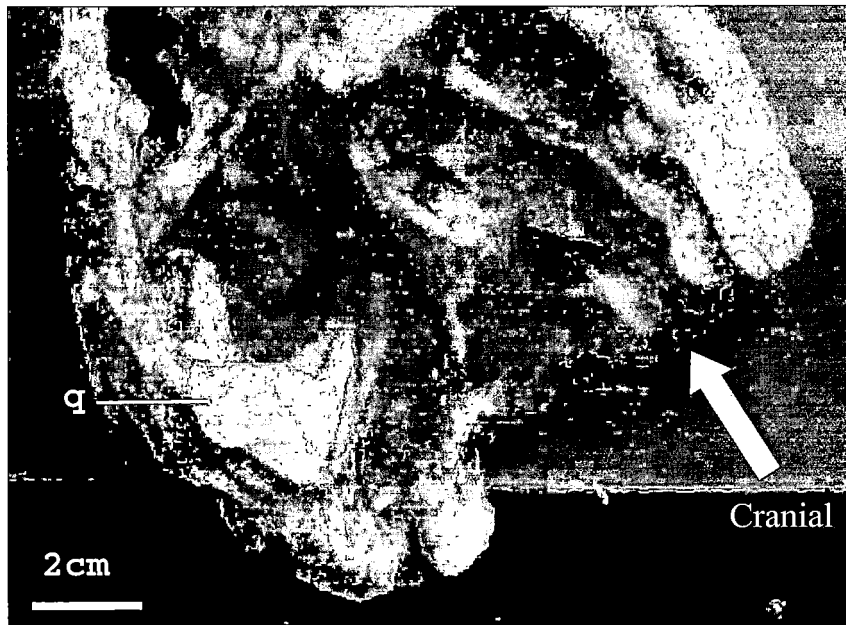
Figure 13. UCLA VP 2908. *Rhodotheratus parvus*,
Quadrate Bone in Ventral View.
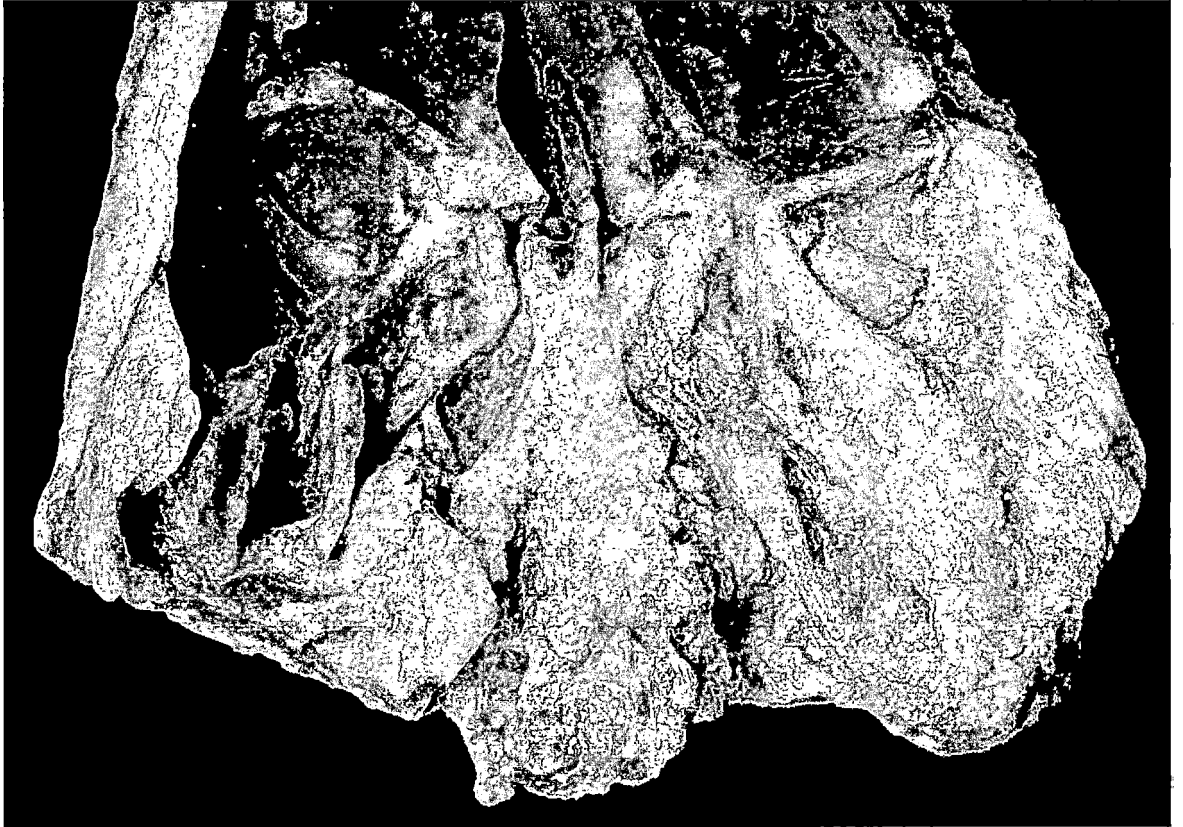
Figure 14A. UCLA VP 2910. *Rhodotheratus parvus*, Braincase in Posteroventral View.
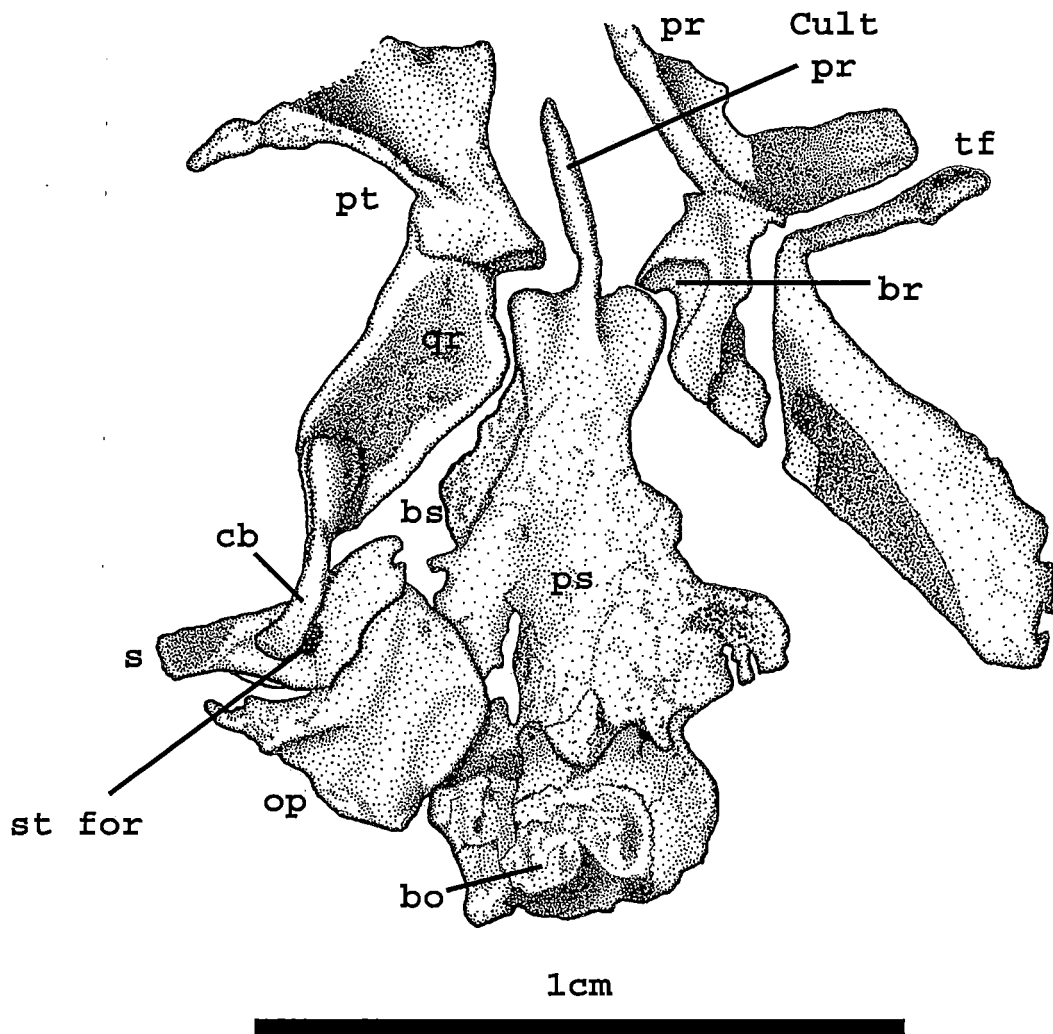
Figure 14B. UCLA VP 2910.   *Rhodotheratus parvus*,
Braincase in Posteroventral View.

Braincase

Parasphenoid. This unpaired braincase element is a flat, diamond shaped (ventral view) bone making up the mid-ventral surface of the braincase (Figures 4,14). It overlies the anterior portion of the parasphenoid dorsally and possesses a broadly acuminate posterior process that articulates between the anteriorly projecting ventral processes of the basioccipital. Only the thinnest of sutures is seen running posterolaterally from the anterior margin of the braincase (lateral to the base of the cultriform process) to the caudal end of the basitubera (in ventral aspect), separating the parasphenoid from the basitubera.

It is noteworthy that the caudal end of the parasphenoid appears to be slightly separated from the rest by very fine sutures. These sutures run perpendicular to the sutures that run posteromedially from the anterior termini of the paired anteriorly projecting processes of the basioccipital, creating a small, somewhat diamond-shaped section of bone separate from the rest of the parasphenoid (Figure 14). The separated section appears to display bilaterally symmetrical morphology, and is therefore not interpreted as being due to simple cracking.

This separated condition of the parasphenoid appears to be unique to *Rhodotheratus* among the Captorhinidae. DeBeer (1937) stated that there are three centers of ossification for the developing parasphenoid in the lizard group Lacertilia, one median and rostral, and two that are lateral and more posterior. Although the organization of these centers appears to be reversed, it is possible that these three centers, though completely ossified, maintain a rudimentary separation in *Rhodotheratus*.

Basisphenoid. The basisphenoid makes up the anterodorsal region of the braincase, just posterior to the base of the cultriform process, and overlays the anterior portion of the parasphenoid. Although the paired basitubera are clearly visible in most of the specimens displaying braincase material (Figures 3,10,11,12), none of those examined showed anything more than a minimal view of its lateral surface. The dorsum sella is not visible in any specimens examined. The lateral surfaces of the basisphenoid of *Rhodotheratus* bear an anterior-posteriorly aligned groove corresponding to Heaton's (1979) groove to accommodate the facial nerve. Not surprisingly, considering *Rhodotheratus'* small size, the groove is

68

relatively larger than in *Captorhinus* ("*Eocaptorhinus*") *laticeps*.

Prootic. The paired prootics are also only minimally visible in the specimens examined. They are irregularly shaped bones making up the dorsolateral aspect of the braincase (in lateral view), and connect with the basisphenoid anteriorly, the supraoccipital posterodorsally, and the stapes ventrally over straight or weakly undulating sutures. No sutures can be confidently identified between the prootic and stapes due to their small size and context of preservation. UCLA VP 2910 displays a prootic structure that is possibly equivalent to Heaton's supratrigeminal process.

Supraoccipital. The presence of a supraoccipital bone is confirmed for *Rhodotheratus*. Although fragmentary in most specimens observed, the holotype specimen displays what appears to be the superior portion of the right side of this cranial element. Although not enough to justify a confident reconstruction of the inferior aspect, it does allow for a confident reconstruction of the superomedial border of the post temporal fenestra (Figure 4).

Exoccipital. The paired exoccipitals, located on the posterior surface of the braincase, are crescent-shaped

elements with convex lateral borders, and make up the lateral walls of the foramen magnum. Ventrally, they are fused to the dorsolateral surfaces of the basioccipital lateral to the occipital condyle. The (dorso) lateral suture between the exoccipitals and the opisthotic is confidently visible (Figures 4,15).

Basioccipital. The single basioccipital bone comprises the posteroventral aspect of the braincase, including the posteriorly projecting, subcircular occipital condyle, for articulation with the atlas (Figures 5,14,15). In posterior view, the condyle articulates bilaterally with the exoccipitals as noted above.
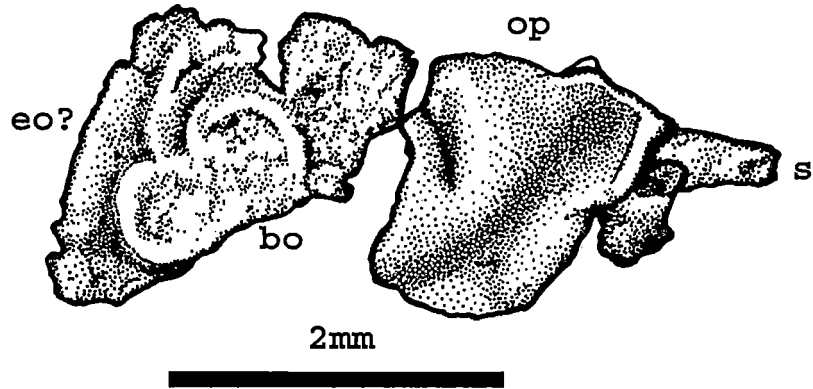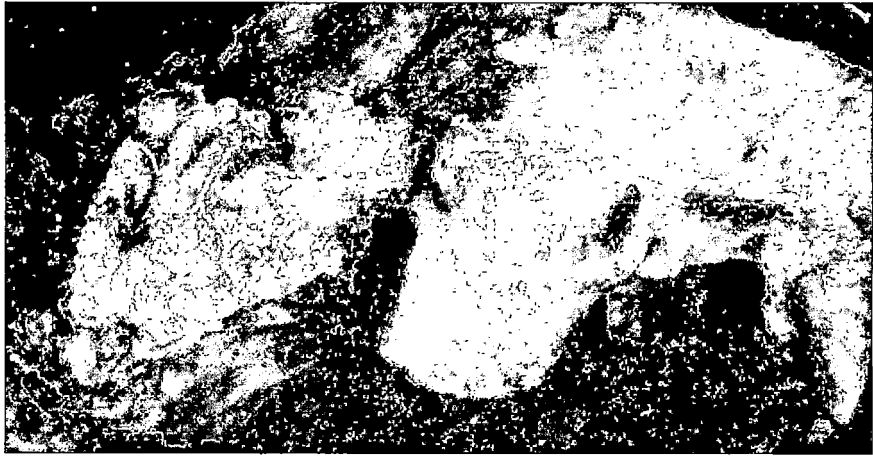
Figure 15. UCLA VP 2910. *Rhodotheratus parvus*, Braincase in Posterior View.

Ventrally, bilateral short and broadly acuminate processes extend anteriorly from the base of the condyle. Nestled in between these processes is the (also broadly acuminate) posterior tip of the parasphenoid. The lateral surface appears to bear a deep groove corresponding to part of the foramen and groove for the facial nerve in *C. laticeps* (Heaton, 1979).

Opisthotic. The opisthotics are irregularly shaped bones making up the posterolateral aspects of the braincase (Figures 5,12,14). They articulate medially with the exoccipitals, ventromedially with the basioccipital, anterolaterally with the footplate of the stapes, and anterodorsally with the prootic.

The general outline of the opisthotic bones in *Rhodotheratus* is not unlike that seen in other, larger captorhinids (Price, 1935; Heaton, 1979). Of note, however, is the presence of a pronounced recess on the posterior aspect of the opisthotic on the paraoccipital process. Similar recesses have been described in *Captorhinus* as an attachment point for the obliquus capitis magnus muscle (Heaton, 1979; Sumida, 1990), and in the ophiacadontid pelycosaur *Ophiacodon* (Romer and Price, 1940). In none of the other organisms, however, is the

72

recess as deep, relative to the size of the organism as that seen in *Rhodotheratus*.

Stapes. The stapes is clearly visible in several specimens (Figures 5,11,12,14,15,16). Proximally, the stapes connects to the body of the braincase at a wide, subcircular medial stapedial footplate. Projecting from the footplate is the lateral process, which is directed laterally and slightly posteriorly and tapers to a cylindrical, blunt end. Located slightly proximal to the center of the lateral process is the stapedial foramen (Figure 14, 16).
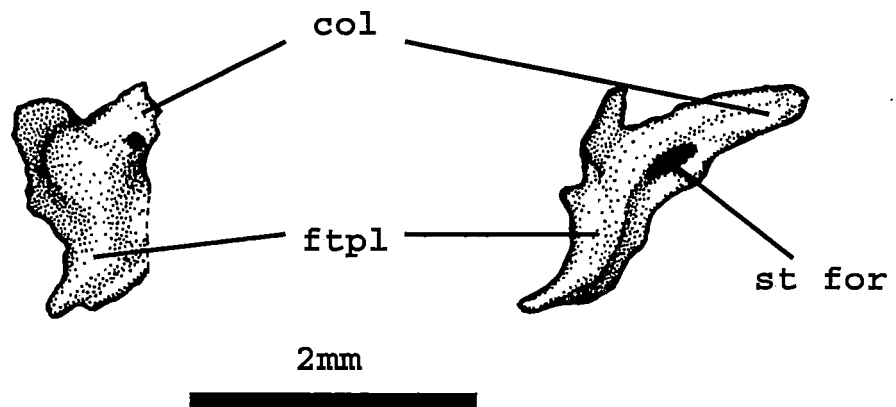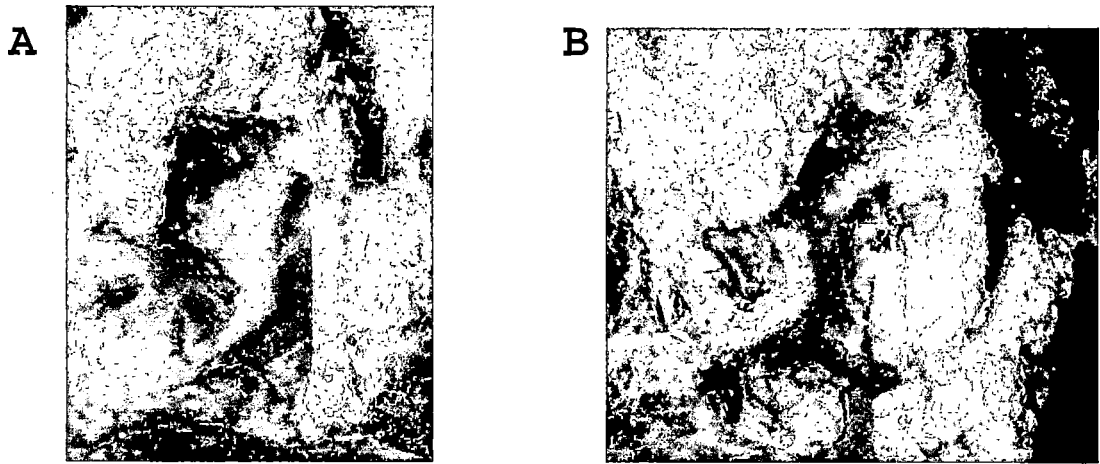
Figure 16. FMNH UR 1256. *Rhodotheratus parvus*, Stapes in A) Ventrolateral and B) Posteroventral View.

Mandible

General. The mandible of *Rhodotheratus* is fairly stoutly constructed, considering its small size. In ventral view, the anterior three fourths of the mandible is primarily straight before turning lingually, creating a laterally convex outline along the caudal portion of its length. A prominent, upwardly projecting coronoid-surangular eminence (equals Heaton's (1979) coronoid-surangular crest) comprises approximately one third of the total length of the mandible. The adductor fossa is also large, encompassing nearly the entire area lingual to the coronoid-surangular eminence. There is no indication of the presence of a Meckelian foramen in any of the examined Rhodotheratus specimens. Light surface sculpturing exists along the lateral exposure, heavier in the area of the coronoid-surangular eminance than further rostrally.

A maximum of 14 teeth, are organized into two rows located on the dorsal surface of the dentary. The mesial three to four teeth are much taller than they are wide, but there is a distinct shortening and widening of the teeth as they progress distally where the teeth are approximately as wide as they are tall. The anterior three teeth are angled rostrally.

Dentary. Comprising the lateral and dorsal surfaces

of the rostral half of the mandible, the dentary is the

tooth-bearing element of the mandible as well as its

largest component (Figures 4,5,6,7,10,11,12,17,18). On the

medial aspect of the mandible, the dentary articulates with

the splenial rostrally, and the lateral edge of the

anterior process of the coronoid. On the lateral surface,

the splenial borders the dentary anteroventrally, the

angular posteroventrally, and the surangula,

posterodorsally. All of the sutures are straight. The

posterior tip is drawn out into a wide, but moderately

sharp point at the junction between the angular and

surangular.
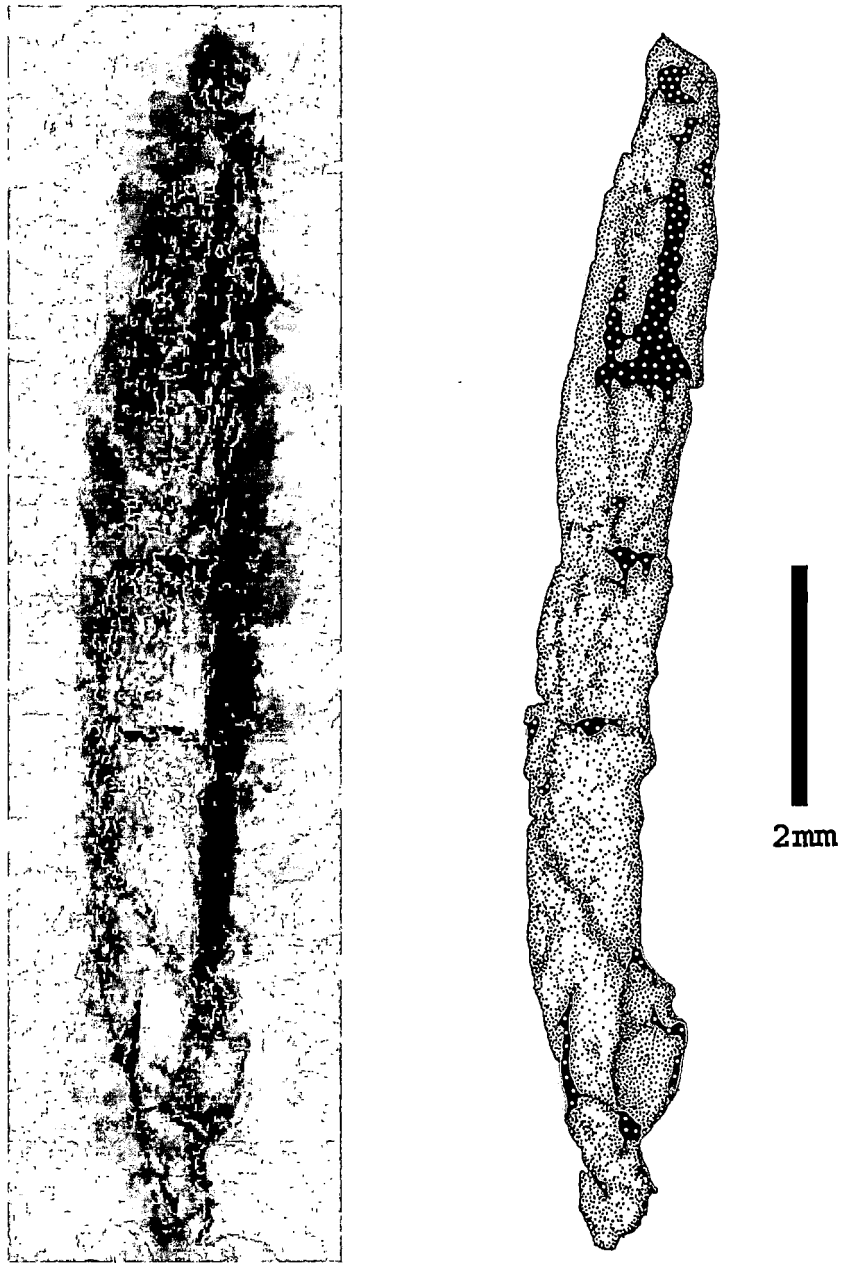
Figure 17A. FMNH UR 1272. *Rhodotheratus parvus*, Lower Jaw in Ventral View.
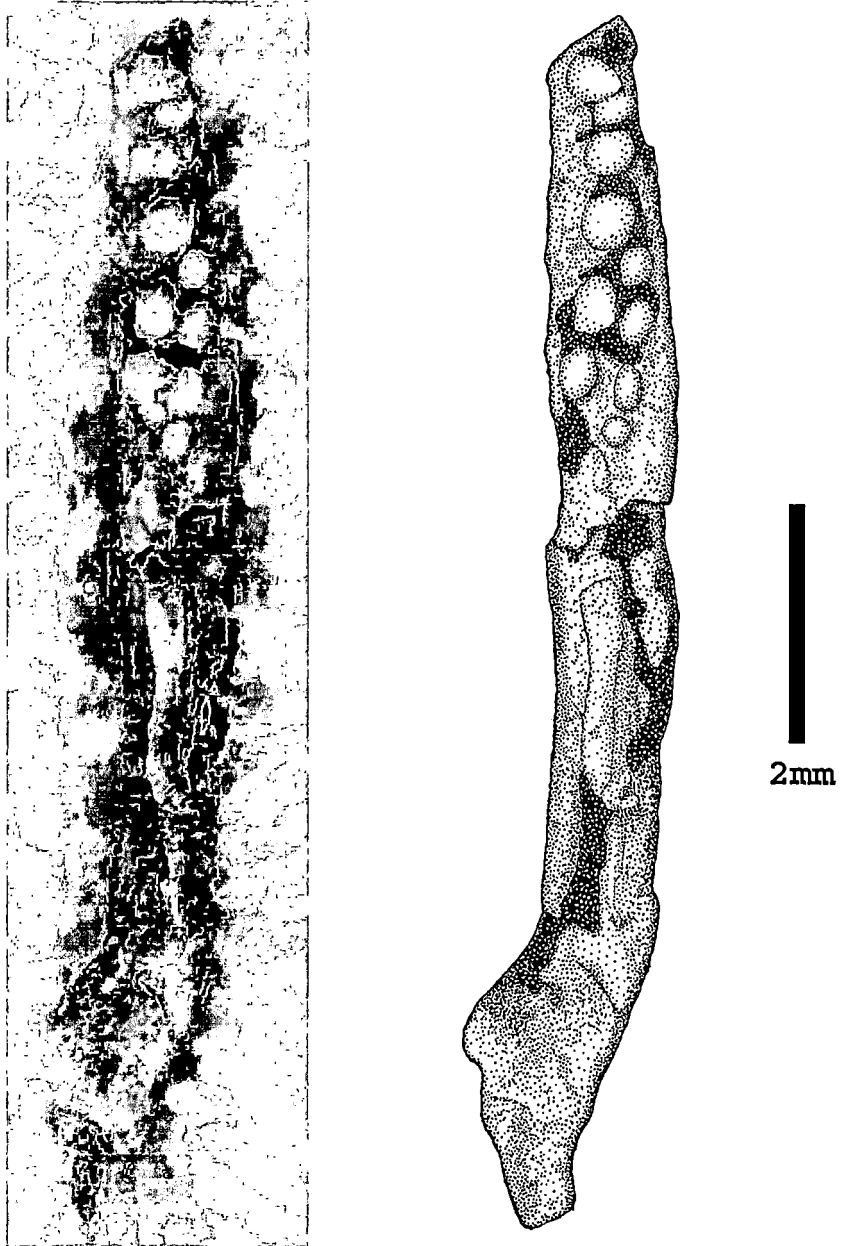
'Figure 17B. FMNH UR 1272. *Rhodotheratus parvus*, Lower Jaw in Dorsal View.
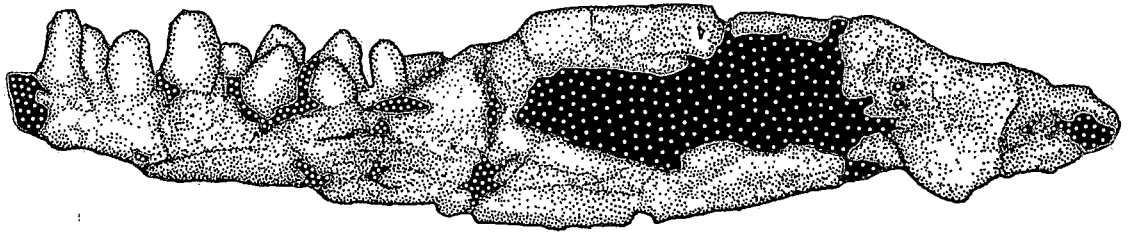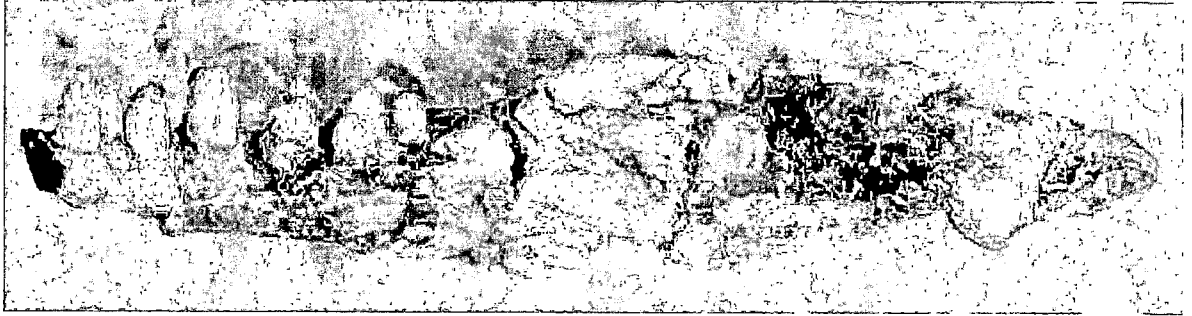
Figure 17C. FMNH UR 1272. *Rhodotheratus parvus*, Lower
Jaw in Mesial View.

Figure 17D. FMNH UR 1272. *Rhodotheratus parvus*, Lower Jaw in Right Lateral View.

Splenial. Whereas, the dentary occupies the dorsal and lateral surfaces of the mandible, the splenial makes up its ventral and medial surfaces. The splenial spans the distance between the rostral tip of the mandible anteriorly, where it articulates with the dentary anteriorly and dorsolaterally, and the angular posteriorly (Figures 4,5,10,11,12). The posteroventral terminus of the splenial tapers to a tip nestled between the two anteriorly projecting process of the angular. Lingually, a narrowly subrectangular flange projects dorsally, articulating with the dentary anterodorsally and the coronoid posterodorsally along straight sutures. Posteriorly, the splenial flange articulates with the prearticular along a slightly undulating suture (Figure 5).

Coronoid. The elongate coronoid is only clearly visible on the lingual aspect of the mandible, though it has a minor dorsal exposure along the ridge of the coronoid-surangular eminence. Its posterior-most point is just anterior to the apex of the coronoid-surangular eminence, and it passes anteriorly to a point lingual to the penultimate dentary tooth. Two posteroventrally directed acuminate processes extend from the body of the coronoid. The more posterior of the two processes extends

81

along the lateral wall of the aductor fossa, whereas the other projects along the anterior margin of the rim of the fossa (Figure 5).

Prearticular. The prearticular is also located primarily on the lingual surface of the mandible. The dorsal edge of the prearticular encompasses the majority of the lingual margin of the rim of the adductor fossa. The rostral end of the prearticular is expanded into a bulbous, dorsally oriented process, which articulates vertically with the coronoid, anteriorly and anteroventrally with the splenial, and ventrally with the angular. Widening posteriorly, the prearticular forms a ventrally visible spatulate process underlying the lingually projecting articular process (Figures 4,5,12).

Surangular. The surangular is the lateral component of the posterodorsal portion of the mandible, visible in both labial and lingual views. In lingual view, it articulates anteroventrally with the dentary and posteroventrally with the angular, both along extended, straight sutures. Lingually, the line of articulation between the surangular and the dentary is more dorsally located than laterally, indicating that there is a great deal of overlap between these two elements. The other

lingual associations of the surangular include the coronoid rostrally, and the articular caudally. The dorsal border of this mandibular element is a convex ridge that, combined with the coronoid anteriorly, makes up the vertically projecting coronoid-surangular eminence. This bone also encompasses the lateral aspect of the retroarticular process (Figure 5).

Angular. The posteroventral component of the mandible, the angular is visible in lingual, lateral, and ventral view. This complex, irregular bone has two primary sections, an anterior flange that wraps around the ventral portion of the mandible, and a posterior portion with a lingual exposure from which, the articular process projects (Figures 4,5,7,10,11,12). The anterior flange has a complex set of associations. Two highly acuminate processes project anteriorly and make up the angular's anterior border. The caudally projecting process of the splenial lies between these two processes. Laterally, the longer of the two processes articulates with the dentary dorsally. Moving caudally along the dorsal border of the angular's lateral aspect, its articulation with the dentary terminates at approximately the midpoint of the coronoid prominence, there initiating its articulation with the

surangular. Lingually, the angular contacts the

prearticular from the tip of the medial anterior process

along its entire dorsal border. All of the angular's

sutural relationships are straight.

Articular. The articular is a short, irregularly

shaped bone located on the lingual aspect of the caudal end

of the mandible (Figure 5). The primary contribution of

the articular to the mandible is the articular surface for

the quadrate dorsally, completing the ventral half of the

jaw joint in *Rhodotheratus* (Figures 4,5,12).
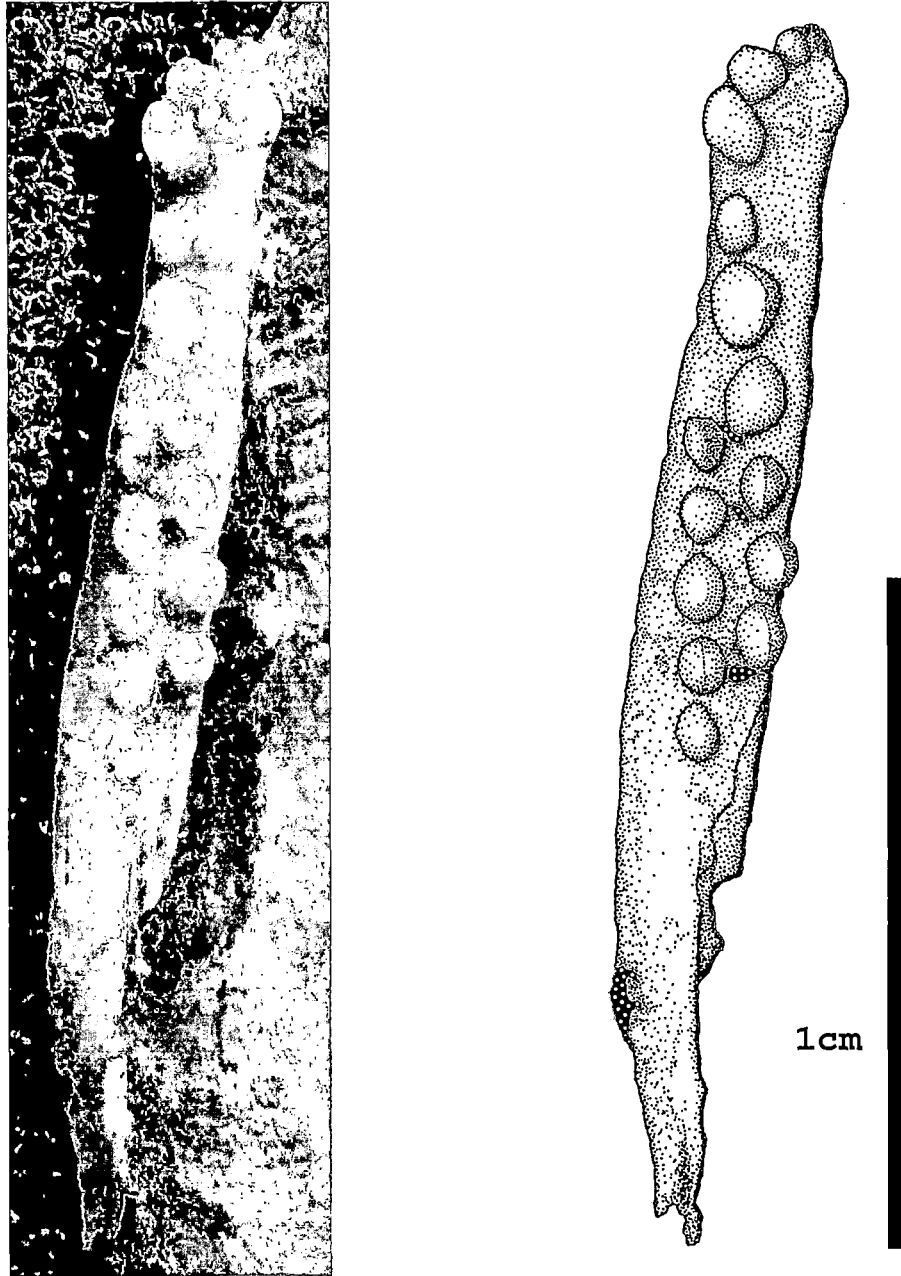
Figure 18. FMNH UR 1278. *Rhodotheratus parvus*, Left Mandible in Dorsal View.

CHAPTER FOUR

DISCUSSION

Degree of Maturity

Rhodotheratus is determined here to be represented by
adult material. This conclusion is based upon a number of
features that indicate bone growth past the juvenile state:
(1) a high degree of sculpturing on the dermal roofing
bones; (2) a high degree of interdigitation of sutures,
particularly those oriented perpendicular to the long axis
of the skull; (3) well-developed facets marking the
articular surfaces between adjacent bones; and (4) multiple
rows of well-developed maxillary and dentary teeth. Dermal
sculpturing (Figures 8,9) takes the form of a "shallow pits
and ridges" pattern commonly seen in other mature
captorhinid species.

The fact that most of the specimens assignable to
Rhodotheratus are nearly complete, articulated specimens is
also a testament to their degree of maturity. The poorly
ossified nature of juvenile skulls predisposes them to
disarticulation and incomplete preservation. Post-mortem
modification of *Rhodotheratus* specimens does occur, but it
is inevitably distortion, not disarticulation. All

86

specimens of *Rhodotheratus* have skulls with sutural articulations robust enough to resist even some post-mortem crushing. At the level of articulation between individual bones, all sutures perpendicular to the long axis of the skull display a high degree of interdigitation, particularly when considering the absolutely and relatively small skull size of the species. This pattern is particularly apparent in the connections between the dermal roofing bones adjacent to the sagittal midline of the skull (premaxilla, nasal, frontal, and parietal bones). In some instances, the region of interdigitation can encompass up to 1 mm in a skull that is less than 25 mm in length.

In UCLA-VP 3024, the frontal bones are absent, exposing their joint surfaces with the parietals. Not only is there a high degree of interdigitation, but the lower lip of the anterior border of the parietal bones clearly underlies, the posterior margin of the frontal bones. Additionally, small extensions of bone connect the superficial parietal interdigitating, sutural projections with the extended, underlying lip of the parietals (see Figure 9). The overall result is, a highly interdigitated scarf joint. Interdigitating sutures between non-dorsally oriented bones occur as well. UCLA VP 2894 displays a high

degree of interdigitation between the jugal and the squamosal plus quadratojugal.

Also indicating maturity past a juvenile stage is the presence of well-developed facets marking the point where one cranial element fits in or onto another element. Further preparation in FMNH UR 1256 revealed that the right maxilla had become separated from the palate, allowing a clear view of the connecting surfaces (Figure 11). There is a wide maxillary process that bears a well-developed maxillary facet, marking the area of connection between the maxilla and the palate. This maxillary process as described here is equivalent to Heaton's (1979) maxillary process in his reconstruction of the palate of *Captorhinus laticeps*. However, the process appears to be much more pronounced in the palate of *Rhodotheratus*. furthermore, there is no apparent facet marking the connection of the palatine to the maxilla in the reconstruction of *C. laticeps*. Modesto (1998), in his update of the cranial structure of *C. aguti*, appeared to include a facet on the articulating surface of the maxillary process. Like *C. laticeps*, however, the process is made up solely of the palatine.

Dentitional characters implying adult age for *Rhodotheratus* are: the variability within the types of teeth present, size differences between teeth of the same type in the same specimen, and the presence of a distinct caniniform region within the maxillary dentition. Although all teeth can be characterized under the general description of "conical", there is variation between teeth in different regions of the jaw. The height of the mesial-most premaxillary teeth is greater than the diameter at their bases. They also show more pointed tips and display a gradual decrease in size proceeding from the proximal to the distal region of the premaxilla. These features suggest that the teeth had reached their full growth potential.

Proceeding distally along the tooth line, the single row of maxillary teeth yields to a multiple-rowed region concomitant with a lingual widening of the maxilla to accommodate the increased number of rows. Teeth within the multiple-rowed region of the upper jaw of *Rhodotheratus* show structural differences when compared with the teeth in the more mesial region of the jaw. The maxillary teeth are typically more stoutly constructed than the more mesial premaxillary teeth, have a more rounded tip with a slight

mesio-distal cutting edge. They show distinct compression, decreasing the width of the teeth linguo-labially. The mesio-distal length of the bases of these teeth is generally much greater than that of the premaxillary teeth with relatively more rounded bases (Figure 4). The teeth within the caniniform region of the upper jaw also differ in size from their maxillary counterparts. The caniniform teeth are relatively more massive compared to the teeth in immediately more mesial and distal positions. The magnitude of the size differences again imply an amount of time to allow for full growth potential of these teeth. Distal to the caniniform region, tooth size tooth size decreases markedly. The teeth of the lower jaw generally follow a pattern similar to that seen in the upper jaw. The two rows of mandibular teeth appear to lie within the gaps in between the three rows of maxillary teeth when the jaws are clenched.

Functional and Feeding
Considerations

The dentitional characteristics of *Rhodotheratus* indicate that it was likely insectivorous. The long conical teeth towards the rostral end of the mouth appear to have been quite well suited to capturing and holding

small prey items. Conversely, the teeth do not demonstrate wear patterns characteristic of the processing fibrous plant material seen in other, herbivorous, captorhinids (Hotton, et al. 1997). Presumably, the three rows of smaller palatal teeth and conical cheek teeth in *Rhodotheratus* might also have aided in holding prey in the mouth, though to a lesser extent. The labio-lingual compression of the cheek teeth in the multiple tooth rowed region of the maxillas may have facilitated gripping or puncture of the chitinous exoskeleton of insects.

Phylogenetic Considerations

The phylogenetic relationships of basal members of the Captorhinidae have been addressed in a number of studies (Gaffney and McKenna, 1979; Ricqlès, 1984; Dodick and Modesto, 1995; Laurin and Reisz, 1995). An analysis of the phylogenetic relationships of all members of the Captorhinidae is beyond the purview of this study; rather, the phylogenetic position of *Rhodotheratus* relative to the taxa for which relationships are well resolved is presented here. As the specimens examined here do not conform to Olson's (1970) definition of the genus *Captorhinikos*, and as specimens assigned to *Captorhinikos chozaensis* and *C.*

valensis were not studied here, that genus is not involved in this study. Similarly, *Riabininus*, *Rothianiscus*, *Hecatogomphius*, *Kahneria*, *Moradisaurus*, and *Acrodontia* are not included in the analysis.

A phylogenetic analysis was performed on a group of basal members of the family Captorhinidae including the genera *Romeria*, *Protocaptorhinus*, *Rhiodenticulatus*, *Captorhinus*, *Labidosaurus*, *Labidosaurikos*, *Rhodotheratus*, *Saurorictus*, and a new, presently unnamed taxon (Taxon X) currently in prep by Sumida, et al. using PAUP* 4.0b (Swofford, 2002). Consistent with Heaton and Reisz's (1986) use of the genus *Protorothyris* as an outgroup for the Reptilia, the genus was utilized here also. Forty-three characters (Appendix B) were subjected to an initial, exhaustive maximum parsimony analysis with no adjustments to the data and yielded a single maximally parsimonious tree (Figure 19). Subsequent analysis utilized addition and subtraction of taxa and characters as described below. Other analyses include the successive re-weighting of homoplasic characters using the rescaled consistency index method (Farris, 1989) as available in PAUP*. All analyses produced a single tree congruent with that presented in Figure 19.

Protorothyris

Romeria

Protocaptorhinus

Rhiodenticulatus

C. laticeps

C. aguti*

Labidosaurus

Labidosaurikos*

Sauroictus

Rhodotheratus*

Taxon "X"

74
49

74
50

98
96

98
69

100
100

98
91

70
48

84
63

5 changes
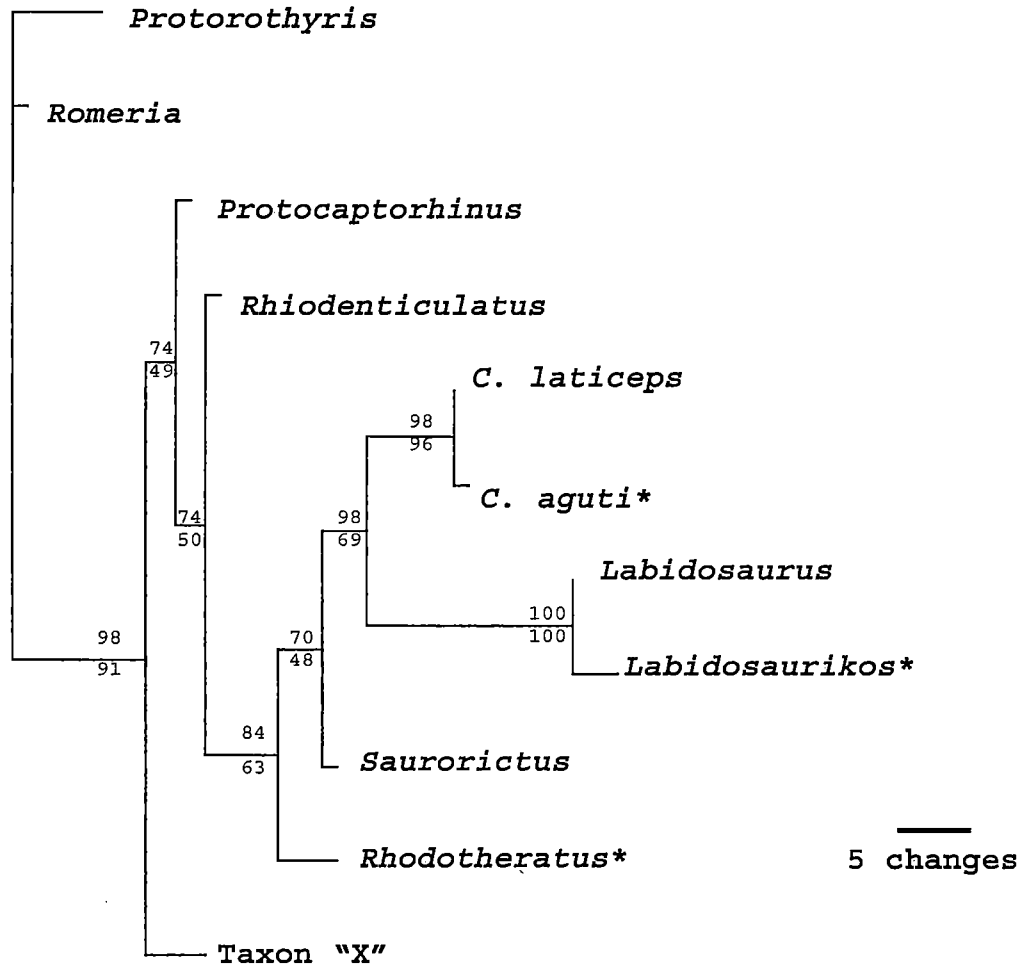
Figure 19. Single Most Parsimonious Phylogenetic Tree (Over 34 Million Trees Searched) Generated by Analysis Using PAUP* 4.0 (Taxon "X" is a new, single tooth-rowed genus of captorhinid reptile currently in prep by Sumida, et al. and is as of yet, unnamed; * in tree represents multiple tooth rowed species; Internal branch numbers represent bootstrap values, both weighted (above) and unweighted (below).

93

With the distinction of *Rhodotheratus* as a new genus, the total number of genera contained in the Captorhinidae increases to 15. As expected, the protorothyridid *Protorothyris* and the basal captorhinid *Romeria* formed a sister group relative to the remaining captorhinid taxa. Also as expected, the two members of the genus *Captorhinus* grouped together, the two genera *Labidosaurus* and *Labidosaurikos* grouped together, and these two groups sorted together, forming a larger monophyletic group. (The recently described *Captorhinus magnus* (Reisz et al., 2002) is based on only fragmentary specimens and was not included in this analysis.) The immediately successive sister taxa to this group are *Saurorictus* and *Rhodotheratus*, respectively. This grouping is stable and highly resistant to change. Subsequent to the initial analysis, multiple variations were applied, including: removal of *Saurorictus*, removal of specific characters common to *Rhodotheratus* and *Saurorictus* (Characters 18 and 40; see Appendix B), and variation of analysis search parameters (branch and bound as well as exhaustive maximum parsimony). Additionally, the reliability of internal branching was tested with 100 bootstrap replications (Felsenstein, 1985) with and without re-weighting of characters (Figure 19). In all cases, the

same basic tree was generated. These results conflict with those of numerous previous studies, including Ricqlès (1984), Ricqlès and Taquet (1982) and Gaffney and McKenna (1979) but are consistent with the more recent study of Dodick and Modesto (1995), whose hypothesis of relationships for more basal captorhinid reptiles is supported in large part, by the results presented here. There are significant morphological differences between *Rhodotheratus* and *Saurorictus*, and phylogenetic analysis confirms their placement in separate taxonomic groups. This suggests that the loss of the supratemporal bone was convergent in these two taxa, rather than lost and then subsequently regained in the subsequent, more derived groups. This may have been a means to increase skull strength and stability in each of these extremely small predators.

It is important to note that *Labidosaurikos* and *Captorhinus* include species with multiple tooth rows. Given that *Rhodotheratus* has multiple tooth rows, the topology of the resulting cladogram indicates that multiple tooth rows would have had to develop on at least two separate occasions. Alternatively, if multiple tooth rows developed only once, and then single tooth rows would have

had to have been redeveloped independently in *C. laticeps* and *Saurorictus* (Figure 19). A homoplastic return to the plesiomorphic condition of single tooth rows is considered here to have been less likely. However, regardless of which of these trajectories proves to be correct, homoplasy in dental features was clearly a feature of the basal reptilian family Captorhinidae.

APPENDIX A:

TABLES

Table 1: List of Cranial Characteristics Currently
Considered to Mark the Amphibian-Amniote Transition (*
indicates cranial character; indicates potentially
ambiguous character).

CHARACTER	CITATION
Frontal bone contacting orbit between the prefrontal and postfrontal*	Laurin and Reisz, 1995; 1997
Lack of contact of parietal lappet to squamosal*	Berman, et al. 1992
Loss of intertemporal bone*	Sumida, et al. 1992
Presence of occipital flange of squamosal (convex)*	Laurin and Reisz, 1995; 1997
Presence of dentition on transverse flange of pterygoid*	Laurin and Reisz, 1995
Convex basioccipital condyle*	Laurin and Reisz, 1995; 1997
Supraoccipital ossification*	Berman, et al. 1992
Absence of coronoid denticles*	Laurin and Reisz, 1997
Single splenial in lower jaw*	Berman, et al. 1992
Presence of labyrinthodont infolding of tooth enamel*	Laurin and Reisz, 1995
Fusion of atlantal pleurocentrum to axial intercentrum	Sumida, et al. 1992
Axial centrum angled anterodorsally	Laurin and Reisz, 1995
Cleithrum restricted to anterior edge of scapulocoracoid	Laurin and Reisz, 1995
Presence of 3 scapulocoracoid ossifications	Laurin and Reisz, 1995; 1997
Presence of astragalus	Laurin and Reisz, 1995; 1997
Dorsal scales long and slender	Laurin and Reisz, 1997

Table 2. Specimens Referred to *Captorhinikos parvus* in
Olson's Initial (1970) Description of the Species, and
Which are Now Referred to *Rhodotheratus parvus*.

SPECIMEN	ELEMENTS REPRESENTED
FMNH UR 1250	Holotype: Skull and part of right lower jaw
FMNH UR 1251	Partial skull, jaws, and skeleton
FMNH UR 1252	Distal end of lower jaw
FMNH UR 1253	Seven vertebrae
FMNH UR 1254	Crushed skull, jaws, and postcranium
FMNH UR 1255	Skull and jaws
FMNH UR 1256	Skull and jaws
FMNH UR 1257	Skull and jaws
FMNH UR 1258	Skull and jaws
FMNH UR 1259	Partial skull and jaws
FMNH UR 1262	Partial skull
FMNH UR 1263	Partial skull showing maxillary teeth
FMNH UR 1264	Partial skull and jaws
FMNH UR 1265	Partial skull and jaw
FMNH UR 1266	Distal end of skull
FMNH UR 1267	Jaws and skull fragments
FMNH UR 1268	Partial skull and jaws
FMNH UR 1269	Partial skull and jaws
FMNH UR 1270	Distal end of skull and jaws
FMNH UR 1271	Part of lower jaw
FMNH UR 1272	Lower jaw
FMNH UR 1273	Lower jaw
FMNH UR 1274	Part of lower jaw
FMNH UR 1275	Lower jaw
FMNH UR 1276	Part of lower jaw
FMNH UR 1277	Part of lower jaw
FMNH UR 1278	Lower jaw
FMNH UR 1279	Parts of skull and jaw
FMNH UR 1280	Lower jaw
FMNH UR 1281	Lower jaw
FMNH UR 1282	Maxillae and dentaries
FMNH UR 1283	Part of lower jaw

Table 3: Individual Skull Elements Visible in Each Specimen Utilized in this Study.

Skull Element	UCLA VP 2894	UCLA VP 2898	UCLA VP 2900	UCLA VP 2908	UCLA VP 2910	UCLA VP 2912	UCLA VP 2915	UCLA VP 2918	UCLA VP 2922	UCLA VP 3023-A	UCLA VP 3023-B	UCLA VP 3023-C	UCLA VP 3024-A	UCLA VP 3024-B	UCLA VP 3025	FMNH UR 1255	FMNH UR 1256	FMNH UR 1257	FMNH UR 1258	FMNH UR 1272	FMNH UR 1273	FMNH UR 1278
Premaxilla				*				*	*		*		*			*	*		*			
Maxilla	*			*			*	*	*		*					*	*		*			
Septomaxilla																*						
Lachrymal	*			*		*	*		*	*	*				*	*	*	*	*			
Nasal				*					*	*	*				*	*	*	*	*			
Prefrontal	*		*	*	*	*	*		*	*	*							*				
Frontal	*	*	*	*	*	*		*		*	*		*			*	*	*	*			
Parietal		*		*						*	*		*			*	*	*	*			
Postparietal	*			*						*		*				*	*	*	*			
Supratemporal			*						*	*	*		*				*					
Postfrontal	*		*		*	*		*	*	*	*						*		*			
Postorbital	*			*				*	*			*				*	*	*	*			
Jugal	*		*	*	*		*			*	*					*	*	*	*			
Squamosal				*				*	*	*						*	*					
Quadratojugal				*				*	*	*												
Vomer				*													*					
Palatine				*													*					
Pterygoid	*			*	*			*		*			*			*	*	*				
Quadrate				*																		
Parasphenoid	*			*				*		*			*			*	*		*			
Basisphenoid				*																		
Prootic				*																		
Supraoccipital						*										*						
Exoccipital					*	*										*						
Basioccipital					*	*							*			*						

Opisthotic					*	*														
Stapes				*	*									*						
Cornua Branchialia					*	*				*										
Dentary	*			*	*	*			*	*	*		*	*		*	*		*	*	*
Splenial																				*	
Coronoid																				*	
Prearticular	*				*										*	*				*	
Surangular	*				*	*			*						*	*				*	*
Angular	*			*	*	*			*						*					*	
Articular	*				*					*				*		*			*	*	

Table 4: Distribution of character-states among the eleven captorhinid taxa included in the phylogenetic analysis presented in chapter three. The numbers in the top rows (1-43) refer to the characters described in Appendix B (A question mark indicates that the character-state could not be determined because of incompleteness of specimen or inaccessibility of examination).

Character / Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Rhodotheratu	0	0	1	0	0	1	1	0	1	0	1	0	?	1	1
Saurorictus	0	0	?	1	1	1	0	0	?	0	1	0	0	0	1
Protorothyris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Romeria	0	0	1	1	0	0	0	0	?	1	0	0	0	1	0
Protocaptorhinus pricei	0	0	1	1	0	?	0	0	1	1	0	0	0	1	1
New Taxon "X"	1	0	1	1	0	1	0	0	?	0	0	0	0	1	1
Rhiodenticulatus	0	0	1	1	0	1	0	0	1	0	1	1	0	1	1
Captorhinus laticeps	0	0	1	1	1	?	0	0	2	0	1	1	0	1	1
Captorhinus aguti	0	0	1	1	1	1	0	0	2	0	1	1	0	1	1
Labidosaurus	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
Labidosaurikos	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1

Character / Taxon	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Rhodotheratus	?	0	2	?	1	0	1	0	1	1	?	?	?	?	0
Saurorictus	1	?	2	?	1	0	?	?	?	?	0	?	?	?	0
Protorothyris	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
Romeria	0	0	0	0	1	0	?	0	0	0	0	?	0	?	0
Protocaptorhinus pricei	1	0	0	1	1	0	?	0	0	0	0	0	0	1	0
New Taxon "X"	1	0	1	1	1	1	1	0	?	?	0	0	0	0	0
Rhiodenticulatus	1	0	?	1	1	?	1	0	0	0	?	0	0	?	0
Captorhinus laticeps	1	1	1	2	1	0	1	1	1	1	0	0	0	1	0
Captorhinus aguti	1	1	1	2	1	0	1	1	1	1	0	0	0	1	0
Labidosaurus	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1
Labidosaurikos	1	1	1	2	1	1	1	1	1	2	2	1	1	1	1

Character / Taxon	31	32	33	34	35	36	37	38	39	40	41	42	43
Rhodotheratus	1	1	0	1	?	1	1	1	0	1	0	1	1
Saurorictus	?	?	?	?	?	?	?	1	0	0	0	1	0
Protorothyris	0	0	0	0	0	0	0	0	0	0	0	0	0
Romeria	0	0	0	?	?	?	0	1	0	0	0	1	0
Protocaptorhinus pricei	0	0	0	?	?	?	1	1	0	0	0	1	0
New Taxon "X"	1	0	?	1	1	?	0	1	0	0	0	1	0
Rhiodenticulatus	0	0	0	1	?	?	?	1	0	0	0	1	0
Captorhinus laticeps	0	1	0	1	0	0	2	1	0	0	1	1	1
Captorhinus aguti	0	1	0	1	0	0	2	1	0	1	1	1	1
Labidosaurus	1	1	1	1	1	1	1	1	1	0	1	2	0
Labidosaurikos	1	1	1	0	1	1	1	1	1	2	1	2	0

APPENDIX B:

SKULL CHARACTERS AND CHARACTER-STATES

USED IN PHYLOGENETIC ANALYSIS

1. SKULL LENGTH: small; less then 5 cm antero-posteriorly in mature specimens (0), or large; greater than 5 cm anteroposteriorly in mature specimens (1) (this study).

2. SNOUT WIDTH: (immediately cranial to orbit): broad; greater than or equal to 35% of skull length (0), or narrow; less than 25% of skull length (1) (Dodick & Modesto, 1995).

3. PREMAXILLA: ventral margin straight (0), or flexed & aligned anteroventrally in lateral view (1) (Berman and Reisz, 1986).

4. MAXILLA: relatively straight (0), or posterior end flexed laterally (1) (Dodick & Modesto, 1995).

5. MAXILLA: posterior most tooth positioned at level of posterior margin of orbit (0), or positioned at level of midpoint of orbit (1) (Dodick & Modesto, 1995).

6. LACRIMAL: suture with jugal small (0), well-developed (1), or posterior to orbit (2) (Dodick & Modesto, 1995).

7. PREFRONTAL: anterior process short; approximately equal to posterodorsal process in anteroposterior length (0), or Long and narrow; approximately twice

the anteroposterior length of the posterodorsal

process (1) (Dodick and Modesto, 1995).

8. FRONTAL: anterior process (from pt. at which frontal contacts orbit) short; less than 55% of the total frontal sagittal length (0), or long; approximately 60% of the total frontal sagittal length (1) (reworded from Dodick & Modesto, 1995).

9. JUGAL: alary process absent (0), present & positioned no higher than the midpoint of the suborbital process of jugal and is distinct from the orbital margin (1), or present & positioned dorsally on the medial surface of the jugal flush with the orbital margin (2) (= "median process" of Berman and Reisz, 1986; Dodick and Modesto, 1995).

10. QUADRATOJUGAL: anteroposteriorly elongate & subrectangular in shape (0), or relatively shorter, almost square in shape (1) (reworded from Dodick and and Modesto, 1995).

11. QUADTRATOJUGAL: convex upward (0), square tipped anteriorly (1), or notched (2) (Dodick and Modesto, 1995).

12. POSTORBITAL CHEEK: mostly straight/little lateral convex (0), or convex/expanded laterally (1) (Dodick and Modesto, 1995).

13. SUPRATEMPORAL: separated from the posparietal (0), or solidly fused with the postparietal (1) (Dodick and Modesto, 1995).

14. PARIETAL (PINEAL) FORAMEN: positioned at midpoint of interparietal suture (0), or anterior to midpoint of interparietal suture (1) (Dodick and Modesto, 1995).

15. POSTPARIETAL: contacts mate fully along dorsal-ventral thickness (0), or dorsally only, postparietals slightly separated ventrally by dorsal aspect of supraoccipital (1) (reworded from Dodick and Modesto, 1995).

16. POSTPARIETAL: in parasagittal section, flat (0), or concave (1) (this study).

17. POSTPARIETAL: majority of postparietal on occipital skull surface and unsculptured (0); or majority of postparietal on dorsal skull surface and sculprured (1) (this study).

18. SUPRATEMPORAL: no contact with postparietal (0), contact with postparietal (1), or absent (2) (this study).

19. OCCIPITAL MARGIN OF SKULL TABLE: embayed bilaterally (0), straight (1), single medial embayment (2) (Dodick and Modesto, 1995).

20. TABULAR: present, resulting in transversely short postparietal (0), or absent, resulting in transversely elongate postparietals (1) (reworded from Dodick and Modesto, 1995).

21. SUPRATEMPORAL HORN: absent (0), or present (1) (this study).

22. ECOPTERYGOID: present (0), or absent (1) (Dodick and Modesto, 1995).

23. PTERYGOID: transverse flange broad-based and distinctively angular in ventral view (0), or narrow and tongue-like in ventral view (1) (Dodick and Modesto, 1995).

24. PARASPHENOID: deep ventral groove absent between cristae ventrolateralis (0), or present between cristae ventrolateralis (1) (Dodick and Modesto, 1995).

25. CULTRIFORM PROCESS OF STAPES: extends anteriorly (0), extends anterodorsally at an angle of approximately 15° to basal plane (1), or extends anterodorsally at

an angle greater than 45° to basal plane (2) (Dodick and Modesto, 1995).

26. SUPRAOCCIPITAL: in lateral view, slopes anterodorsally (0), vertical (1), or angled posterodorsally (2) (Dodick and Modesto, 1995).

27. SUPRAOCCIPITAL LATERAL ASCENDING PROCESS: accounts for less than one half of height of supraoccipital (0), or greater than two thirds of height of supraoccipital (1) (Dodick and Modesto, 1995).

28. OCCIPITAL CONDYLE: at level of quadrate condyles in ventral view (0), immediately anterior to quadrate condyles in ventral view (1), or posterior to condyles in vent view (2) (Dodick and Modesto, 1995).

29. PAROCCIPITAL PROCESS: short; less than one half the length of the stapedial columella (0), or long and "rod-like;" greater than one half the length of the stapedial columella (1) (Dodick and Modesto, 1995).

30. MANDIBULAR RAMUS SHAPE: in ventral view, relatively straight (0), or sigmoidal shape (1) (Dodick and Modesto, 1995).

31. MANDIBULAR RAMUS SIZE (width): less than 8% of total jaw length (0), greater than 8% of total jaw length (1) (Dodick and Modesto, 1995).

32. MANDIBULAR RAMUS POSTERIOR END: rectilinear (broadly expanded) (0), or acuminate (1) (Dodick and Modesto, 1995).

33. MANDIBLE LATERAL SHELF BELOW CORONOID PROCESS: absent (0), or present (1) (Dodick and Modesto, 1995).

34. MANDIBLE, ANTERIOR PROCESS OF CORONOID: short (0), or long (1) (Reworded from Dodick and Modesto, 1995).

35. MECKELIAN FORAMEN (= posterior foramen intermandiularis caudalis): small; anterior-posterior length less than 9% of lower jaw (0), or large; anterior-posterior length greater than 14% of lower jaw (1) (Dodick and Modesto, 1995).

36. CORONOID PROCESS, POSTERODORSAL PROCESS: slender and does not form wall of adductor fossa (0), or deep and forms dorsal most third of lateral wall of adductor fossa (1) (Dodick and Modesto, 1995).

37. RETROARTICULAR PROCESS: absent (0), present & slender (1), or present & broader transversely than long (& short) (2) (Dodick and Modesto, 1995).

38. MAXILLARY DENTITION: tooth stations number 30 teeth or more (0), or 25 or less (1) (Berman and Reisz, 1986).

39. MAXILLARY CANINIFORM TEETH: present (0), or absent (1) (Dodick and Modesto, 1995).

40. MAXIMUM NUMBER OF TOOTH ROWS (maxillary and mandibular): single (0), two to three (1), four or more (2) (Modified from Ricqlès, 1984).

41. MARGINAL DENTITION: cheek teeth conical (0), or chisel-shaped (1) (Dodick and Modesto, 1995).

42. DENTARY TEETH: isodont (0), caniniform region present anteriorly (1), or caniniform tooth present mesially with caniniform region absent (2) (reworded from Dodick and Modesto, 1995).

43. DENTARY: 1st tooth oriented mainly vertically (0), or 1st tooth leans strongly rostrally (1) (reworded from Dodick and Modesto, 1995).

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