Wise men speak because they have something to say; fools because they have to say something.

—— Plato, 429 – 347 B.C.E.

You can't depend on your eyes when your imagination is out of focus.

—— Mark Twain, 1889

I may not have gone where I intended to go, but I think I have ended up where I needed to be.

—— Douglas Adams, 1988

University of Alberta

SYSTEMATICS OF PLATYNOTAN LIZARDS

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
in
Systematics and Evolution

Department of Biological Sciences

Fall 2012
Edmonton, Alberta

For Crystal,

Madeline,

Finley

and

Violet.

ABSTRACT

Living platynotan lizards are represented by two families: Helodermatidae, consisting of two species limited to south-western North America and north-western Central America; and Varanidae, with 54 species distributed throughout Africa, south-east Asia and Australia. Modern members of Platynota, universally adapted to a predaceous lifestyle and often specializing in relatively large vertebrate prey, include the largest living lizard and three species known to employ venom. Although relatively depauperate, in terms of extant taxa, the 100 million year record of fossil Platynota reveals a widely distributed and morphologically diverse clade of predatory lizards. Several new taxa have been introduced in the past 30 years, many represented by complete skulls and skeletons yet the relationships among taxa found at the base of Platynota remain largely unresolved. Many basal platynotans have been placed within family Necrosauridae, the type genus of which is the most widely distributed and well represented fossil platynotan. As currently constituted the Necrosauridae is presumed to be paraphyletic and lacks a clear and concise diagnosis as does the type genus *Necrosaurus*. Amended diagnoses are provided for *Necrosaurus* and the Necrosauridae and the membership of taxa previously placed within Necrosauridae is examined. Phylogenetic analysis of fossil platynotans recovers a monophyletic Necrosauridae in a sister-group relationship to a clade containing modern varanids. Description of a new genus and species of platynotan from the

Maastrichtian of southern Saskatchewan reveals unusual anatomical features, adding to the already diverse morphology represented within Platynota. The newly described species is the oldest member of the Necrosauridae and one of two North American species.

ACKNOWLEDGEMENTS

I owe a debt of gratitude to Dr. Michael Caldwell for taking me on as a graduate student on very short notice, and for patiently guiding me through the process of researching and writing the Ph.D. dissertation contained herein. Dr. Caldwell played the role of supervisor deftly, supplying a great deal of financial and moral support, providing specific guidance on structure and content only when requested, and generally leaving me to make (and hopefully correct) my own mistakes. In addition to his academic supervisory role Dr. Caldwell has proved a bona fide mentor and friend, opening his home as well as his lab, making explicit his intent to treat students as junior colleagues; a goal he undoubtedly achieves.

I must also thank those who have served as members of my supervisory committee including Drs. Phillip Currie, Heather Proctor, Robert Holmes, and Randall Nydam as well as Drs. Alison Murray and Brian Chatterton for having served on my candidacy examination committee. Though little availed, I obtained no small amount of comfort knowing that the advice of these individuals was little more than an email away. Dr. Nydam in particular has provided many thoughtful comments and queries, his encouragement made efficacious by virtue of the quality of its source.

I wish to recognize several members of the Department of Biological Sciences who have contributed to my efforts either directly or indirectly. Members of the office of the Associate Chair Graduate studies, specifically Dr.

Heather McDermid, Dr. Rolf Vinebrooke, Chesceri Mason, Michelle Green and Melany Rattray, provided a great deal of administrative support helping with grant applications, awards and program extensions. The dedication and professionalism these individuals bring to their respective roles is of no small benefit to the many graduate students in our department and the quality of the support they provide cannot be overstated. In addition to it being my academic home, I feel fortunate to call the Department of Biological Sciences my employer as well. The challenge of completing my academic program while fulfilling my duties as an employee has been met thanks to the considerable patience shown by my employment supervisors Maggie Haag, and Dr. Alison Murray, as well as the Associate Chair Undergraduate Dr. Cindy Paszkowski and the Assistant Chair Administration David Howatt. I am fully cognisant of the fortunate position I find myself in, having acquired employment prior to completing my degree, and of the risk taken by the above individuals on my behalf in offering said employment. I look forward to demonstrating my gratitude in the form of a greater focus on my assigned duties and hope to validate the choice made by my hiring committee three years ago.

During the course of researching this thesis, many individuals provided necessary access to specimens and the following collections managers and curators have my thanks: Sandra Chapman and Dr. Colin McCarthy of the Natural History Museum in London; Dr. Meinolf Hellmund of the Geiseltal Museum at the Martin Luther University in Halle, Germany; Dr. Matthew Carrano of the Smithsonian Institution in Washington D.C.; Alan Resetar and

William Simpson of the Field Museum, Chicago; and Dr. Richard Cifelli of the Oklahoma Museum of Natural History in Norman Oklahoma. Special thanks is owed to Dr. Magdalena Borsuk-Białynicka of the Paleobiological Institute of the Polish Academy of Sciences in Warsaw, Poland with whom I had the pleasure of interacting with over the course of one month during an extended research trip facilitated in part by her hosting my visit. Dr. Borsuk-Białynicka was very generous with her time and with the outstanding collections in her care, providing me with temporary office space and with frequent discussions about my research in its early stages. It is clear to me that Dr. Borsuk-Białynicka maintains a special fondness for the specimens I was examining and I remain humbled that she would be so willing to share and discuss them with me.

The holotype specimen of the new genus and species described in chapter four of this thesis, was collected and provided by Tim Tokaryk of the Royal Saskatchewan Museum. The extended loan of the specimen as well as the access he provided to materials under his care have been crucial to the completion of this thesis and have left me indebted to Mr. Tokaryk. Equally vital to my work was the expert and painstaking preparation of the holotype by Alan Lindoe. The level of detail revealed under his steady hands leads me to wonder if Mr. Lindoe knows the specimen better than I do, and I am grateful to him for going the extra mile in prepping both dorsal and ventral surfaces of the specimen. Finally, I must thank Dr. Eric Snively, Dr. Benedikt Hallgrimsson and Michael Burns for facilitating and performing High Resolution X-Ray Computed Tomographic scans of the holotype in the Micro-CT Laboratories at the University of Calgary and the University of Alberta. These scans greatly enhanced the level of detail I was able to observe, illustrate and describe, and contributed significantly to the final result.

As with any place of work, the quality of ones co-workers can greatly enhance or detract from the experience of being a graduate student. I am happy to say that my interactions with fellow graduate students have been almost universally positive and I feel quite fortunate to have been a member of this particular cohort. In particular I would like to thank Dr. Takuya Konishi and Dr. Alessandro Palci for their conversation and insights on mosasauroid morphology and systematics. Dr. Erin Maxwell, Dr. Craig Scott, Dr. Todd Cook, Lindsay MacKenzie, Victoria Arbour, Brian Rankin and Scott Persons have all contributed positively to my graduate studies experience either acting as a sounding boards, by directing my attention to pertinent papers or by lending some technical expertise and for that I thank them.

While the above list of individuals covers those related to my time as a graduate student on campus, I would surely not have found myself in a Ph.D. program without the considerable encouragement and support of several family members. I thank my parents, Stewart Barr and Gwenyth Cartmell-Barr, for instilling in me a healthy respect for and a modest facility with the English language. My mother has also supported my family and myself financially and through helping care for my three children at times when I was otherwise occupied. Additional family members who have provided support in myriad forms include Kathy Tracy, Hayward Tracy, Maureen Barr, Mary Tropak, Sean

Barr, Ian Barr, Deborah Barr and Jordan Tracy and they have my sincere gratitude.

Lastly I must attempt to put into words the overwhelming gratitude I feel toward my partner, Crystal Tracy and our three children. The pursuance of a graduate degree has naturally placed a burden on my time, finances and mental health. As a result, several of my familial commitments have had to be rescheduled, postponed or outright cancelled and my family has felt this burden very keenly. Despite this my wife has continued to support this endeavour and it is this support more than any other's which has meant the most to me. I could not have done (and likely would not have attempted to do) this without her backing and encouragement. Above all others, I dedicate this work to Crystal Tracy.

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LIST OF ABBREVIATIONS

INSTITUTIONAL

BMNH	British Museum of Natural History, United Kingdom.
GM	Geiseltal Museum, Martin Luther University, Germany.
FMNH	Field Museum of Natural History, United States of America.
MNHN	Muséum National d'Histoire Naturelle, France.
SNB	Senckenberg Natural History Museum, Germany.
UALVP	University of Alberta Laboratory for Vertebrate Paleontology, Canada.
UAMZ	University of Alberta Museum of Zoology, Canada.
USNM	United States National Museum, United States.
ZPAL	Polish Academy of Sciences Institute of Paleobiology, Poland.

ANATOMICAL

Ala.Pro	Alar process of the prootic
Ant.Sa.For	Anterior surangular foramen
Ant.V.C.	Anterior opening of Vidian canal
At	Atlas
B.Occ	Basioccipital
B.Tub	Basl tubercle
C3	3rd cervical vertebra
C4	4th cervical vertebra
C.N.VI	Abducens foramen

C.N.VII	Facial foramen
C.N.X	Vagus foramen
C.N.XII	Hypoglossal foramen
Con	Vertebral condyle
Cot	Vertebral cotyle
Cr.Int	Crista interfenestralis
Cr.T	Crista tuberalis
D.Sel	Dorsum sella
EcPt	Ectopterygoid
Fr.Pro	Frontal process of postfrontal
HSCC	Horizontal semi-circular canal
Hypo	Cervical hypopophysis
J	Jugal
Lac	Lacrimal
LPrM	Lacrimal process of maxilla
Mx	Maxilla
Occ.C	Occipital condyle
Oto	Otooccipital
Ot.Rec	Otic recess
Pa	Parietal
Pa.Pro	Parietal process of postfrontal
Para.Pro	Paraoccipital process
PO	Postorbital

PoF	Postfrontal
PreF	Prefrontal
PSCC	Posterior semi-circular canal
P.S.R.	Parasphenoid rostrum
PsZyg	Pseudo-zygantrum
PT	Pterygoid
Sq	Squamosal
St	Supratemporal
V	Vomer
Ves	Vestibule

CHAPTER ONE

GENERAL INTRODUCTION

INTRODUCTION TO PLATYNOTA

Platynotans are a clade of lizards currently composed of the three morphologically distinct genera, *Heloderma*, *Lanthanotus* and *Varanus*. Of the estimated 10,100 species of living squamates (Zug et al. 2001) only 56 are platynotan, with the bulk of that diversity being represented by a single genus, *Varanus* (Pianka and King 2004). The geographic distribution of extant platynotans is also limited with all but *Heloderma* being restricted to Africa, Southeast Asia and Australia. The two living species of venomous *Heloderma* occupy a thin geographic band running from the Sonoran desert of North America, south along the Pacific coast of Mexico and Guatemala (Beck 2005), while the monospecific and enigmatic *Lanthanotus* is confirmed only from the north western coast of Borneo (McDowell and Bogert 1954). The largest living group, referred to commonly as monitor lizards, is represented by 53 species of *Varanus*; six in Africa, 23 in south east Asia, and 24 in Australia (Bennett 1998). Monitor lizards in particular have captured the imagination of researchers, and in quoting a colleague the preeminent varanid systematist Robert Mertens (1942) described them as "..these 'proudest, best proportioned, mightiest and most intelligent' lizards."

In addition to being taxonomically and geographically limited, extant platynotans are almost universally adapted to a predaceous lifestyle, many specializing on relatively large vertebrate prey. Despite this and the morphological constraints associated with their predaceous habits, platynotans, especially the monitors, have occupied a surprisingly wide array of niches, and include species adapted to arboreal, semi-aquatic, and terrestrial lifestyles living in both mesic and arid habitats. Though conservative in their morphology, monitors range nearly three and a half orders of magnitude in size. The smallest living varanid species, the Australian pygmy monitor (*Varanus brevicauda*), measures under 24cm and with documented weights between 8 and 17 g (Pianka 2004) while the largest is the 3 meter long Komodo dragon from the islands of Komodo and Flores, known to weigh as much as 70 kg (Ciofi 2004). *Varanus* also includes the largest land lizard known, the Pleistocene *Varanus* (*Megalania*) *prisca* Owen 1860. At six meters long and an estimated maximum mass of 2200 kg (Hecht 1975) this lizard appears to be a sister-taxon to the Komodo dragon (Head et al. 2009) and has recently been suggested to share the ability of that species to produce venom (Fry et al. 2009).

Impressive though they may be, modern platynotan lizards represent a small portion of the diversity known from the fossil record of the group. Thought by many (Owen 1877; Marsh 1880; Baur 1890; Williston 1898; Nopsca 1903; Camp 1923; McDowell and Bogert 1954; Russell 1967; Rieppel 1980; Carroll and DeBraga 1992; DeBraga and Carroll 1993; Lee 1997) to include the giant marine mosasaurs, Platynota was relatively poorly represented in terrestrial deposits and for a long time taxa were few and fragmentary. The first fossil platynotans were described in the late 19th century (Owen 1860; Leidy 1870; Filhol 1873) with fragmentary specimens steadily being added throughout the early to mid 20th century (Gilmore 1922, 1928, 1942, 1943; Kuhn 1940; Hoffstetter 1962; Estes 1964). Beginning in 1977 with the discovery of

Eosaniwa (Haubold 1977), the fossil record of Platynota began to expand rapidly as numerous articulated specimens displaying disparate morphologies began to be described in the literature (Stritzke 1983; Borsuk-Białynicka 1984; Norell et al. 1992; Nydam 2000; Gao and Norell 2000; Conrad 2006; Norell et al. 2008). Along with this newfound platynotan diversity came a renewed interest in determining the origins of the major platynotan radiations (Borsuk-Białynicka 1984; Norell and Gao 1997; Lee 1997; Gao and Norell 1998; Nydam 2000; Balsai 2001; Conrad 2006, 2008; Rieppel et al. 2007; Conrad et al. 2010). Despite this increased interest in platynotan relationships and the growing body of morphological data in the form of several new platynotan genera, the relationships between many platynotans (those with no obvious affinity to *Varanus*, *Lanthanotus* or *Heloderma*) continue to lack resolution. The traditional use of the term Platynota as representative of anguimorphans more closely related to *Varanus, Lanthanotus* and *Heloderma* than to anguids or xenosaurs, has been used for some time (McDowell and Bogert 1954; Rieppel 1980; Borsuk-Białynicka 1984; Pregill et al. 1986) and was phylogenetically defined by Lee (1997). This 'stem-based' definition is useful in light of the many platynotans whose relationships remain unresolved and the term 'basal platynotan' will be used throughout this thesis to refer to those taxa.

One particular group of basal platynotans, the Necrosauridae has become a 'waste basket' into which a variety of primitive platynotan forms have been placed. Almost certainly paraphyletic in its current usage (Estes 1983; Borsuk-Biłynicka 1984; Gao and Fox 1996) the Necrosauridae is named, ironically, for one of the most well represented basal platynotan genera. Lying as it does near the base of Platynota a better understanding of Necrosauridae, and *Necrosaurus,* may provide crucial insights into the radiation of more derived platynotan groups.

INTRODUCTION TO THE THESIS

For over one hundred years, the fossil record of terrestrial platynotans was one of small fragmentary specimens displaying a few clear platynotan characters and little else. Early efforts to classify fossil platynotans were limited to alpha-taxonomy (Gilmore 1928; Hoffstetter 1943, 1962; McDowell and Bogert 1954; Estes 1983) and basal platynotans were grouped together based as much on characters they lacked as on characters they shared (Estes 1983). Additionally, the treatment of new specimens representing previously known taxa has at times been perfunctory (Rieppel and Grande 2007) while the description of new taxa has occasionally lacked sufficient comparative scope (Conrad 2006).

If increased resolution of platynotan relationships is to be achieved, an effort must first be made to diagnose clearly, those taxa for which ample material is available. Long established taxa may be carefully re-evaluated in light of new specimens and new evidence, while newly discovered specimens should be evaluated within the ever-broadening concept of what platynotans are or may be defined as. The following chapter introductions outline the scope of the thesis presented therin.

Introduction to Chapter Two

First introduced in 1870, *Saniwa ensidens* (Leidy) has consistently been described as a varanoid lizard more closely related to *Varanus*, than to *Heloderma* (Gilmore 1922, 1928; Camp 1923; McDowell and Bogert 1954; Estes 1983). Though many species of *Saniwa* have been subsequently proposed (Marsh 1872; Dollo 1923; Brattstrom 1955), few have been widely accepted within the scientific community, and only the type species, has warranted inclusion in phylogenetic analyses of varanoid phylogeny. In 2007, a complete skeleton of *Saniwa* (FMNH PR2378) was described and referred to the type species, the authors purporting to dramatically amplify the list of known phylogenetic characters for that taxon (Rieppel and Grande 2007). A review of the generic and specific diagnoses along with a reinvestigation of FMNH PR2378, suggests that while it certainly is a member of the genus *Saniwa*, it cannot conclusively be referred to *S. ensidens*.

Introduction to Chapter Three

The genus *Necrosaurus* Filhol 1876 is traditionally comprised of two species represented by numerous complete and fragmentary dentaries, maxillae, parietals, frontals, vertebrae and other post-cranial bones and is the most commonly occurring platynotan in the Eocene of Europe (Filhol 1873; Lydekker 1886; Fejérváry 1935; Kuhn 1940; Hoffstetter 1943; Hecht and Hoffstetter 1962; Godinot et al. 1978; Rage 1978, 1988; Rage and Ford 1980; Estes 1983; Augé

1990, 2005; Alifanov 1993; Rage and Augé 2010; Klembara and Green 2010) . Despite a relative abundance of material, and an important phylogenetic position as a platynotan on the stem leading to modern varanoids, *Necrosaurus* is under-studied and lacking a clear generic diagnosis. Numerous fossil taxa, both from North America and Eurasia, have been appended to the Necrosauridae (Estes 1983; Borsuk-Białynicka 1984), their inclusion based on their possession of a 'necrosaurian-grade' of evolution resulting in an almost certainly paraphyletic assemblage of diverse platynotan taxa. A review of the members of the genus *Necrosaurus* is here presented along with an amended generic diagnosis, and a discussion of other fossil taxa that may warrant inclusion in a monophyletic Necrosauridae.

Introduction to Chapter Four

Taxa found on the platynotan stem leading to Varanoidea can vary considerably from one another and they remain a taxonomically problematic group the monophyly of which is clearly in doubt (Estes 1983; Borsuk-Białynicka 1984; Gao and Fox 1996). A new platynotan lizard, *Vulpesaurus magdalenae* gen. et sp. nov. is here described. The first semi-articulated lizard specimen described from the Frenchman Formation (late Maastrichtian) of Southern Saskatchewan (Tokaryk 1997), *Vulpesaurus* is represented by much of the skull, several cervical and dorsal vertebrae, and fragments of sacral, costal and appendicular elements. The specimen is described in detail employing High Resolution X-Ray Computed Tomography (HRXCT). Unique features of the braincase and palate help to distinguish *Vulpesaurus* from all other known platynotans.

Introduction to Chapter Five

Basal platynotans have traditionally been regarded as possessing a mosaic of primitive and derived anguimorphan characters (Gilmore 1928; Hoffstetter 1943; Estes 1983; Borsuk-Białynicka 1984; Gao and Fox 1996) and phylogenetic analyses of platynotan relationships consistently reconstruct a paraphyletic assemblage of ‘stem’ taxa basal to the Varanoidea (Borsuk-Białynicka 1984; Lee 1997; Norell and Gao 1997; Gao and Norell 1998; Nydam 2000; Balsai 2001; Conrad 2006, 2008; Rieppel et al. 2007; Conrad et al. 2010). A recent increase in the number of platynotan taxa described (Norell et al. 1992; Gao and Norell 2000; Conrad 2006; Norell et al. 2008) has done little to resolve our understanding of basal platynotan relationships. As currently compiled, data sets continue to rely on characters constructed to address the anatomical variability present in extant taxa, and fail to address variability present within fossil taxa. A phylogenetic revision of Anguimorpha is presented here, with the aim of introducing new character data relating to patterns of variability observed within basal platynotans.

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CHAPTER TWO

A TAXONOMIC REVIEW OF THE GENUS *SANIWA* LEIDY 1870

(VARANOIDEA, ANGUIMORPHA, SQUAMATA)

INTRODUCTION

Since its introduction, the genus *Saniwa* has held a unique and important place within varanoid phylogeny, as both the most primitive taxon referable to Varanidae, and the only one found in North America. Several other fossil varanoids have been discovered in North America (Gilmore 1928, 1942; Estes 1964; Stevens 1977; Gao and Fox 1996; Nydam 2000) but among them, only *Paleosaniwa* (Gilmore 1928) finds placement as a varanid (Gilmore 1928; Estes 1964; Gao and Fox 1996), though many express doubts (McDowell and Bogert 1954; Hoffstetter 1969; Estes 1983) based on that taxon's considerably more primitive and fragmentary nature; the most recent analysis focusing on *Paleosaniwa* (Balsai 2001) placed it within the Monstersauria (sensu Norell and Gao 1997) outside the Varanidae. Thus, among North American squamates, *Saniwa* remains the only taxon consistently assigned to the Varanidae.

The presence of a varanid in the Eocene/Oligocene of North America has obvious implications for the biogeography of varanids, but perhaps more importantly, the genus provides insight into early varanid morphology. Fossils attributed to the Varanidae in Eurasia are relatively widespread and have been recovered from the Late Cretaceous of Mongolia and Kazakhstan (Borsuk-Białynicka 1984; Kordikova et al. 2001; Norell et al. 2007); the early Eocene of

Kirghizia (Averianov and Danilov 1997); the middle Eocene of the former USSR (Reshetov et al. 1978) the late Eocene and early Oligocene of Egypt (Smith et al. 2008; Holmes et al. 2010); the middle Eocene and early Oligocene of Mongolia (Alifanov 1993); the Miocene of Kenya (Clos 1995); the middle Miocene of Spain and Portugal and the late Miocene of Germany, France and Spain (Roger 1898; Hoffstetter 1969); and the Pliocene of Greece (Weitofer 1888). Pleistocene and Holocene specimens attributable to *Varanus* have been recovered in India (Lydekker 1886), Java (Fejérvary 1935), and Australia (Rage and Bailon 2005), and the giant monitor *Varanus (Megalania) prisca* Owen 1860 of Pleistocene Australia is often referred to that genus (Lydekker 1888; Head 2009). Accounts of most of these taxa are fairly brief, being described from vertebral material only. The late Cretaceous *Cherminotus* (Borsuk-Białynicka 1984) and *Ovoo* (Norell et al. 2007) appear to be more closely related to *Lanthanotus* than to *Varanus* and others, such as *Varanus prisca* (Owen 1860) and *V. rusingensis* (Clos 1995), are very like modern *Varanus* in their anatomy and do little to add to our understanding of early varanid evolution. In this context, *Saniwa* appears to offer the best opportunity to examine the early evolution of Varanidae (Conrad et al 2008) and has important implications for the diagnosis and phylogenetic analysis of this species-rich clade.

The phylogenetic significance of *Saniwa* has resulted in its inclusion into most recent studies of anguimorphan and varanoid systematics (Norell et al. 1992; Norell and Gao 1997; Lee, 1997; Gao and Norell 1998; Lee 2000; Nydam 2000; Balsai 2001; Conrad 2006, 2008; Norell et al. 2007;Conrad et al. 2008, 2010; Gauthier et al. 2012). All the above studies recover a sister group relationship between either *Saniwa* and *Varanus* or between *Saniwa* and a clade containing *Varanus* and *Lanthanotus*. This consistency of placement is relatively rare within varanoid analyses and serves to emphasize the importance *Saniwa* holds in helping define varanid synapomorphies.

TAXONOMIC HISTORY

Joseph Leidy published an initial brief description of *Saniwa ensidens* in 1870 (Leidy 1870), a large *Varanus*-like lizard from the middle Eocene Bridger Formation of Sweetwater county, Wyoming, discovered by a Dr. F.V. Hayden in that same year. Leidy followed with a more detailed description and accompanying illustrations three years later (Leidy 1873) adding at that time a second species, *S. major* (Leidy 1873), based on two dorsal vertebrae and the distal end of a humerus. The latter element was later determined to be non-squamate by Feyérvary (1918), and Gilmore (1922), and Leidy himself had already pointed out similarities with the humerus of birds [in a curious case of history repeating itself, Smith (2009a) made the same error identifying a similar specimen (an avian distal humerus) as *Saniwa*, though he promptly corrected the error (Smith 2009b)]. *S. major* was deemed a junior synonym by Estes (1983) without direct explanation, though possibly based on the lack of sufficient material.

The type material of *S. ensidens* was deposited in the United States National Museum (USNM 2185) and remained unprepared for 50 years. After preparation in 1921, Charles W. Gilmore undertook a redescription of the type specimen along with a review of several closely related taxa that had been introduced in the interim (Gilmore 1922). Shortly thereafter, the entire set of holotype material was articulated into a composite skeleton to be used for exhibition (the missing elements modeled largely on those of *Varanus griseus*) obscuring margins of many of the preserved elements with paint, plaster and/or modeling compound. 1872 had seen the introduction by Othniel C. Marsh of five species within the new genus *Thinosaurus*: *paucidens*, *leptodus*, *crassa*, *agilis* and *grandis* all from the Bridger Formation in Wyoming (Marsh 1872). Gilmore (1922) noted that *Thinosaurus leptodus* "is apparently identical" with the *Saniwa* type material and treated it as a junior synonym. The other four species introduced by Marsh were retained by Gilmore (1922, 1928) as species within *Saniwa*.

The descriptions of all five species introduced by Marsh (1872) were preliminary and the promise of more detailed descriptions and illustrations to come never materialized. Of the four species introduced by Marsh and retained by Gilmore, only *Saniwa paucidens* was represented by more than jaw fragments and vertebrae, and that specimen (the greater part of a skeleton) is now lost (Estes 1983). The remaining Marsh species *S.crassus*, *S. grandis*, and *S. agilis*, are differentiated from *S. ensidens* solely on the basis of vertebral characters that may be attributable to size difference and regional variation (Gilmore 1928; Estes 1983), and though he retained them, Estes (1983) noted that the size range represented is equaled within several species of *Varanus*. Estes (1983) along with others (Molnar 2004; Rieppel and Grande 2007) suggests a better understanding of vertebral variation within *Saniwa* and within *Varanus* is required before the validity of these taxa can be definitively assessed.

Dollo (1923) erected *Saniwa orsmaelensis* on the basis of a maxillary, femur and a dorsal vertebra from the early Eocene of Belgium, though he did not figure the specimens nor did he designate a type. Hoffstetter (1969) did illustrate a trunk vertebra from the original material and Estes (1983) designated this the lectotype. Hecht and Hoffstetter (1962) compared all material referred to *S. orsmaelensis* with *S. ensidens* and noted that the maxilla and femur were similar to undescribed *Necrosaurus* material from Quercy, France, while the vertebral material was indistinguishable from *S. ensidens*. Provisionaly retained by Estes (1983) based on geographic separation but dismissed by Rieppel and Grande (2007) for the above reasons, *S. orsmaelensis* at a minimum provides evidence of the genus in Europe.

Stritzke (1983) briefly described a well preserved, nearly complete skeleton from the middle Eocene of Germany (Messel) as *Saniwa feisti.* Augé (2005), Conrad (2008) and others have questioned this assignment, pointing out numerous similarities between '*S.*' *feisti* and *Necrosaurus*, the most common platynotan of the European Paleogene. Pending a forthcoming redescription by Smith (in prep) '*S.*' *feisti* is here considered not to be a member of *Saniwa*.

An additional North American species *Saniwa brooksi* was introduced by Brattstrom (1955), based on vertebrae from the late Eocene of San Diego and distinguished from other known species on the basis of size and the relative height of the condylar ball. Estes (1983) again provisionally retains *S. brooksi* based on geographic separation, and the fact that it seems to differ more greatly from *S. ensidens* than do any of the other proposed species. However Estes (1983) again points to our lack of knowledge regarding the potential variation within *Saniwa* or *Varanus*, stating that in light of this "…it is difficult to comment on the validity of any species of *Saniwa* other than *S. ensidens*." Additional specimens from the early and middle Oligocene of Wyoming have been referred as *Saniwa* sp. (Gilmore 1928) and were noted by Estes (1983) only as confirmation of varanids in the Oligocene of North America.

Lastly, Smith (2006) erected *Saniwa endura* based on a holotype partial left dentary and paratype partial parietal from the late Eocene Chadron Formation of North Dakota. *S. endura* is differentiated from *S. ensidens* on the basis of the paratype parietal which is markedly different from those referred to *Saniwa*. Smith (2006) points out the size discrepancy between the paratype parietal and the holotype dentary, but unites them based only on their shared varanid morphology. It is entirely possible then that the holotype dentary of *S. endura*, indistinguishable from *S. ensidens*, is of that species while the paratype parietal may represent an altogether different, non-saniwine taxon.

The taxonomic difficulties outlined above, relate exclusively to the recognition of several possible species within the genus *Saniwa*. The generic diagnosis and acceptance of *Saniwa* as a valid taxon is unaffected. The inclusion of *Saniwa* in phylogenetic analyses has from a practical standpoint often relied on character scores derived from multiple specimens, some of which were formerly referred to now defunct species (Conrad 2008; Gauthier et al. 2012). This practice seems entirely reasonable given the consistency of both the resulting character scores and the retrieval of *Saniwa* as a basal member of the Varanidae. Nonetheless, the suggestion that a clade of several large predatory varanid lizards may have occupied parts of North America during the Paleogene is interesting in light of the abundant species of *Varanus* currently occupying Africa, Asia, Indonesia and Australia, with numerous examples of multiple species co-occurring (Molnar and Pianka 2004). More complete examples of *Saniwa*, allowing for direct comparison to the cranial elements of the *S. ensidens* holotype, as well as examination of intervertebral variation would help greatly in any investigation of the possible species diversity within the genus and recently discovered specimens of *Saniwa* offer up just such an opportunity.

MATERIALS AND METHODS

A remarkably complete and well-preserved specimen of *Saniwa* was recovered from 'locality H' of Grande and Buchheim (1994) from the Fossil Butte Member of the Green River Formation in Lincoln County Wyoming. The locality is of late early Eocene, and produces a diverse assemblage of aquatic vertebrates as orange-brown colored bone in a buff to white micritic limestone (Grande and Buchheim). Housed in the Field Museum of Natural History, Chicago, the specimen (FMNH PR2378) was described and illustrated by Rieppel and Grande (2007) along with a second, somewhat less well-preserved, specimen from the Fossil Butte Formation ('locality K' of Grande and Buchheim

1994). The second specimen is held in a private collection at the Black Hills Institute and a cast of its cranial material is held at the Field Museum as FMNH PR2380.

Comparisons between the Fossil Butte Formation material and the Type material of *Saniwa ensidens* (USNM 2185), were made by direct observation of the complete skeleton of FMNH PR2378, the cranial cast FMNH PR2380 and the cranial material belonging to the holotype USNM 2185. The mandible and post-cranial material of USNM 2185 were unavailable at the time of viewing, vertebral material included in FMNH PR2378 is ventrally embedded in the matrix and, as noted above, the cast specimen FMNH PR2380 consists of cranial material only. These factors severely limit the opportunity for detailed comparisons of mandibular and post-cranial material at this time.

SYSTEMATIC PALEONTOLOGY

ANGUIMORPHA Fubringer, 1900

VARANOIDEA Boulenger, 1891

VARANIDAE Gray, 1827

SANIWINAE Camp, 1923

SANIWA LEIDY, 1870

Saniwa Leidy, 1870 p.124; Leidy 1872 p.370;

Thinosaurus Marsh, 1872 p.299;

Saniwa leptodus Gilmore, 1922.

Type species–*Saniwa ensidens* Leidy, 1870.

Other species considered potentially valid (following the logic of Estes 1983), *S. orsmaelensis* Dollo, 1923, and *S. brooksi* Brattstrom, 1955.

Diagnosis–Estes (1983) provides a thoughtful and detailed diagnosis of the species outlining the principal characters in relation to their presence or absence in *Varanus*, laying out three distinct categories as follows:

Characters derived relative to *Varanus*–Premaxilla much reduced (though see Caldwell 2003); dorsal posterior lacrimal foramen bounded completely within the lacrimal; pseudo zygosphenes and zygantra present; reduction of cervical intercentra; anteroposteriorly expanded neural spines extending into the caudal region.

Characters primative relative to *Varanus*–presence of palatine and pterygoid teeth; palatines closely approaching the midline; reduced posterior retraction of external bony naris; posterior process of maxilla long, with 2-3 maxillary teeth underlying the orbit; neck elongation greatest anterior to the 5th cervical vertebra; neural spine low; caudal intercentra with intracentral articulation but closer to the condyle than in *Varanus*; precondylar constriction less well developed; coracoid with a single coracoid fenestra.

Characters considered primitive but occasionally present in *Varanus*– longitudinal sulcus on medial surface of quadrate process of pterygoid deep; vomers relatively wide; snout moderately blunt; separate postorbital and postfrontal; postorbital arch complete; ilium narrow; cervical ribs beginning on 5th vertebra.

As *Saniwa ensidens* was the only well represented species at the time, Estes (1983) offered the above diagnosis for the entire genus, but for the purposes of the following comparison it will be applied specifically to the holotype of *S. ensidens.*

ANATOMICAL COMPARISON

The following discussion details the observed similarities and differences between the holotype of *Saniwa ensidens* (USNM 2185) and the comparable elements preserved in FMNH PR2380 specifically with occasional reference to FMNH PR2380 where distinct variation in the latter specimen warrants inclusion. As FMNH PR2380 is a cast of a privately held specimen, and as the cast itself lacks clear resolution between matrix and fossilized bone as well as bubble and pit artifacts, detailed discussion of the morphology and taxonomic identification of FMNH PR2380 are specifically avoided here. Rieppel and Grande (2007) report the likely sub-adult status of FMNH PR2378 citing incomplete ossification of distal and proximal epiphyses of the right humerus and femora, whereas described by Gilmore (1922) the postcranial material of USNM 2185 would seem to represent that of an adult. Despite this the cranial material of both specimens appears to represent individuals of very similar size and potential ontogenetic variation between the two specimens is presumed to be minimal. Lastly, when used in this paper, the name *Saniwa ensidens* refers exclusively to the type specimen (USNM 2185).

Maxilla–In describing the holotype of *S. ensidens*, Gilmore (1928) noted a distinct medial inflection of the dorsal-most portion of the nasal process of the maxilla, describing it as a flattened turbinarial process. A similar extension is apparent on the right maxilla of FMNH PR2378, and though that element is considerably flattened, a clear longitudinal fracture, as would be expected from such taphonomic distortion, is visible at the precise point at which the element would have deflected medially. In addition, the relatively long 'zygomatic' or posterior process of the maxilla suggested by Gilmore (1922, 1928) is also present in FMNH PR2378 with the likelihood of 2-3 teeth underlying the orbit. The cast specimen, FMNH PR2380, preserves this element in medial view with no apparent distortion and also bears a medial inflection at its apex and an equally long posterior process. In the presence of the above features, FMNH PR2380 is consistent with the Holotype of *S. ensidens*.

The maxillary tooth count In FMNH PR 2378 can only be inferred as the element is preserved in lateral view with the teeth interdigitating with those of the right dentary, but the size and spacing of the teeth are consistent with FMNH PR2380 which clearly shows a minimum of 16 tooth positions. This is in accordance with the conservative estimate of Caldwell (2003) being somewhat more than 9 and less than 22, and the estimate provided by Rieppel and Grande (2007) of 17-18. It should be noted however, that the broad range estimate provided by Caldwell is necessitated by the fragmentary nature of the type specimen, and that as defined by the type, there can be no certainty as to the number of maxillary teeth in *Saniwa ensidens*.

Rieppel and Grande (2007 p.646), in discussing the posterior margin of the nasal process point out that in *Varanus* there exists a 'posteriorly pointed process that enters between the prefrontal and nasal'. No such process exists in *Varanus* and the description of this region in FMNH PR2378 provided by Rieppel and Grande (2007) clearly indicates that they were referring to the posterior process of the maxilla which projects between the prefontal and lacrimal. In discussing this feature, Rieppel and Grande (2007) note its complete absence in FMNH PR2380, and the possibility of a small projection in FMNH PR2378, though they suggest that the fracturing of the latter specimen renders that assessment equivocal. They go on to suggest that *S. ensidens* also possesses no such projection and indeed, Gilmore (1922, 1923) fails to adequately describe this portion of the element and in the plates provided appears to illustrate the left maxilla with fairly linear anterodorsally to posteroventrally tapering posterior margin much like that observed in FMNH PR2370. In his description of the prefrontal however, Gilmore (1928) notes an indented articular surface on its ventrolateral margin which he concluded was for a posterior projection of the maxilla. Direct observation of the Holotype reveals a small posteriorly directed projection of the left maxilla entering between the prefrontal and lacrimal, though the nature of preparation of that specimen appears to include some intervening material. The projection observed on USNM 2185 is somewhat larger than that suggested by the element in FMNH PR2378 (Fig. 2-1).

Prefrontal–Most of the left prefrontal of USNM 2185 was preserved and it was described by Gilmore (1922, 1928) as proportionately longer and more broad than that of a *Varanus* specimen of corresponding size. The same can be said for the preserved left prefrontal of FMNH PR2378 though some considerable fracturing of that element has occurred. In both specimens, the prefrontal bears a thickened dorsolateral crest where the anterodorsal surface forms an angle with the lateral surface. Both Gilmore (1922, 1928) and Rieppel and Grande (2007) interpret this ridge as evidence of a support for the attachment of a substantial palpebral, an element preserved in FMNH PR2378 but not in the type material. Other than in general shape, proportion and presence of a dorsolateral ridge, little can be compared between the prefrontals of USNM 2185 and FMNH PR2378 due to the compression of the element in the latter. Insofar as they can be compared however, the prefrontal of FMNH PR2378 appears very much like that of *Saniwa ensidens*.

Lacrimal–The lacrimal of *Saniwa ensidens* is considered phylogenetically important as it possesses two posterior lacrimal foramina (a varanid synapomorphy), both of which are bounded entirely within the lacrimal (an apomorphy of *Saniwa ensidens*). Both left and right lacrimals appear to be well preserved though incompletely exposed in FMNH PR2378. Despite this, Rieppel and Grande (2007) limit their description of this element to three sentences, noting only the presence of a small posterior projection on the lateral surface of the right lacrimal, and the impossibility of ascertaining the nature of the posterior lacrimal foramina citing a lack of exposure and preservation. In fact, an element lying just posteroventral to the posterodorsal tip of the left maxilla, figured but not labeled or referred to in the text (Rieppel and Grande 2007), shows evidence of two foramina (Fig. 2-2).

The size of this element as well as the size and relative position of the two foramina, and the position of the element in relation to the left maxilla strongly support its identification as the left lacrimal, though its visible surface does not permit conclusion as to its exact orientation in the preserved specimen. Gilmore accurately (1922) figured the posterior (orbital) surface of the left lacrimal of USNM 2185, showing its characteristic double foramina, but wrote that they ‘appear to have a common exit’ on the anteromedial surface of the bone. The anteromedial surface of the lacrimal of USNM 2185 cannot currently be observed as a result of the mounted preparation of that specimen, and so no confirmation of Gilmore’s apparently uncertain description of the internal exit of the lacrimal foramina is possible. If Gilmore’s interpretation in this regard is correct, and FMNH PR2378 is presumed to posses the same arrangement of the lacrimal foramina, then we can assume that the visible surface of the left lacrimal in FMNH PR2378 includes a portion of the orbital surface as the foramina present are definitely separated. Alternatively, the visible surface of this element may represent the anteromedial exit of continuously separate double lacrimal foramina. The right lacrimal of FMNH PR2378 is also perfectly well preserved though only visible on its lateral surface, matrix obscuring the posteriorly facing orbital surface. There appears to be ample room to remove some of the matrix from the orbital surface exposing at least some portion of the lacrimal foramina. In either case, a modest amount of further preparation of both the right and left lacrimals, would go a long way to determining the orientation and arrangement of the lacrimal foramina and in doing so, might prove critical to the accurate taxonomic assignment of FMNH PR2378.

Postfrontal/postorbital–Contrary to Rieppel and Grande (2007), both left and right postorbitofrontals are preserved and visible in FMNH PR2378. Those authors figured and identified the left postorbitofrontal as the surangular, a portion of which does lay posteromedial to it. Of the two, the right postorbitofrontal is better preserved and is dislocated, lying just posterior to the right anterolateral process of the parietal. In their description of this element Rieppel and Grande (2007) note the full exposure of the anteromedial prong that would have contacted the posterolateral surface of the frontal, the incomplete exposure of the posteromedial prong that would have contacted the anterolateral surface of the parietal, a small anteroventral projection that would have made or approached contact with the right jugal, and a posterior process that would have contacted the squamosal, completing the upper temporal arch. In fact, the visible portion of the right postorbitofrontal of FMNH PR2378 consists of three branches only, not the four described by Rieppel and Grande (2007), the orientation of which makes their individual identification problematic. The right postorbitofrontal appears as a triradiate structure with a relatively broad posteriorly directed and tapering process, the tip of which is overlain by the alar process of the right prootic, a dorsomedially projecting, slender prong, the tip of which is broken off, and an anteriorly projecting triangular process roughly equal in length to the preserved portion of the medial process (Fig. 2-3). Rieppel and Grande (2007) detail the position of the posterior process of the postorbital, relative to the right squamosal and to the alar process of the prootic, indicating that in their interpretation, it represents the postorbital contribution to the temporal arch. Following their logic then, the dorsomedially projecting prong could only be identified as the posteromedial prong of the postfrontal where it contacts the parietal, yet the above authors describe that portion of the postfrontal as 'incompletely exposed'. If we continue with the landmark of the posterior process provided as context, then the anterior (and only remaining) process would necessarily be interpreted as the anteromedial prong of the postfrontal where contact with the frontal occurred, yet the authors clearly indicate the presence of an anteroventrally directed 'short and slightly curved' process, much like that seen in *Varanus*, which would have approached or contacted the right jugal, a description that matches well the appearance of the anterior process in the specimen. In short, the description of the right postorbitofrontal of FMNH PR2378 provided by Rieppel and Grande (2007) doesn't correlate with the specimen or the figures provided. Their explicit interpretation of the element, as evidence of a fused postorbitofrontal, contra Gilmore's description of the Holotype (1922, 1928), is also not supported, as an isolated postfrontal could conceivably consist of three processes such as those present. The interpretation of the right postfrontal presented here is that of a discrete element with the medial and posterior branches representing the anteromedial and posteromedial prongs of the postfrontal respectively. The anteriorly directed, small triangular process appears consistent with the anteroventrally directed process for contact with the jugal, with its distal tip fractured through compression resulting in an anterior projection. It is important to note that the only alternative interpretation available is that the anterior and medial processes represent the anteromedial and posteromedial prongs of the postfrontal respectively, and that if they were rotated into an articulating position with the frontal and parietal, the third, posterior projection, would be oriented in a markedly lateral direction, swinging well away from the upper temporal fenestra and articulation with the squamosal. If correct, this interpretation does not allow for a clear assessment of the fusion or lack of fusion between the postfrontal and postorbital as the articular surface for the postorbital would be embedded in matrix, but it also does not preclude the possibility that like those of *Saniwa ensidens* the posfrontal and postorbital were separate elements.

Under the interpretation presented above, the postfrontal of FMNH PR2378 differs somewhat from that of *Saniwa ensidens* (USNM 2185). The angle created by the relatively gracile posteromedial (parietal) and anteromedial (frontal) processes of the postfrontal in the *Saniwa ensidens* holotype is acute, being slightly less than 70 degrees. The relative contributions of the postfrontal and postorbital to the anteroventral process that approaches and sometimes articulates with the dorsal ramus of the jugal are variable. In anguids, where the two elements are typically unfused, contact with the jugal may be formed exclusively by the postorbital (*Gerrhonotus* and *Diploglossus*), or by roughly equal contributions of the postfrontal and postorbital (*Ophisaurus* and *Elgaria*).

In *Saniwa ensidens* (USNM 2185) the sutural contact is visible between the left postfrontal and postorbital indicating the exclusion of the postfrontal from any potential contact with the jugal. Rather, the postorbital laterally overlaps the postfrontal and forms a small but distinct anteroventral projection approaching contact with the jugal. By contrast, the postfrontal of FMNH PR2378, appears to incorporate a relatively large and robust anteroventral process that very likely would have contacted the jugal behind the orbit. Also, the posteromedial process of the postfrontal in FMNH PR2378 is considerably more robust than that of *Saniwa ensidens* (USNM 2185) and the angle formed between it and the anteromedial process is less acute, approximately 90 degrees, matching well the outer margins of the parietal and frontal where it laterally cupped those elements in articulation. It is worth noting that the parietal and frontal of the cast specimen FMNH PR2380 when articulated would have formed an acute lateral angle similar to that displayed by *Saniwa ensidens* (USNM 2185), thus differing from FMNH PR2378.

Jugal–Owing to a fractured posterodorsal tip and some distortion along its length, Gilmore (1922, 1928) was unable to conclusively reconstruct the precise contact of the jugal with surrounding elements. The element does however allow for size comparison, appearing considerably more robust than that of *Varanus*, its length and size suggesting that contact with the postorbitofrontal, and completion of the postorbital bar was likely; a condition suggested by Gilmore (1922, 1928) and Estes (1983) as well. The left jugal of FMNH PR2378, well preserved and broadly exposed, corresponds favorably with the type material, though its posterodorsal ramus appears somewhat more broad that that of the *Saniwa ensidens* (USNM2185), the latter showing a continuous tapering towards its posterior tip. This feature in combination with the robust nature of the anteroventral process of the postfrontal described above strongly suggest the formation of a complete postorbital bar.

Exoccipital–As noted by Rieppel and Grande (2007) the right paroccipital process of the exoccipital has flipped over with the ventral surface visible in dorsal view. Gilmore (1922) described a thin horizontal wing-like plate anteroventral to the vagal foramen joining to the lateral border of the basioccipital. Termed the crista tuberalis by Oelrich (1956), this structure is common in squamates, highly developed in *Varanus* and considerably less developed in other varanoids. In position and degree of development, the crista tuberali of USNM 2185 and FMNH PR2378 are equivalent, as are the relative contribution of that element to the foramen magnum. The degree of development of the ridge present on the anterior surface of the paroccipital process dividing the upper, articular surface from the lower free surface is also equivalent between USNM 2185 and FMNH PR 2378. The degree to which the posterolateral tip of the paroccipital process of expands dorsoventrally seems greater in USNM 2185 than the corresponding surfaces in FMNH PR2378 though the latter appear somewhat abraded. In all aspects that can be compared, the paroccipitals of FMNH PR2378 and USNM 2185 appear very similar to one another, and fall well within the morphological range ascribed to varanoids.

Supraoccipital–The supraoccipital of FMNH PR2378 is well preserved with no sign of dorsoventral compression or subsequent distortion. It is accurately described by Rieppel and Grande (2007) as trapezoidal in outline with a modest convexity, and a low sagittal ridge that slopes gently outward creating a saddle-like shape. Gilmore failed to adequately illustrate the supraoccipital of USNM 2185 including it only in plates of the composite skull as mounted for exhibition, but direct observation of the element reveals it to be proportionately far narrower and more steeply convex than that of FMNH PR2378 (Fig. 2-4). Gilmore's (1928) description of the particularly strong keel (processus ascendens of Fejérváry 1915) flanked by deep longitudinal grooves is quite accurate as are his superficial comparisons with the supraoccipitals of *Varanus niloticus* and *Megalania prisca*. Gilmore (1928) also suggests that the form of the supraoccipital is evidence of *Saniwa ensidens* possessing the 'high type' of skull seen in some species of *Varanus* but not in others. Speculation on overall skull height aside, it is clear that FMNH PR2378 differs considerably from *Saniwa ensidens* in the overall form and surface sculpturing of the supraoccipital. The cast specimen FMNH PR2380 shows the disarticulated supraoccipital in ventral view lying between the left and right dentaries. The position of this element doesn't allow for a clear description of its dorsal surface but the general shape contour appear trapezoidal and shallow, much like that of FMNH PR2378.

Pterygoid–Little of the right pterygoid of FMNH PR2378 is visible, but that which is compares favorably to the complete left pterygoid of USNM 2185. The longitudinal sulcus visible on the quadrate ramus of the right pterygoid of

FMNH PR2378 appears to be correctly interpreted by Rieppel and Grande (2007) as the dorsomedial site of attachment for the protractor pterygoidei muscle. The sulcus present on the ventromedial surface of the pterygoid in *Varanus* and *Saniwa ensidens* (the ‘internal side’ of Gilmore 1922, 1928; ‘median sulcus’ of Estes 1983; ‘lateroventrally? facing groove’ of Rieppel and Grande 2007), site of insertion for the pterygoideus internus muscle, is deeper in the latter and listed as diagnostic for the genus (Estes 1983). Since this feature is not visible in FMNH PR2378, a diagnostic assessment of its pterygoid anatomy cannot be made.

Ectopterygoid–That portion of the left ectopterygoid of FMNH PR2378 which is visible, appears to be much the same as the ectopterygoid of *Saniwa ensidens*, though no features of this element are considered diagnostic for the taxon. The anterior portion of the ectopterygoid is obscured eliminating the possibility to determine the nature of its contact with the maxilla and/or palatine, but the morphology of the preserved portion of the maxillary process of the left palatine suggests that such a contact did occur (see palatine below).

Palatine–Much of the dorsal surface of the left palatine is visible in the region of the left orbit of FMNH PR2378. The location of the infraorbital foramen on the dorsal surface of the maxillary process as well as the shallowly forked posterior edge of the pterygoid process correspond favorably with both *Saniwa ensidens* and *Varanus*. In addition, though not in contact with the displaced left maxilla and ectopterygoid, the degree of posterior extension of the maxillary process of the left palatine seems adequate to assume contact between it and the ectopterygoid, excluding the maxilla from the border of the suborbital fenestra. Presence of palatine teeth (present in *Saniwa ensidens* and absent in *Varanus*) cannot be determined due to lack of any ventral exposure.

As noted above, the mandible and post-cranial material of USNM2185 were unavailable at the time of viewing while the axial skeleton of FMNH PR2378 is ventrally embedded in matrix and only the dorsal surface of the vertebrae are visible. Though direct detailed comparison of these regions was impossible, several features can be compared based on illustrations and descriptions in Gilmore (1922, 1928) and descriptions provided by Estes (1983).

Mandible–Descriptions and drawings made by Gilmore (1922, 1928) and Estes (1983) of *Saniwa ensidens* correlate favorably with the visible morphology of FMNH PR2378 and FMNH PR2380, including the presence of fully pleurodont tooth attachment; teeth trenchant, recurved, with dilated, fluted bases; tooth replacement interdental, lacking resorption pits; dentary-surangular articulation not deeply notched; coronoid with relatively long anterior extension with posterior edge not extending well behind the coronoid eminence; surangular and prearticular forming a long narrow adductor fossa on the medial surface; articular facet broad with raised anterior buttress; and retroarticular process with slight expansion and medial inflection. Gilmore (1928) estimated a dentary tooth count of 22 for the fragmentary type material while the preservation of FMNH PR2378 does not allow for an accurate assessment. Rieppel and Grande again rely on the cast specimen FMNH PR2380 to provide their estimate of 17 tooth positions, assigning that number to *Saniwa ensidens*.

Axial skeleton–diagnostic features of the axial skeleton of *Saniwa ensidens* including anteroposteriorly expanded neural spines extending into the caudal region; presence of pseudozygosphenes/zygantra; and greatest elongation of centra occurring in the cervical region, with those anterior to the fifth cervical vertebra being the longest. These characteristics are also present in FMNH PR2378.

DISCUSSION

Since its introduction by Leidy in 1870, there has been little doubt as to the phylogenetic significance of the holotype material of *Saniwa ensidens* (USNM 2185). The close relationship of *Saniwa* to modern *Varanus* allowed for a broadening of the diagnosis of the varanid family, formerly represented by extant species only. Despite this, many authors of important phylogenetic studies of the group chose not to include *Saniwa* in their analyses ostensibly based on the incomplete nature of the specimen (Pregill et al. 1986; Estes et al. 1988). In describing the beautifully preserved Fossil Butte specimen (FMNH PR2378) Rieppel and Grande (2007) purport to fill in this long standing need for additional morphological information regarding *Saniwa ensidens* and its phylogenetic position. The problem presented here, is that while FMNH PR2378 does generally compare favorably to the type specimen of *Saniwa ensidens* (USNM 2185), as prepared it lacks crucial diagnostic features of the species and displays some morphological elements that are decidedly different from the holotype.

Many of the observed similarities between *Saniwa ensidens* (USNM 2185) and FMNH PR2378 (nature of the dentition, moderate retraction of the external bony naris, exclusion of the maxilla from the suborbital fenestra, reduction of the jugal, formation of an intramandibular hinge) are shared by *Varanus* as well as by more basal members of the Varanoidea, and as such, do not offer grounds on which to assign FMNH PR2378 to the genus *Saniwa*. A review of the characters important for the diagnosis of *Saniwa ensidens* is needed to assess the potential assignment of FMNH PR2378 to that species or genus. As noted above, in the diagnosis provided by Estes (1983), few characters are considered apomorphic, distinguish *Saniwa* from *Varanus*. The first of these, (premaxilla much reduced) was demonstrated by Caldwell (2003) to be inaccurate as the premaxillary material assigned to the holotype (58 years after the original description) by Gilmore (1928), is very likely that of a xenosaur. The remaining apomorphies diagnosing *Saniwa ensidens* are:

1. Double posterior lacrimal foramina, housed completely within the lacrimal.

2. Presence of pseudozygosphenes and zygantra.

3. Reduction of cervical intercentra.

4. Anteroposteriorly expanded neural spines extending into the caudal region.

Of these four features, only two (2 and 4), both post-cranial are observable in FMNH PR2378, the others being obscured by matrix. The preserved elements of the dermal skull roof of the type specimen of *Saniwa ensidens* (USNM 2185) are few and fragmentary, with the palatal elements relatively better represented. As FMNH PR2378 is exposed on its dorsal surface, the comparisons that can be made with USNM 2185 are limited.

In the general form and topology of most cranial elements, FMNH PR2378 (and FMNH PR2380) compare favorably to USNM 2185 but there are descrepancies. A posterior process of the maxilla that intercedes between the lacrimal and prefrontal, is present in *Saniwa ensidens* (USNM 2185), reduced in FMNH PR2378, and completely absent in FMNH PR2380. The overall shape of the supraoccipital of *Saniwa ensidens* (USNM 2185) is markedly narrow and sub-triangular, with steeply sloped sides leading to a distinct sagittal ridge flanked by longitudinal troughs, while the supraoccipital of FMNH PR2380 is trapezoidal in shape with a broad, smooth and gently convex dorsal surface. The postfrontal of *Saniwa ensidens* forms an acute medial angle between slender anteromedial and posteromedial prongs, and is excluded by the postorbital from contact with the jugal, whereas the postfrontal of FMNH PR2378 displays a more robust posteromedial prong, a medial angle of approximately 90 degrees, and a considerable contribution to an anteroventral process likely contacting the jugal.

Given the taxonomic history of *Saniwa*, including the proposition of numerous species within the genus, and its close phylogenetic relationship to the species-rich *Varauns*, the appearance of the Fossil Butte specimens provides an excellent opportunity to test the hypothesis of species diversity within *Saniwa*. Estes (1983) was non-committal in tentatively recognizing multiple species of *Saniwa*, but did not preclude the possibility citing their overlapping distribution with the Paleocene-Eocene maximum tropicality in North America. Interestingly, a recent faunal diversity assessment of Paleocene-Eocene mammals notes a Wasatchian peak in generic diversity within the Clark's Fork Basin of Wyoming (Gingerich 2003), while studies on squamates suggest increased diversity associated with shifts in faunal composition and climate (Gauthier 1982; Smith 2006, 2009).

CONCLUSIONS

Throughout their paper, Rieppel and Grande (2007) more often compare and discuss FMNH PR2378 in relation to *Varanus* than to the type material for *Saniwa ensidens* (USNM 2185). Indeed, the authors appear to have not made any direct observations of the type material, as they state in their review (p.662) of the species diagnosis provided by Estes (1983), that the nature of the dorsal lacrimal foramen as described by Gilmore (1922, 1928) 'if correctly identified, would be an autapomorphy for *Saniwa ensidens*'. Direct observation of USNM 2185 reveals the accuracy of Gilmore's assessment. The holotype is not listed by Rieppel and Grande (2007) under 'material examined' and instead, they seem to have relied on the comparatively brief description of Gilmore (1922, 1928) as well as the rather poorly produced figures of the reconstructed cranium (Gilmore 1928). As a result, the description of FMNH PR2378 provided by Rieppel and Grande (2007) fails to note observable differences between it and the holotype of *Saniwa ensidens* (USNM 2185). Although many general comparisons are made in the description of FMNH PR2378 provided, Rieppel and Grande (2007) make no explicit statements as to the diagnostic features supporting its identification as

Saniwa ensidens. On the contrary, the authors present it and the cast FMNH PR2380, perforce as representatives of *Saniwa ensidens* without overcoming the burden of proof.

The single cranial feature distinguishing *Saniwa ensidens* from all other varanoids is the presence of an upper lacrimal foramen housed completely within the lacrimal. Both lacrimals are well preserved in FMNH PR2378, though their orbital surfaces are in part obscured by matrix. Rieppel and Grande (2007, p.649) argue in favor of the phylogenetic significance of the relative number and placement of the lacrimal foramina within varanoids. It seems bizarre then that in describing the FMNH PR2378 the authors make no effort to expose the lacrimal foramina in order to confirm their taxonomic assignment. As prepared and preserved, FMNH PR2378 may be confidently assigned to the genus *Saniwa* based on similarities of the neural spines and the presence of pseudozygosphenes/zygantra and a turbinarial process of the maxilla, but as yet it cannot be confirmed to be of the species *S. ensidens*. Concomitantly, the amended diagnosis presented by Rieppel and Grande (2007) may be applied to the genus *Saniwa*, but not to *S. ensidens*.

Further preparation of FMNH PR2378 (specifically in the area of the lacrimals) and the potential revelations (features of the palate and ventral surfaces of the vertebral column) that might be provided through High Resolution X-ray Computed Tomography of the specimen would go a long way to confirming or dispelling the doubts presented here. The historical dispute over the validity of additional *Saniwa* species based on vertebral material might also be resolved through a thorough examination of the degree of intervertebral variation present in FMNH PR2378. In addition, the disposition of the holotype of *Saniwa ensidens* (USNM 2185) should be addressed. USNM 2185 as currently mounted, bears little resemblance to the overall appearance of FMNH PR2378 and FMNH PR2380, undoubtedly better representatives of the genus. As well, some of the morphological details of USNM 2185, as figured and described by Gilmore (1922, 1928), are obscured in the mounted specimen by what appear to be molding compound, plaster, paint and glue. A complete restoration of the type material should accompany any future investigations of possible species diversity within the genus *Saniwa*.

FIGURE 2-1. a. & b. Lateral view of the posterior region of the left maxilla of *Saniwa ensidens* (holotype USNM 2185). c. Lateral view of the right maxilla of FMNH PR2378. Scale bar = 20mm.

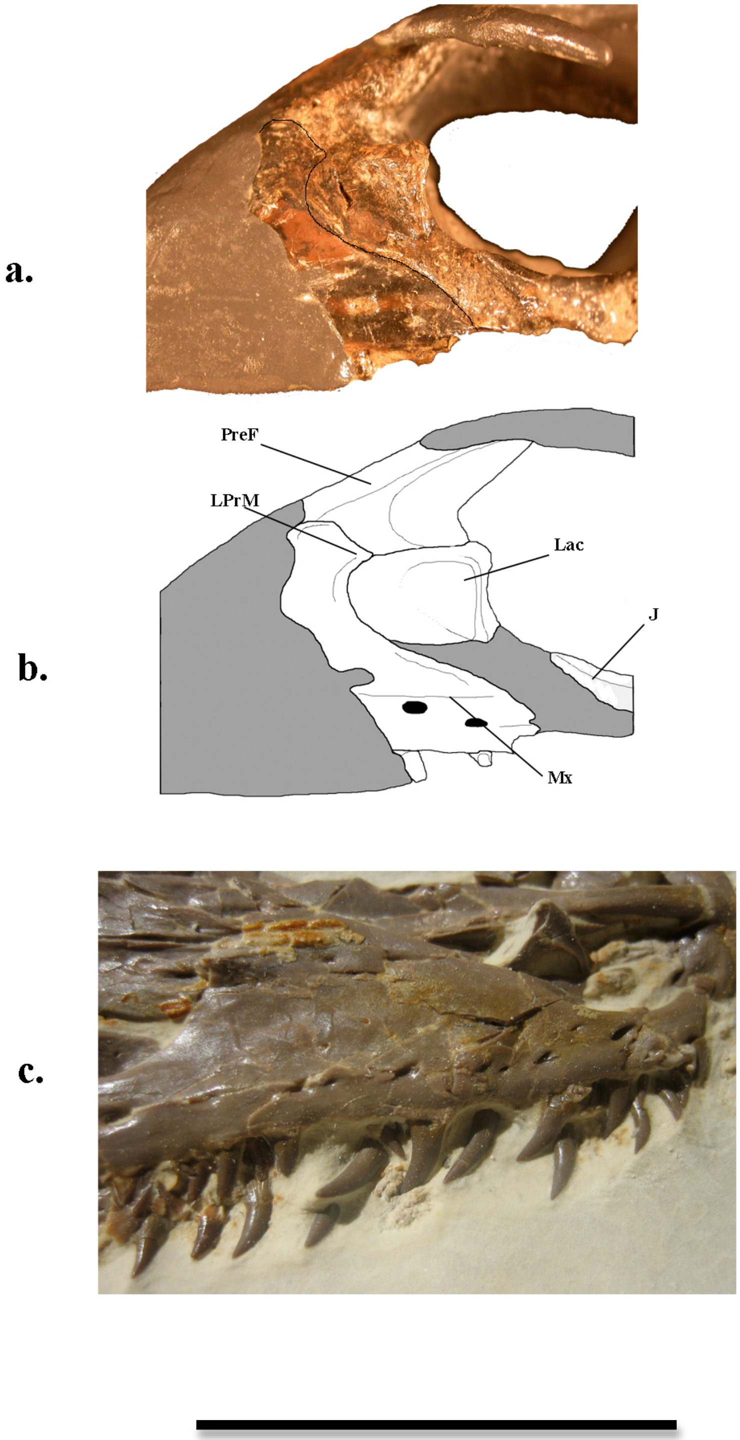
a.
PreF
LPrM
Lac
J
b.
Mx
c.

FIGURE 2-2. a. Photograph of left lacrimal of FMNH PR2378. b. & c. Photograph and line drawing of orbital view of the left lacrimal of *Saniwa ensidens* holotype (USNM 2185). Scale bar = 20mm.

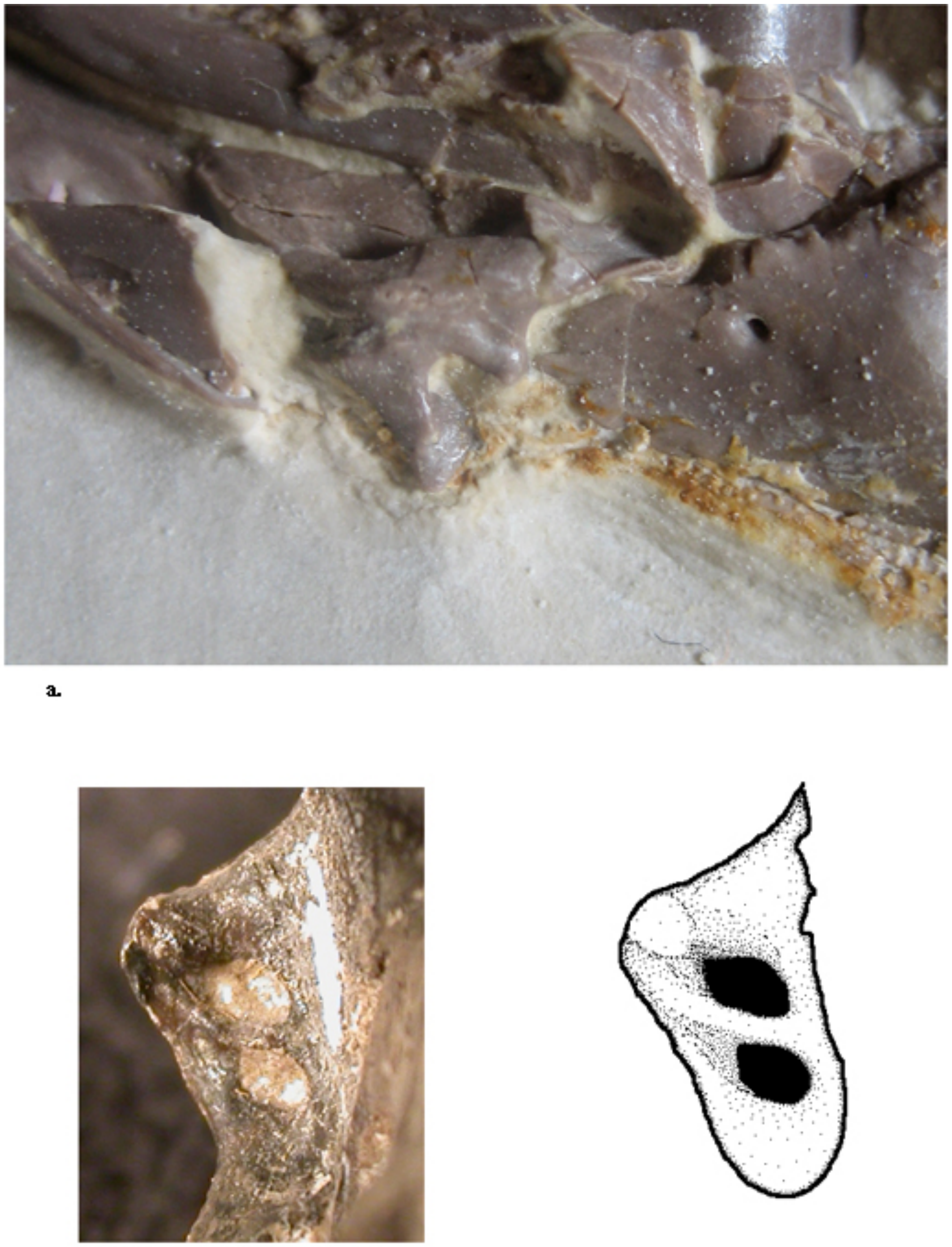
a.
b.
c.

FIGURE 2-3. Dorsal view of the region of the right postfrontal of FMNH PR2378. Scale bar = 20mm.

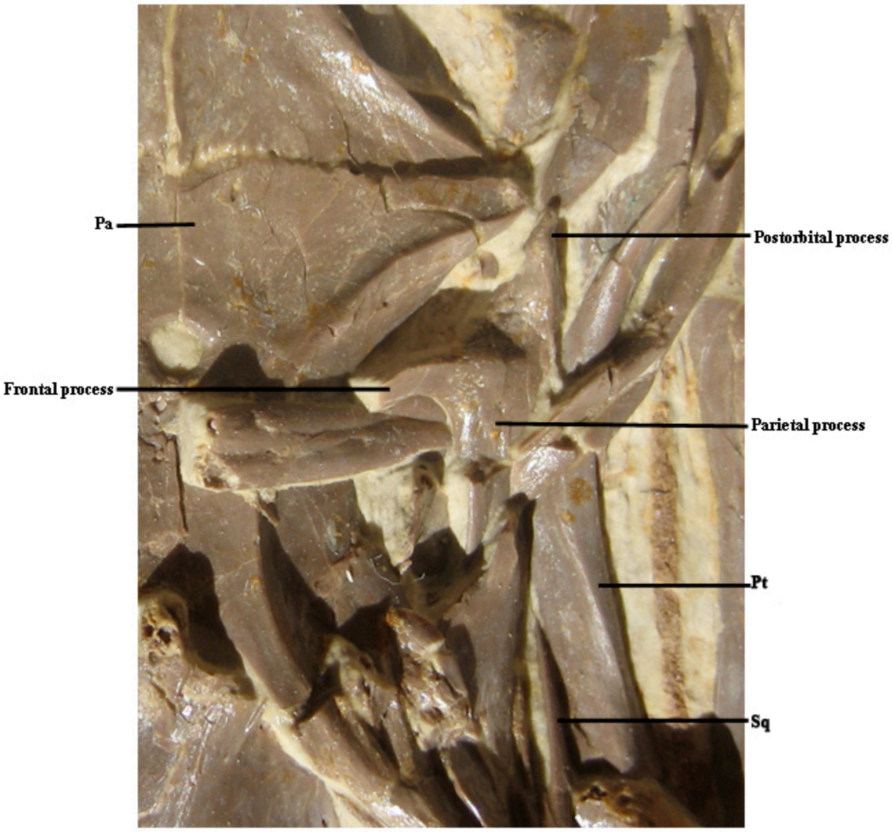
Pa
Postorbital process
Frontal process
Parietal process
Pt
Sq

FIGURE 2-4. Posterodorsal views of, a. supraoccipital of *Saniwa ensidens* holotype (USNM 2185) and b. FMNH PR2378. Scale bar = 20mm.

a.

b.

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CHAPTER THREE

ON THE ANATOMY AND AFFINITIES OF THE GENUS *NECROSAURUS* (PLATYNOTA, ANGUIMORPHA, SQUAMATA)

INTRODUCTION

The introduction of *Necrosaurus cayluxi* Filhol 1873, marks the earliest documentation of fossil platynotans in Europe. Originally described (1873) and later figured by Filhol (1877, plate 26, fig. 434) the holotype of *N. cayluxi* (holotype: MNHN ?) consists of a single nearly complete left dentary from the late Eocene/early Oligocene of the Phosphorites du Quercy, France. A second species *Necrosaurus eucarinatus* Kuhn 1940 (holotype: GM 402; referred- GM 4139), from the mid Eocene of Geiseltal Germany, is represented by a hind limb with associated osteoscutes and a disarticulated skeleton including parietal, frontal, maxillary, mandibular and vertebral elements. The two species of *Necrosaurus* appear very similar to one another (though their congeneric status has been questioned – see Conrad 2008), being separated traditionally only on the basis of the presence of a sagittal crest on the parietal of *N. cayluxi*, and a putative difference in the dentary tooth number (Estes 1983). Many additional specimens attributed to *Necrosaurus* have been recovered from the late Paleocene France (Hoffstetter 1943), Germany (Kuhn 1940), and Mongolia (Alifanov 1993); the early Eocene of France (Hoffstetter 1943), and Belgium (Hecht and Hoffstetter 1962; Godinot et al. 1978); the middle Eocene of France (Rage and Augé 2009); the middle and late Eocene of southern England (Klembara and Green 2010); the late Eocene of Switzerland (Hoffstetter 1943, 1962; Augé 1990), France (Rage 1988), and Isle of Wight, UK (Rage and Ford 1980); and the early Oligocene of Belgium (Hecht and Hoffstetter 1962).

Subsequent to the original description of *Necrosaurus cayluxi* several fossil genera described as 'necrosaurian' have been discovered and tentatively assigned to the Necrosauridae including *Ekshmer bissektensis* Nessov 1981 (holotype: CMG 2/11727), from the Bissekty Formation of Uzbekistan, Coniacian in age; *Colpodontosaurus cracens* Estes 1964 (holotype: UCMP 46608), from the late Cretaceous Lance Formation of Wyoming; *Parasaniwa wyomingensis* Gilmore 1928 (holotype: USNM 10797), also from the Lance Formation, Wyoming; *Provaranosaurus acutus* Gilmore 1942 (holotype: PU 14243), a form similar to *Colpodontosaurus* from the late Paleocene Fort Union Formation, Wyoming; *Eosaniwa Koehni* Haubold 1977 (holotype: GM XXXVIII/57), of the mid Eocene Geiseltal, Germany; and *Parviderma inexacta* Borsuk-Białynicka 1984 (holotype: ZPAL MgR I/43), from the late Cretaceous of Mongolia. Borsuk-Białynicka (1984) also assigned *Gobiderma pulchra* Borsuk-Białynicka 1984 (holotype: ZPAL MgRIII/64) and *Proplatynotia longirostrata* Borsuk-Białynicka 1984 (holotype: ZPAL MgR I/68) to a 'necrosaurian-grade' allied with but outside of Necrosauridae.

From the outset, *Necrosaurus* has been described as exhibiting a mosaic of characters including both primitive aguid-like characters, and derived varanoid characters, with the only apparent generic synapomorphies being the presence of ovoid, keeled body osteoderms and osteodermal sculpturing on the parietal and frontal. As currently conceived the Necrosauridae are held together primarily by plesiomorphic characters and any taxa in possession of dermal sculpturing of the frontals and parietal combined with one or more varanoid characters has been granted entrance into the family resulting in a paraphyletic grouping to which Estes et al. (1988) applied the term metataxon. This grouping has not aided the study basal platynotans as it fails to provide an accurate diagnostic shorthand for its constituent members, arguably the point of supra-generic groupings, and its use is typically qualified by authors pointing out its likely paraphyly (Borsuk-Białynicka 1984; Estes 1983; Gao and Fox 1996; Gao and Norell 1998, as well as many others). Despite this, as a taxon Necrosauridae may yet be worth saving if it can be demonstrated to contain a subset of basal platynotans with at least a claim to monophyly. Before any taxa may be assessed for potential necrosaur affinity, a clear examination of potential necrosaur synapomorphies must be undertaken and a stable generic diagnosis derived there from.

TAXONOMIC HISTORY

Hoffstetter (1943) dealt with the problems of synonymy long associated with the *Necrosaurus cayluxi* material (*Paleosaurus* of Filhol 1873; *Paleovaranus* of Filhol 1877; *Odontomophis* of de Rochebrune 1884; *Paleovaranus* of de Stephano 1903; and *Varanus* of Fejérváry 1918) and also identified the Geiseltal material described by Kuhn (1940) as *Melanosauroides giganteus* (=*Ophisauriscus eucarinatus* Kuhn 1940) as belonging to *Necrosaurus*. The characteristics of *Necrosaurus cayluxi* and *N. eucarinatus* as outlined by Hoffstetter (1943) comprised the first concise description of the genus and he erected the Necrosauridae based on them though no formal diagnosis for the family or genus was offered.

Hoffstetter's (1943) initial concept of the family Necrosauridae was based on *Necrosaurus cayluxi* and *N. eucarinatus* alone. Long associated with *Varanus*, Hoffstetter noted the lack of narial retraction and expanded vertebral condyles in necrosaurs, regarding them as basal platynotans. McDowell and Bogert (1954), citing these primitive features of *Necrosaurus*, as well as the presence of shinisaurid-like keeled osteoscutes, fusion of post-dentary bones, a presumed lack of expanded tooth bases and a misguided notion that the teeth are blunt, recurving only on the distal tip (again like *Shinisaurus*), allied the Necrosauridae with *Xenosaurus*, *Shinisaurus* and the Anguioidea well outside of the Platynota. Hoffstetter (1954) initially agreed with McDowell and Bogert's (1954) assessment but also pointed out their error in describing the dentition of *Necrosaurus* as being fully pleurodont and lacking basal dilation, and later (1962) returned Necrosauridae to the Platynota based on the following derived characters: laterally compressed, recurved teeth with striated and expanded bases, fusion of frontals and caudal chevrons articulating partially with centra. Estes (1983) retained a platynotan placement for the family noting also the presence of loose epiphyses on the cervical hypapophyses of *Necrosaurus*. Other features of *Necrosaurus* that would seem to suggest placement within Platynota are the lack of resorption pits and interdental tooth replacement, characters not present in Anguioidea. The characters cited by McDowell and Bogert (1954) in allying *Necrosaurus* with the anguioids, are plesiomorphic for Anguimorpha, and the specific comparisons made between the osteoderms of *Shinisaurus* and *Necrosaurus* are erroneous, as the former are without surface sculpture and triangular in section, while the latter are decidedly more compressed with numerous visible pits and ridges on either side of the median keel. The placement of *Necrosaurus* as a basal platynotan is accepted and considered well-supported here, based predominantly on the highly predaceous and varanoid-like suite of dental characters.

Estes (1983) provided a formal diagnosis for the Necrosauridae based largely on the work of Hoffstetter (1943, 1962), and in addition to *Necrosaurus cayluxi* and *N. eucarinatus*, placed four additional fossil taxa within it. *Parasaniwa wyomingensis* Gilmore 1928 was placed in its own family by Estes (1964) based on its particular combination of anguioid scutellation and vertical anterior margin of the nasal process of the maxilla combined with varanoid tooth morphology and replacement as well as a presumed presence of an intramandibular hinge. Hoffstetter (1969) allied Parasaniwidae with Necrosauridae based on shared dental characteristics and the presence of osteoderms on the skull. Estes (1975, 1976) initially maintained separation between these two families based on differences in scutellation but subsequently assigned *Parasaniwa* to Necrosauridae based on direct observations of necrosaur material and a discussion with J. Gauthier. Unfortunately Estes (1983) did not detail the reasons for this change but stated only that he was convinced "…one family is represented." (Estes 1983, pg.174). *Provaranosaurus acutus* Gilmore 1942 was noted by Estes (1965) to be similar to *Parasaniwa* in the lack of a free ventral border of the intramandibular septum, the lack of narial retraction and in general tooth form including basal striations. Based on this he included

Provaranosaurus in his Parasaniwidae (= Necrosauridae of Estes 1983). In naming and describing *Colpodontosaurus cracens*, Estes (1964) originally placed it within the Anguioidea based on plesiomorphic traits but later (1983) tentatively assigned it to Necrosauridae based on similarities of the intramandibular septum, and thin tooth walls it shares with *Provaranosaurus*. Lastly, Estes (1983) assigned *Eosaniwa koehni* Haubold 1977 to Necrosauridae based again on plesiomorphic traits of the dentition and scutellation noting supposed similarities between the osteoscutes of *Eosaniwa* and *Necrosaurus*.

Three additional taxa were assigned to or affiliated with the Necrosauridae by Borsuk-Białynicka (1984). *Proplatynotia longirostrata* Borsuk-Białynicka 1984 was described by Borsuk-Białynicka as exhibiting a 'necrosaurian-grade' citing similarities with *Necrosaurus* in the presence and type of cranial osteoderms, the dorsal attachment of adductor musculature and modest narial retraction, but refrained from including it in Necrosauridae on the basis of an apparently primitive braincase and a lack of fluting or striae on the tooth bases. *Parviderma inexacta* Borsuk-Białynicka 1984 was included in the Necrosauridae by Borsuk-Białynicka, despite the differences noted in the narrowing of the frontals and the type of osteodermal ornamentation (both described as xenosaurid-like); her assignment of it to this family presumably based on the dorsal attachment of adductor musculature, and the presence of basal fluting on the teeth. Finally, *Gobiderma pulchrum* Borsuk-Białynicka 1984 was assigned by the author to an indeterminate family of 'necrosaurian-grade' since it differed from necrosaurs in the ventral placement of adductor musculature on the parietal and in the form of the thick osteodermal covering, both showing a strong resemblance to *Heloderma*.

The familial diagnosis presented by Estes (1983) for Necrosauridae includes the following primitive characters: unretracted nares; ventral processes of frontals not underlying the olfactory tract; weak development of an intramandibular hinge; and the presence of osteoderms. The derived characters included in Estes (1983) diagnosis are: teeth trenchant, with slight recurve and basal striations; fusion of frontals; free epiphyses of the cervical hypapophyses; and caudal chevron articulations not fully intercentral. In this form, the diagnosis for the Necrosauridae is unnecessarily broad with respect to *N cayluxi* and *N. eucarinatus*. The lack of narial retraction, lack of contact between the subolfactory processes of the frontals, and presence of osteoderms are all plesiomorphic for Anguimorpha and are present to varying degrees and qualities within xenosaurs and anguids. As such these characters may be expected to occur commonly in basal platynotans and while descriptive, do not differentiate necrosaurs from their common ancestry with anguids and xenosaurs. Such broadly distributed plesiomorphies should not be included in any formal diagnosis of Necrosauridae unless they are considered to be apomorphic in the form of reversals, a position for which there is no evidence. The remaining characters in Estes (1983) diagnosis largely relate to the predatory habits presumed for necrosaurs and evidenced in modern varanoids. Estes (1983) appears to qualify some of these characters ('slightly recurved' teeth) while not including other potential ones (expanded tooth bases, presence of plicidentine infolding) thus allowing for a more inclusive grouping. As conceived by Estes (1983) the diagnosis of the Necrosauridae could potentially encompass all basal platynotans that show no clear affiliation with *Heloderma, Lanthanotus* or *Varanus*, its practical application being effectively synonymous with basal or stem Platynota.

MATERIALS AND METHODS

In an effort to understand the interspecific and intraspecfic variation of the anatomies of *Necrosaurus cayluxi* and *N. eucarinatus*, multiple specimens of both taxa were examined and compared with other putative necrosaurs. From this data a revised diagnosis for the Necrosauridae was compiled with an aim to restricting characters to more closely conform to those known for the type genus *Necrosaurus*.

MATERIALS EXAMINED–*Necrosaurus cayluxi*: BMNH R3486, BMNH R6842, MNHN QU 17172, MNHN QU 17173, MNHN QU17174, MNHN QU17175. MNHN QU17176, MNHN QU17605, MNHN QU17610, MNHN QU17611, MNHN QU17613, MNHN QU17620, MNHN QU17621, MNHN QU17631, MNHN QU17635, MNHN QU 17738, MNHN SNB1007, MNHN SNB1009, MNHN SNB1010, MNHN SNB1011, MNHN SNB1013, MNHN SNB1016, MNHN SNB1017, USTL ECX53, USTL PRA7. *Necrosaurus eucarinatus*: GM CeIII-4139, MNHN QU17177, MNHN QU17609, MNHN QU17622, MNHN QU 17623, MNHN QU17624, MNHN QU17625, MNHN SNB1014, USTL BFI1873**.** *Necrosaurus sp.*: BMNH R1303, BMNH R6823,

MNHN QU17604, MNHN QU17606, MNHN QU17607, MNHN QU17608, MNHN QU17612, MNHN QU17614, MNHN QU 17615, MNHN QU17617, MNHN QU17618, MNHN QU17619, MNHN QU17632, MNHN QU17633, MNHN QU17634, MNHN QU 17637, MNHN QU17641, MNHN QU17642, MNHN QU17649, MNHN QU17654, MNHN QU17657.

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758

SQUAMATA Oppel, 1811

ANGUIMORPHA Fubringer, 1900

PLATYNOTA Baur, 1890

NECROSAURIDAE Hoffstetter, 1943

Necrosaurus Filhol, 1876.

Type species–*Necrosaurus cayluxi* Filhol 1873.

(*Paleosaurus* Filhol, 1873; *Paleovaranus* Filhol, 1877; *Odontomophis* de Rochebrune 1884; *Paleovaranus* de Stephano 1903; *Varanus* Fejérváry 1918)

Additional species–*Necrosaurus eucarinatus* Kuhn 1940.

(*Melanosauroides giganteus,* Kuhn 1940; *Ophisauriscus eucarinatus*, Kuhn 1940; *Necrosaurus giganteus*, Hoffstetter 1943)

Generic diagnosis–See below.

DISSCUSSION PART I – GENUS *NECROSAURUS*

The material examined for this study includes specimens referred both to *Necrosaurus cayluxi* and to *N. eucarinatus* as well as numerous elements referred to *Necrosaurus* sp. That the two species do in fact represent a single genus must first be established if the indeterminate specimens are to be considered informative at the generic level. The congeneric status of *N. cayluxi* and *N. eucarinatus* has been challenged in recent phylogenetic work by Conrad (2008; although see Conrad et al. 2010) while other studies frequently code *Necrosaurus* at the generic level, presumably drawing on specimens of both species for character data (Gao and Norell 1998; Nydam 2000; Balsai 2001), thus ignoring any potential interspecific variation. Close examination of the data matrix provided by Conrad (2008) reveals six characters in which the author's codings differ between *N. cayluxi* and *N. eucarinatus*. These are:

1. Character 10 (Conrad 2008)- Dermal sculpturing, parietal/frontal: (0) absent; (1) present on frontal and parietal: Conrad scores this character as (0) for *N. cayluxi* and as (1) for *N. eucarinatus*. An examination of numerous parietals and frontals collected from the Phosporites du Quercy France, and assigned to both necrosaur species reveals that frontals are universally encrusted with osteodermal sculpture (Fig. 3-1) while parietals vary in the degree of sculpturing among *N cayluxi* specimens. It is important to note that parietals of *N. cayluxi* are assigned to that species with a high degree of confidence based of the unique (for platynotans) and prominent sagittal keel formed on their posterior half. Such keeled parietals have been illustrated by Rage (1978), Estes (1983) and Augé (2005) and indeed

those authors illustrate the element without any ornamentation other than the keel itself, supporting Conrad's (2008) coding of absent. However, though the anterolateral edges of the parietal table form contiguous ridges with the sagittal keel and overshadow the flattened region surrounding the pineal foramen, several keeled parietals assigned to *N. cayluxi* bear bumps and ridges similar in size to, though fewer in number than, those found on the parietals assigned to *N. eucarinatus* (Fig. 3-2). Therefore the coding of character 10(0) (Conrad 2008) is wrong for *Necrosaurus cayluxi* and the two species of necrosaur cannot be differentiated by dermal sculpturing of the parietal or frontal as it is present on both elements in both taxa.

2. Character 55 (Conrad 2008)-Frontals (0) separate in adults; (1) fused in adults: For this character Conrad (2008) codes *N. cayluxi* as (1) and *N. eucarinatus* as (0). The coding for separate frontals in *N. eucarinatus* is erroneous. The frontal of the (*Melanosauroides*) type specimen (GM CeIII-4139) described by Kuhn (1940) is azygous (and illustrated as such by Estes 1983) as are numerous frontals from du Quercy assigned to *N. eucarinatus*.
3. Character 74 (Conrad 2008)-Parietal, frontal tabs (0) absent; (1) present within the contact and visible dorsally; (2) present on the ventral surface: Conrad (2008) codes (0) for the absence of frontal tabs on the parietal for *N. eucarinatus* and (1) for the presence of dorsally visible frontal tabs on the parietal in *N. cayluxi*. The coding for this character in Conrad (2008) appears generally accurate. Parietals of *N. cayluxi* show reasonable development of anterolateral tabs overlapping the posterolateral surface of the adjoining frontal. The Geiseltal

specimen of *N. eucarinatus* cannot be confidently scored for this character but several du Quercy specimens assigned to it show little or no frontal tab development. One parietal in particular (MNHN QU17177) figured by Augé (2005 fig.194, p.285) and assigned to *N. eucarinatus* does show modest development of frontal tabs but also exhibits a much higher degree of osteodermal ornamentation and a greater thickness of the parietal table and may not be representative of the form by and large.

4. Character 75 (Conrad 2008)-Parietal, median adductor crest expressed as a keel (0) absent, flat parietal table extends to the posterior margin; (1) present: Here Conrad (2008) correctly codes for the presence of a keel in *N. cayluxi* and the absence of one in *N. eucarinatus*.
5. Character 178 (Conrad 2008)-Dentary, shape of long axis (0) ventrally convex; (1) straight: Conrad (2008) codes for a straight ventral edge of the dentary in *N. cayluxi* and a convex ventral edge in *N. eucarinatus.* The degree of ventral convexity of the dentary appears somewhat variable in both necrosaur species. Among the du Quercy specimens reviewed here, few dentaries are determined to species and all bear at least some ventral curvature. Those that are assigned to one or the other species are done so presumably on the basis of tooth count (thought to be higher in *N. eucarinatus*) and so are limited to reasonably complete elements. Among the dentaries assigned to *N. cayluxi*, MNHN QU17605 (figured by de Stephano 1903), MNHN QU17738 and MNHN QU17172 (both figured by Augé 2005) as well as BMNH R3486 show a modest though distinct ventral convexity. The Geiseltal type material of *N. eucarinatus*

(GM CeIII-4139) figured by Estes (1983) shows somewhat greater curvature though USTL ECX (figured by Augé 2005), also assigned to *N. eucarinatus,* is among the least ventrally convex of all the dentaries examined. Variable in expression, the degree of ventral convexity presents no consistent pattern with respect to delineating the two species of necrosaur and the most that can be said is that none of the dentaries observed exhibits a particularly straight ventral margin.

6. Character 303 (Conrad 2008)-Squamation, imbrication (0) absent; (1) present: Conrad (2008) chooses to code (0) for absence of imbrication of squamation in *N. cayluxi* and (1) for presence of imbrication in *N. eucarinatus*. It can only be assumed that this assessment is based on evidence in the holotype *of N. eucarinatus* (GM CeIII-4021) of overlapping osteoscutes preserved in situ on the knee region of that specimen (figured by Estes 1983) and a lack of any evidence of imbrication on the surface of osteoscutes assigned to *N. cayluxi*. It must be pointed out that the disarticulated Geiseltal specimen of *N. eucarinatus* (GM CeIII-4139) preserves numerous examples of isolated body osteoscutes identical to those assigned for *N. cayluxi*, (Fig. 3-3) and equally free of any evidence of imbrication, indicating the possibility that some but not all osteoscutes were arranged in an overlapping pattern perhaps in relation to their position on the body. In light of this, and the absence of positive evidence for non-imbrication in the limbs of *N. cayluxi*, that taxon should be scored as missing data for this character.

Of the six characters coded by Conrad (2008) as differentiating the two species of *Necrosaurus*, only those relating to the parietal, presence of a sagittal keel and frontal tabs, are demonstrably valid differences. The presence or absence of a sagittal keel was posited as variation possibly due to ontogeny by Estes (1983) and was not considered strong enough evidence on which to split the genus. The presence of frontal tabs of the parietal was noted by Estes et al. (1988) as a possible varanid synapomorphy and would appear to relate to the broad anterolateral expansion of the parietal seen within *Varanus*. Fossil and living forms thought to be closely related to *Varanus* (*Saniwa, Telmasaurus, Saniwides, Ovoo, Cherminotus,* and *Lanthanotus*) as well as members of the Monstersauria lack frontal tabs, strongly suggesting that their presence in *N. cayluxi* is the result of convergence. The presence of rudimentary frontal tabs on the particularly robust and ornamented parietal (MNHN QU17177) assigned by Augé to *N. eucarinatus* may indicate a developmental relationship between osteodermal thickening of the parietal surface and the development of some frontal overlap. Equally possible, in the case of *N. cayluxi,* the increased thickness of the parietal along the bifurcating ridge leading from the sagittal keel to the anterolateral corners may also influence the overlapping relationship of the parietal to the frontal. In either case, the variable development of frontal tabs observed for *Necrosaurus cayluxi* would seem to be indicative of interspecific variation only.

Traditional separation of *Necrosaurus cayluxi* from *N. eucarinatus* is based on the presence of a sagittal keel of the parietal in the former and an increased dentary tooth count in the latter (Estes 1983). While the difference in development of a sagittal crest is unquestionable, a survey of the dentaries from du Quercy suggests that the reported difference in dentary tooth counts is unwarranted. The holotype of *N. cayluxi* as figured by Filhol (1877 plate 26, fig. 434) is a fragmentary left dentary bearing three complete teeth, three broken tooth bases and space for roughly two additional teeth. This fragment does not preserve either the anterior or posterior tips of the dentary and cannot be used to infer a dentary tooth count other than to specify a number greater than eight. Fejérváry (1935) who figured and described a nearly complete left dentary (plate X, Fig. 7-8) makes no explicit estimate of tooth count but frequently references individual tooth numbers as landmarks when describing the relative positions of adjacent structures. In one particular reference to a tooth number, Fejérváry (1935) remarks that the posterior most alveolar foramen lies beneath the twelfth tooth. The figure presented by Fejérváry (1935) shows two small teeth as well as space for at least two more posterior to the tooth referred to as the twelfth, indicating a total tooth count of at least 16. This is contrary to Estes (1983) who reproduced Fejérváry's (1935) figure yet describes *N. cayluxi* as possessing a dentary tooth count of 13. It is unclear where Estes (1983) derives this tooth count from as he does not cite a specific source of this information nor does he offer any figures other than that of Fejérváry (1935) discussed above.

The right dentary figured by Augé (2005 figs. 186a ,186b; MNHN QU17172) bears five intact teeth, four broken tooth bases and space for at least three more. The distal and proximal tips of this element are missing and at least three additional tooth positions can be estimated for the missing portions, allowing for an estimated total tooth count of approximately 15. An additional complete right dentary (BMNH R3486) assigned to *N. cayluxi* bears 17 tooth positions (Fig. 3-4) though it should be noted that the element is fractured in two and while the contours of the alveolar margin, ventral margin and Meckelian sulcus align perfectly, the fractured surfaces of the two halves do not and the specimen may represent posterior and anterior halves of two separate elements. The most compete dentary examined (USTL ECX53) is assigned in collection to *N. cayluxi* but figured by Augé (2005, figs. 197a, 197b) as *N. eucarinatus* and bears 15 tooth positions with the likelihood of at least one more on the missing posterior tip. Lastly, the type material included in Kuhn's (1940) description of *N. eucarinatus* (GM CeIII-4139) and figured by Estes (1983, fig. 43e) includes a partial right dentary bearing eight intact teeth and space for two more. Contrary to Haubold (1977), who provided a dentary tooth count of 18, the preservation of this specimen is particularly bad and it does little to inform an estimate of dentary tooth count for *N. eucarinatus*.

There appears to be little evidence to support the tooth counts reported by Estes (1983) for either *Necrosaurus cayluxi* (=13, too few), or *N. eucarinatus* (=18, too many). Rather, when viewed as a whole, the specimens here examined provide only enough data to provide an estimate of 15 to 17 tooth positions with reasonable estimates for both necrosaur species overlapping within that range. It should be pointed out that in all specimens where the distal and proximal tips of the dentaries are preserved, the tooth size diminishes rapidly as they approach the anterior and posterior ends of the tooth row (Fig.3-4). Thus, the fact that the majority of dentaries described and figured do not posses either or both ends of the element may have lead to considerable inaccuracies when estimating tooth counts.

As outlined above, the verifiable differences between *Necrosaurus cayluxi* and *N. eucarinatus* (presences of a sagittal keel and frontal tabs on the parietal of *N. cayluxi*) seem to provide a level of variation worthy of specific, though not generic, distinction. Numerous characters shared between the two taxa may be used to form the basis of a generic diagnosis and these are outlined below.

Frontal– (Fig. 3-1) Frontals fused, tapering abruptly anterior to contact with the parietal forming parallel margins above and anterior to the orbit. Surface of frontal bearing a modest raised supraorbital ridge with a small but distinct sagittal keel formed by a median row of fused osteoderms. Anterior tip of frontal underlies nasals, the surface forming a W-shaped articulation with one medial and two anterolateral prongs. The examined material from du Quercy shows remarkable consistency in the above features while the frontal of the type of *N. eucarinatus* (GM CeIII-4139) differs somewhat in the apparent lack of a raised lateral margin and sagittal keel, as well as a different pattern of osteodermal sculpturing. All frontals that could be examined ventrally bore paired indentations on the ventral edge of the posterior one third of the subolfactory processes (cristae cranii). As far as is known, this feature has not been described or figured for any basal platynotan and its appearance in the material examined here may be unique. Equally uncertain is the function of these indentations, though they may be indicative of a particularly robust attachment of the planum supraseptale, a portion of interorbital chondrocranium that lies dorsal to the interorbital septum and attaches to the posterior edges of the cristae cranii (de Beer 1930; Bellairs 1950; Bellairs and Kamal 1981; Guerra and Montero 2009).

Parietal–(Fig. 3-2) The site of established interspecific differences, the parietals of *Necrosaurus cayluxi* and *N. eucarinatus* also display some similarities worth noting. As discussed earlier, the ornamentation of the parietal table though less obvious in *N. cayluxi* appears very similar in structure between the two species. Both possess a raised ridge encircling the pineal foramen with additional median crests branching off from it anteriorly in *N. cayluxi,* and anteriorly and posteriorly in *N. eucarinatus*. Adjacent to the pineal foramen there are several (*N. eucarinatus*) or few (*N. cayluxi*) tubercles that in larger specimens are joined by ridges that parallel the diverging anterolateral margins of the parietal table. In *N. cayluxi* , the proliferation of these tubercles is much reduced owing to the posterior truncation of the parietal table and presence of a sagittal keel. The parietal of the *N. eucarinatus* specimen from Geiseltal (GM CeIII-4139) again differes from its du Quercy counterparts in the form of its osteodermal ornamentation, expressing the same pattern (pineal osteoderm with anteromedial ridge and adjacent tubercles) but with relatively fewer and larger tubercles.

Another feature of the combined necrosaur parietals that stands out in comparison to other basal platynotans is the marked narrowing of the posterior parietal table. Though not keeled like *Necrosaurus cayluxi*, *N. eucarinatus* parietals nonetheless show far greater expansion of the adductor musculature onto the posterodorsal surface than other platynotans for which the parietal is sufficiently known. In all specimens examined, the narrowest width of the parietal table is smaller than the narrowest point on the frontals of equal proportion as judged from the width of the sutural contact shared by the elements. Within terrestrial platynotans, this condition is approached in some *Varanus* and is in fact present to a similar degree in *Bahndwivici ammoskius* Conrad 2006, a putative shinisaurid from the early Eocene of Wyoming. Though the two species of necrosaur differ in the degree of posterior constriction of the parietal table, the uniqueness of this feature within Platynota marks its importance in the diagnosis of the genus.

Maxilla–The maxillae of *Necrosaurus. cayluxi* and *N. eucarinatus* are important to the generic diagnosis insofar as they demonstrate a varanoid type of tooth morphology and implantation combined with a primitive (compared to crown varanoids) unretracted narial margin. Here the plesiomorphic state of the external nares only serves to differentiate *Necrosaurus* from more derived forms and does little to inform their potential relationships with other basal platynotans. However, the character transformation presumed to result in the posteriad position of the bony external naris as typified by *Varanus* would very likely have passed through at least some intermediate forms and *Necrosaurus cayluxi* has been suggested to posses some small amount of narial retraction (Estes 1983). There is some evidence to support a modest degree of narial retraction in *Necrosaurus* in the form of a gradually sloping anterodorsal margin of the nasal process of the maxilla in specimens assigned to *N. cayluxi*. Also, Hoffstetter (1943) describes *N. cayluxi* as having relatively tall and somewhat elongated snout based on the form of the nasal process of the premaxilla. The condition of the nasal process of the maxilla in *N. eucarinatus* cannot be established as the only maxilla examined and assigned to that species belongs to the type (GM CeIII-4139) wherein it is poorly preserved and partially obscured.

Dentary–The key diagnostic characters present on the observed dentaries of *Necrosaurus* have already been introduced in the above discussions on the dentary tooth count (15-17), tooth form (trenchant, recurved), implantation and replacement (‘varanoid type’). The teeth themselves are accurately depicted by Hoffstetter (1954) as having dilated bases and basal fluting indicative of the presence of plicidentine. Many specimens observed include broken tooth crowns allowing verification of this in the form of internal views of infolded tooth bases. Kearney and Rieppel (2006) and Maxwell et al. (2011) both report the presence of plicidentine as a varanoid synapomorphy though neither study included any terrestrial fossil platynotans. Most basal platynotans possess basal striae or fluting on the marginal teeth suggesting the presence of plicidentine, with larger species/specimens tending to show a higher degree of infolding. Though its specific distribution cannot be confirmed as many taxa lack conveniently broken and well-preserved tooth crowns, plicidentine may well be a platynotan synapomorphy and as such its presence does little to distinguish necrosaurs from other basal platynotans.

Osteoderms–(fig. 3-3) Hoffstetter (1943) emphasized the importance of the similarity in form between the osteoderms of *N. cayluxi* and *N. eucarinatus*. Indeed, this characteristic alone seems to have convinced him of the need to synonymize Kuhn's *Melanosauroides* (1940) with *Necrosaurus*. The osteoderms of *Necrosaurus* are consistently ovoid with a median longitudinal keel. The keel is strong and distinct but relatively low-lying and restricted to the center of the osteoderm, which in cross section would still appear fairly flat. By contrast, the keeled osteoderms of *Shinisaurus* are steeply triangular in cross section, the dorsolateral surface of the keel running to the outer edges of the osteoderm. *Eowsaniwa koehni* Haubold 1977, also possesses a form of keeled osteoderm although with a morphology distinct from *Necrosaurus*. The osteoderms of *Eowsaniwa* appear less consistent in shape than those of *Necrosaurus*, most appearing as sub-circular with one end more blunt than the other. Also, in *Eosaniwa* the keel is flanked by a network of few coarse ridges fanning out from the median keel, while in *Necrosaurus* the pits and ridges decribed by Estes (1984) are far more numerous and fine-grained. Rieppel et al. (2007) provided a redescription and phylogenetic analysis of *Eosaniwa* including the body osteoderms in which he makes no reference to any similarity with those of *Necrosaurus.*

The form of the osteoderms of *Necrosaurus* have been described as unique among Platynota (Hoffstetter 1943) and continue to be of great significance in diagnosing the genus. They may be equally important in understanding the distribution of the group as they are often preferentially preserved, signaling the presence of necrosaurs in localities where cranial material has not yet been discovered (Hecht and Hoffstetter 1962; Godinot et al. 1978; Klembara and Green 2009).

Generic Diagnosis–*Necrosaurus* may be distinguished from all other known platynotans on the basis of the following combination of characters: Frontal with an extremely regular pattern of osteodermal sculpturing including a median series of keeled and fused osteoderms and possessing parallel margins on the anterior two-thirds; Ventral edge of subolfactory process of frontals bearing a posteriorly located groove; Parietal with osteodermal sculpturing including a pineal eminence and keel and a posterior constriction of the parietal table its minimum width equaling that of the frontal; Narial margin of maxilla inclined, not vertical though nares unretracted and posterior maxillary teeth partially underlying the orbit; Dentary ventrally convex, with a reduced subdental shelf bearing 15-17 teeth; Teeth pleurodont, trenchant and widely spaced with expanded and fluted bases, recurved and lacking resorption pits; Osteoderms ovoid with median keel flanked by fine grained pit and ridge surface texture.

DISSCUSSION PART II – PUTATIVE NECROSAURIDAE

Family Necrosauridae as erected by Hoffstetter (1943) was not clearly circumscribed and since Estes expanded its membership in 1983 it has become a catch-all taxon for numerous basal platynotans. As demonstrated above, the type genus *Necrosaurus* can be effectively diagnosed and theoretically a family based upon it may be argued to be monophyletic provided it includes only members which appear more closely related to *Necrosaurus* than to any other platynotans. The taxa previously assigned to the Necrosauridae (Estes 1983) are discussed below and their potential membership in the family is evaluated. In addition, two other fossil taxa, not yet formally assigned to Necrosauridae, are evaluated for their potential inclusion in the family based on similarities they share with *Necrosaurus*.

Parasaniwa wyomingensis Gilmore 1928–Parasaniwidae was allied with Necrosauridae by Hoffstetter (1969) based on the its shared combination of varanoid tooth characteristics and osteodermal ornamentation of the frontal and parietal. Estes (1975, 1976) agreed with this assessment and eventually went further (1983) abandoning Parasaniwidae in favor of Necrosauridae without direct explanation. Osteodermal ornamentation in platynotans is more widespread than once thought. Prior to McDowell and Bogert's (1954) assessment of *Heloderma* as a basal platynotan, most classifications followed Camp (1923) in allying it with *Glyptosaurus* and the Anguidae. McDowell and Bogert (1954) also pointed out the platynotan affinities of *Lanthanotus* and documented the presence of osteoderms in that taxon as well as some species of *Varanus*. This evidence combined with the subsequent placement of numerous osteoderm-bearing taxa within Platynota (Estes 1964; Haubold 1977; Borsuk-Białynicka 1984; Gao and Fox 1996; Norell and Gao 1997) demonstrates the wide distribution of this character within the clade. As such, mere presence of osteoderms on the skull roof provides no foundation for inclusion in the Necrosauridae. The pattern of ornamentation in *Parasaniwa* differs considerably from *Necrosaurus*, as does the orientation of the anterior margin of the nasal process of the maxilla (nearly vertical) and the width of the posterior parietal table. There appear to be no special similarities between *Parasaniwa* and *Necrosaurus* and the inclusion of *P. wyomingensis* in the Necrosauridae is here rejected.

Provaranosaurus acutus Gilmore 1942–Estes (1983) placed *Provaranosaurus* in the Necrosauridae based on a combination of derived tooth characters (basal infolding) and the primitive characters of unretracted nares and a free ventral border of the intramandibular septum. As discussed above, the maxilla of *N. cayluxi* shows evidence of a modest retraction of the nares, and the presence of a free posteroventral projection of the intramandibular septum is a plesiomorphy of Platynota. The needle-like teeth of *Provaranosaurus* are more similar to *Parasaniwa* as noted by Estes (1965) as is the vertical margin of the nasal process of the maxilla.

Colpodontosaurus cracens Estes 1964–Descsribed by Estes (1983) as an acceptable ancestor to *Provaranosaurus*, *Colpodontosaurus* is very poorly known and Estes (1983) appears to include it in the Necrosauridae based on its association with *Provaranosaurus*, which in turn he affiliates with the osteoderm bearing *Parasaniwa*. Compared directly with *Necrosaurus* there are no features of *Colpodontosaurus* or *Provaranosaurus* that would suggest a close relationship with the former. Rather, based on similarities of the dentition and the completely unretracted nares, there may be justification for the ressurection of the Parasaniwidae with *Parasaniwa, Provaranosaurus* and *Colpodontosaurus* as members. Based on a paucity of material and a greater overall similarity to *Parasaniwa* than to *Necrosaurus*, *Colpodontosaurus* and *Provaranosaurus* are here rejected as members of the Necrosauridae.

Eosaniwa koehni Haubold 1977–First described by Haubold (1977) as an anguid, *Eosaniwa* displays a number of bizarre characters, unique among basal platynotans. *Eosaniwa* is large for a platynotan (skull length = 19cm) with an elongate rostrum and broad flanges on the angle of the jugal and the suborbital lamina of the pterygoid. Rieppel et al. (2007) report a count of 35 in the maxilla and 16 in the anterior two thirds of the dentary. The teeth of *Eosaniwa* are long and thin and in the view of Estes (1983) suggest a piscivorous diet. Rieppel et al. (2007) described the teeth as lacking plicidentine; however, some of the larger teeth lying midway along the left maxilla show basal fluting and at least one broken tooth of the distal right dentary appears to have internal plicae formed either of the dentine itself or by an interaction with it by the bone of attachment (see also Caldwell 2012). If present, the plicidentine of *Eosaniwa* is not nearly so obvious as that displayed by numerous specimens of *Necrosaurus*. The frontals of *Eosaniwa* were demonstrated by Rieppel et al. (2007) to be paired and direct observation of CT data provided by O. Rieppel shows them to be covered in a non-regular fashion by small tubercles. The parietal of *Eosaniwa* is not preserved. The osteoderms of *Eosaniwa* are distinct from those of *Necrosaurus* and are discussed in detail above. The presence of osteodermal ornamentation of the head and body and the possession of a varanoid type of dentition are the only characteristics shared by *Eosaniwa* and *Necrosaurus* and the specific forms taken by those features differ significantly in the two taxa. Additionally, the paired frontals, lacking a sagittal ridge, as well as the dramatic elongation of the rostral region serve to distinguish the former from the latter and the inclusion of *Eosaniwa* in the Necrosauridae is rejected.

Saniwa feisti Stritzke 1983–Typically referred to as *'Saniwa' feisti,* the necrosaurian affinities of this taxon have been noted by others who have included it in phylogenetic analyses, with those authors consistently recovering a position close or adjacent to *Necrosaurus* (Rieppel et al. 2007; Norell et al. 2007; Conrad 2008) and examination of photographs provided by M. Caldwell and R. Nydam of a complete skeleton of *'S'. feisti* (SMF ME10954) held at the Senckenberg Natural History Museum, Frankfurt, reveals important similarities with *Necrosaurus* (Fig.3-5).

The azygous frontal and parietal both bear osteodermal ornamentation in a pattern consistent with that of *Necrosaurus.* The osteoderms of the frontal are more numerous, smaller and less organized than those of *Necrosaurus* but the pattern of placement is quite regular including a median row forming a raised keel between slightly raised supraorbital ridges. The frontal further resembles *Necrosaurus* in possessing a W-shaped suture where it contacts the nasals while the overall shape of the element shows an increased interorbital constriction. The pattern of ornamentation on the parietal is very consistent with *N. eucarinatus* though the posterior portion of the parietal table in *'S.' feisti* does not narrow to the same degree and the adductor musculature appears to be relegated to the mostly laterally facing decensus parietalis. Like *Necrosaurus* (and unlike

Parasaniwa) the parietal table of *'S.' feisti* does not extend posteriorly onto the dorsum of the supratemporal processes. The maxilla of *'S.' feisti* possesses a slightly inclined anterior margin of the nasal process approximately the same as that of *Necrosaurus eucarinatus*, but somewhat more steep than that of *N. cayluxi*. Strizke (1983) reported 20 teeth in the maxilla of *'S.' feisti* and the Senckenberg specimen corroborates this count. None of the *Necrosaurus* specimens examined were complete enough to allow for an accurate estimate of maxillary tooth number but the fragments available show proportions (tooth size relative to location on maxilla) very like those found in *'S.' feisti*. Lastly, the Senckenberg specimen of *'S.' feisti* preserves numerous osteoderms in the form of spicule-like structures surrounding the trunk, tail and limbs. These structures are interpreted here as the sagittal keel of somewhat reduced necrosaur-like osteoderms and indeed, more robust osteoderms can be found lying adjacent to the cervical vertebrae that are virtually identical to those found in *Necrosaurus* (Fig. 3-3). Pending a redescription of the taxon by K. Smith (in prep.), *'Saniwa' feisti* is here considered to be at the very least a strong candidate for inclusion in a monophyletic Necrosauridae if not an actual member of the genus *Necrosaurus*.

Bahndwivici ammoskius Conrad 2006–Conrad (2006) described and reconstructed the early Eocene form *Bahndwivici ammoskius* as a shinisaurid. Before the possible necrosaurian affinities of this taxon can be discussed, the taxonomic assignment provided by its author, one quite separate from the position of *Necrosaurus,* must be dealt with. Direct observation of the type and only specimen of *B. ammoskius* (FMNH PR2260) reveals numerous misinterpretations on the part of Conrad (2006). As that author has erected and diagnosed the family Shinisauridae (including *Shinisaurus* and *Bahndwivici*) based on a set of seven synapomorphies derived from phylogenetic analysis, it seems appropriate to address these characters first. They are:

1. Character 1 (Conrad 2006)- Skull, muzzle shape: (0) tapering; (1) blunt and rounded: For this character Conrad (2006) scores both *Shinisaurus* and *Bahndwivici* as (1) blunt. Questions relating to the vagueness and potential utility of such a poorly conceived character aside, there is simply no evidence to suggest a blunt snout in *Bahndwivici*. As Conrad (2006) himself points out, the premaxilla of *Bahndwivici* is "…narrow and only forms the anterior tip of the skull" while there certainly does not appear to be any marked medial inflection of the premaxillary process of the well-preserved right maxilla. If a reconstruction of the profile of the snout must be undertaken then surely the conditions seen in these two elements would more strongly support a relatively tapered snout. The premaxilla of *Bahndwivici* is also dorsoventrally gracile and its posterodorsally sloping nasal process is thin and pointed. By way comparison, the premaxilla of *Shinisaurus* is relatively more robust, forming a thick parapet below and medial to the external nares, while its nasal process is equally broad contacting the anterior as well as anteromedial edges of the nasals (Conrad 2004; pers. obs). The form of the premaxilla in *Bahndwivici* and its posterolateral contact with the maxilla is consistent with that seen in *Necrosaurus*.

2. Character 2 (Conrad 2006)-Skull, raised crest on temporal arch: (0) absent; (1) present, strongly developed: Here Conrad scores both *Shinisaurus* and *Bahndwivici* (1) for presence of a strongly developed crest on the supratemporal arch. To be clear, this character has not been optimized for *Bahndwivici* but rather it has been coded by the author as (1) in the matrix provided. How this was done in light of the fact that the temporal arches of *Bahndwivici* are in no way preserved is unclear. Its worth noting, that the author's first statement regarding the form of the skull of *Bahndwivici* points out the lack of preservation of the temporal arches (Conrad 2006, pg. 113).
3. Character 7 (new) (Conrad 2006)-Nasofrontal suture, articulated shape in dorsal view: (0) W-shaped; (1) frontal forming anterior wedge: Despite Conrad's (2006) coding of this character as (1) for *Bahndwivici* the anterior tip of the frontal in that taxon is clearly W-shaped (Fig. 3-6) and similar in all respects to the frontonasal suture seen in both species of *Necrosaurus* and *'Saniwa' feisti*. Newly created, this character clearly pertains to the shinisaurian condition where the frontal (1) forms an anterior wedge between the nasals and lacks any anterolateral projections, a character state it shares with *Xenosaurus*.
4. Character 9 (New) (Conrad 2006)-Prefrontal, dorsolateral tuberosity: (0) absent; (1) present: This character was constructed de novo by Conrad (2006) and appears to address the thick crenulated ridge that ornaments the dorsolateral angle of the prefrontal and runs confluent with the supraorbital ridge of the frontal in *Shinisaurus*. The coding provided by Conrad (2006) for this character is (1) or present, for *Shinisaurus* and *Bahndwivici.* The prefrontals of latter are

very well preserved and closely resemble those of more derived varanoids (*Varanus*, *Saniwides, Telmasaurus, Cherminotus, Estesia* and *Saniwa ensidens*) insofar as the lateral angle formed at the juncture of the vertical, orbital surface and the horizontal, dorsal surface is fairly acute. This feature is typically associated with the site of attachment of a palpebral ossification and is developed into a dorsolaterally projecting crest in *Bahndwivici* though no palpebral elements are preserved in the specimen. Medially, this raised dorsolateral crest gives way to a slightly concave dorsal surface of the prefrontal in *Bahndwivici* which is particularly reminiscent of the condition seen in *Telmasaurus* (pers obs.) but is in no way similar to the dorsal convexity created by the raised tuberosity on the prefrontal of *Shinisaurus* (Conrad 2004).

5. Character 10 (New) (Conrad 2006)-Prefrontal, blocks contact between maxilla and nasal: (0) absent; (1) present, extends anteriorly to naris: This is another new character introduced by Conrad (2006) and is presumably designed to deal with the uncommon (for anguimorphans) feature represented by state (1) and present in *Shinisaurus*. Conrad (2006) codes *Bahndwivici* as (1), having an anterior extension of the prefrontal that intercedes between the nasal and maxilla and reaching the posterior border of the naris. This despite the fact that the nasals are not sufficiently preserved to allow for their reconstruction and that the prefrontal facets, visible on either side of the frontal, demonstrate an anteroposterior position of the prefrontals that lies well posterior to the position of the external naris as suggested by the nasal process of the right maxilla. The prefrontal of *Shinisaurus* is diamond shaped in dorsal view with the anterior narial extension,

described as a thin lamina (Conrad 2004), forming a point. By contrast, the prefrontals of *Bahndwivici* both display a triangular dorsal surface with a relatively straight and transversely oriented anterior margin, lacking a lamina. Topological reconstruction of the elements surrounding the external nares of *Bahndwivici* is not possible given the level of preservation of FMNH PR2260. As preserved the element discussed appear consistent with those of other platynotans for which they are known and bear no special similarity to the condition seen in *Shinisaurus*.

6. Character 11 (New) (Conrad 2006)-Prefrontal, presence of a subpalpebral fossa: (0) absent; (1) present: Conrad (2004) describes and illustrates a subpalpebral fossa on the prefrontal of *Shinisaurus,* outlined by a 'telescoping' rim of bone lying immediately posterior to the contact with the maxilla. In Conrad's (2006) illustration of *Bahndwivici*, he labels the site of a proposed subpalpebral fossa on the left prefrontal at a point where the element has undergone significant fracturing. The far better preserved right prefrontal does not possess a circular fossa or associated raised bony rim but instead displays a longitudinally oriented sulcus on the anterolateral surface just below the dorsolateral crest. A similar but shallower sulcus is observed in *Varanus*, its delineation in *Bahndwivici* made more clear by the increased development of the prefrontal crest in that taxon. The subpalpebral fossa of *Shinisaurus* is distinct in its morphology and does not appear to be present in *Bahndwivici*.
7. Character 30 (Conrad 2006)-Articular, retroarticular process; (0) posteriorly directed; (1) medially deflected: Conrad's (2006) analysis of this character finds

a state of (0) posteriorly directed retroarticular process for both *Shinisaurus* and *Bahndwivici*. Only the left retroarticular process is preserved in *Bahndwivici* and is accurately decribed by Conrad (2006) as having a faint "posteromedial inflection".

Having addressed the shinisaurid synapomorphies of Conrad (2006), one other significant difference between *Shinisaurus* and *Bahndwivici* is worth noting. The skull form of *Shinisaurus* is very tall, the continuous margin outlined by the premaxilla, nasals prefrontals and frontal tracing a broad curve from the tip of the snout to the parietal table. This form results in a marked dorsal convexity of the long axis of the frontal, a feature not present in *Bahndwivici.* If the frontal of *Bahndwivici* were curved in such a way, it should show signs of transverse fracturing in the flattened preserved specimen, as are present in the posteroventrally directed supratemporal processes of the parietal. In fact it does not, but instead appears to be undamaged and quite flat along its longitudinal axis as does the parietal table.

Characters shared by *Necrosaurus* and *Bahndwivici ammoskius* include: osteodermal ornamentation of the frontal forming a median keel; lateral margins of the frontal parallel in its anterior two thirds; W-shaped fronto-nasal suture; osteodermal ornamentation of the parietal including a pineal eminence and anterior median keel; maxilla with inclined anterior margin of the nasal process; posterior constriction of the parietal table resulting in a minimum width equal to that of the frontal; and ovoid body osteoderms bearing a median keel flanked by a fine grained pit and ridge surface texture. *Bahndwivici* differs from

Necrosaurus in lacking any evidence of plicidentine, and in the less organized pattern of osteodermal ornamentation of the frontal which appears to be more consistent with the condition seen in *'Saniwa' feisti*.

Perhaps the most striking feature of *Bahndwivici* is the similarity between its osteoderms and those of *Necrosaurus*. It can be safely assumed that if the osteoderms possessed by *Bahndwivici* were discovered in isolation in and sediments ranging anywhere from the late Cretaceous to the Oligocene, they would be interpreted as conclusive evidence of the presence of 'necrosaurs'. Despite this, Conrad (2006) makes no reference to the osteoderms of *Necrosaurus* but instead interprets the caudal osteoderms of *Bahndwivici* as taking the form of an inverted V rather than possessing a dorsal keel. The author offers no explanation supporting this interpretation other than pointing out that the inverted V-shape is the condition in *Shinisaurus*. In contrast to this interpretation, several areas lateral to the caudal vertebrae show a double layer of osteoderms with the keels pointing dorsally in the upper layer and ventrally in the lower layer. The evidence preserved in the specimen clearly supports an interpretation of the osteoderms of *Bahndwivici* as possessing a dorsal keel.

The above evidence supports the inclusion of *Bahndwivici ammoskius* in the Necrosauridae, contradicting the interpretation of Conrad (2006) that it forms a sister group relationship with *Shinisaurus*. In light of this, a thorough review of *Bahndwivici* needs to be undertaken but lies outside the scope of the current study. Pending such a review, it is recommended that *Bahndwivici ammoskius* be considered a strong candidate for membership within Necrosauridae.

CONCLUSIONS

The discussion presented above suggests that a reconstitution of the family Necrosauridae and its membership is needed. In its current form and recent historical usage Necrosauridae is very likely paraphyletic (Estes 1983; Borsuk-białynicka 1984; Estes et al. 1988, Gao and Fox 1996) and in practical terms serves as a stem-based taxon representing fossil forms that cannot be confidently allied with Helodermatidae, Lanthanotidae or Varanidae yet appear to be more closely related to those forms than to *Xenosaurus, Shinisaurus* and the Anguidae. The retention of such a stem-based taxon is useful given the lack of resolution among the relationships of fossil forms found on the stem leading to Varanoidea Camp 1923 and fortunately, such a taxon already exists. The term Platynota Duméril and Bibron 1836 has been consistently applied to a group comprised of living varanoids and their fossil relatives (McDowell and Bogert 1954; Rieppel 1980; Borsuk-Białynicka 1984; Pregill et al. 1986; Evans 1994) as was pointed out by Lee (1997) who offered the first phylogenetic definition of Platynota as a stem-based taxon representing Varanoidea (*Varanus, Lanthanotus* and *Heloderma*) and all taxa more closely related to varanoids than to other anguimorphs. Thus defined, Platynota has been widely used (Lee 1998, 2000; Bernstein 1999; Balsai 2001; Conrad 2004, 2006, 2008, 2010; Norell et al. 2008; Rieppel et al. 2007; Bhullar and Smith 2008) particularly where phylogenetic hypotheses of fossils with varanoid affinities are concerned.

There is unnecessarily broad overlap between the Necrosauridae as currently conceived and the Platynota as commonly used. There is no reason to treat all platynotans bearing no demonstrable relationship to a particular group of crown varanoids as a 'necrosaurs' and there exists no barrier to the diagnosis and construction of more than one basal platynotan family. If the terms 'necrosaurid/necrosaur/necrosaurian' are to have merit and warrant usage, a revised and more exclusive familial diagnosis for Necrosauridae is needed. To that end, an amended definition of Necrosauridae is offered here:

Diagnosis of Necrosauridae–Basal platynotans in possession of the following: external nares little retracted, with an inclined anterior border of the nasal process of the maxilla and broad naso-maxillary contact; Frontals fused with parallel anterolateral margins with little (*'Saniwa' feisti)* or no interorbital constriction and a W-shaped suture between frontal and nasals; frontal and parietals bearing osteodermal ornamentation forming a pineal eminience and a sagittal keel (derived further in *Necrosaurus*); posterior parietal table constricted with a minimum width equal to that of the frontal (except *'Saniwa' feisti*) and little or no contribution to the supratemporal processes; ovoid body osteoderms with a distinct sagittal keel flanked by fine grained pit and ridge surface texture.

It is hoped that the preceding argument provides adequate justification for the retention of a clearly circumscribed and potentially monophyletic Necrosauridae. The construction and retention of family level groupings among fossil Platynota provides a conceptual framework for discussing relationships among basal platynotans. This is particularly important as many phylogenetic reconstructions of platynotan relationships do not include certain taxa (based on lack of data) and/or fail to resolve the interrelationships among basal platynotans due to a lack of homological hypotheses. Lastly, the suite of characters described above may provide the basis for the construction of character statements pertinent to the phylogenetic reconstruction of basal platynotan relationships.

FIGURE 3-1. Frontal of *Necrosaurus. cayluxi* (MNHN QU17610) in a. dorsal view and b. ventral view; and frontal of *N. eucarinatus* (MNHN QU17609) in c. dorsal view and d.ventral view. Scale bar = 10mm.

a.

b.

c.

d.

FIGURE 3-2. Parietals of a. *Necrosaurus eucarinatus* (MNHN QU17625) and b. *N. cayluxi* (MNHN QU17620) in dorsal view. Scale bar = 10mm.

a.

b.

FIGURE 3-3. Osteoderms of a. *Necrosaurus eucarinatus* (GM CeIII-4139), b. Isolated *Necrosaurus sp.* (MNHN CB17439), c. *Eosaniwa koehni* (GM XXXVIII/57) and d. Caudal region of *Bahndwivici ammoskius* (FMNH PR2260). Scale bar = 10mm.

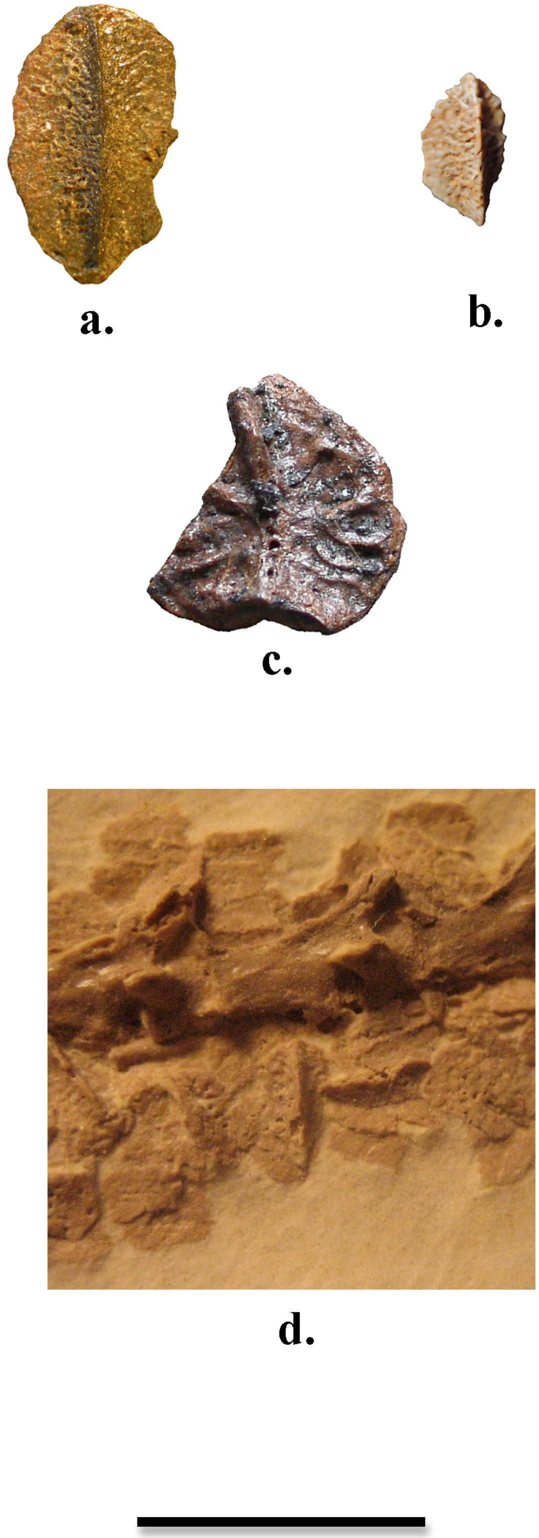
a.
b.
c.
d.

FIGURE 3-4. Right *Necrosaurus cayluxi* dentary (BMNH R3486) in a. medial view and b. lateral view; Vertical lines mark 17 tooth positions. Scale bar = 10mm.


a.
b.

FIGURE 3-5. Dorsal view of skull of *'Saniwa' feisti* (SMF ME10954). Scale bar = 10mm.

FIGURE 3-6. Dorsal view of skull of *Bahndwivici ammoskius* (FMNH PR2260).

Scale bar = 10mm.

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CHAPTER FOUR

A NEW PLATYNOTAN LIZARD (ANGUIMORPHA, SQUAMATA) FROM THE LATE CRETACEOUS OF SOUTHERN SASKATCHEWAN, CANADA

INTRODUCTION

The past thirty-five years, has seen a considerable increase in the number of described platynotan taxa, with several occurring in central Asia, (Borsuk-Białynicka 1984, Norell et al. 1992; Gao and Norell 2000; Norell et al. 2007), two in Europe (Haubold 1977; Stritzke 1983) and two in North America (Nydam 2000; Conrad 2006). Despite this increase, the phylogentic relationships of basal platynotans remain largely unresolved (Gao and Norell 1998; Nydam 2000; Balsai 2001; Rieppel et al. 2007; Conrad 2008) due in part to the fragmentary nature of many taxa, especially those found in North America. Apart from *Bahndwivici ammoskius* Conrad 2006 and newly described specimens of *Saniwa ensidens* Leidy 1870 Rieppel and Grande 2007), the record of platynotans in North America consists of isolated and fractured cranial, mandibular and post-cranial elements (Gilmore 1928; Estes 1983; Gao and Fox 1997). A new, semi-articulated platynotan from the Frenchman Formation of Southern Saskatchewan (RSM P 2622.2) is here described. The specimen was investigated using high resolution X-ray computed tomography (HRXCT) enabling illustration and description of features otherwise obscured my matrix and bone.

GEOLOGICAL SETTING

The specimen, RSM P 2622.2, (Figs. 4-1, 4-2) was collected in the spring of 1997 from the Killdeer Badlands locality of the Frenchman Formation of Southern Saskatchewan (Tokaryk 1997), (Fig. 4-3 Map). The specimen was discovered serendipitously while excavating the underside of a theropod ankle

(Tokaryk, pers. comm.). Furnival (1946) described the Frenchman Formation as "thick, massive or coarsely crossbedded, medium-grained fluvial sandstones". Sweet et al. (1999) point out the existence of much finer shale silt and sandstones toward the top of the formation and it was one of these fine-grained beds from which the Holotype was collected. A *Triceratops*-bearing formation, the Frenchman is of "latest Maastrichtian age, its top more or less corresponding to the K-T boundary" (Sweet et al. 1997). Correlative strata within North America include the Scollard Formation of Alberta, the Hell Creek Formation of Montana and the Lance Formation of Wyoming.

MATERIALS AND METHODS

The specimen was transferred to The University of Alberta by Dr. Michael Caldwell and preparation of dorsal and ventral surfaces of the specimen was performed by Alan Lindoe. High resolution X-ray computed tomographic scans were prepared with the assistance of Dr. Benedikt Hallgrímsson and Dr. Eric Snively in the 3D Morphometrics Lab at the University of Calgary. The 38.5mm cranial block was scanned along its axis for a total of 1325 slices 30 μm apart. HRXCT data was explored using OsiriX DICOM viewer v.3.5.1 32 bit version (Pixmeo, Geneva, Switzerland) employing 3D surface rendering and individual elements were isolated for viewing from all directions using crop and scissor tools. Illustrations provided were drawn from image captures of 3D surface rendering with visual confirmation of features using standard light microscopy where possible.

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758

SQUAMATA Oppel, 1811

ANGUIMORPHA Fürbringer, 1900

PLATYNOTA Baur, 1890

VULPESAURUS, gen. nov.

Etymology–"*Vulpes*" from the Latin for fox, and "*sauros*", the Greek word for lizard. Named for the Swift Fox, a narrow-snouted and diminutive predator maintaining a tenuous toehold in the Killdeer Badlands of today.

Generic Diagnosis– A Late Cretaceous platynotan possessing: varanoid type tooth replacement with teeth trenchant, and expanded at the bases but lacking plicidentine; dorsally attached jaw adductor musculature and considerable posterior constriction of the parietal table; free epiphyses (peduncle) on fused hypapophyses of anterior cervical vertebrae. Differing from other terrestrial platynotans in the possession of: supratemporal facets on the supratemporal processes of the parietal exceeding the parietal notch; posterior rami of the parietal and accompanying suspensoria with minimal ventral inflection; pterygoids toothed, possessing a single row of 18-20 socketed teeth extending posteriorly to the point of pterygoid/basisphenoid articulation; palatine processes of pterygoids elongate and tapering to dorsoventrally thin lamellae of bone likely contacting vomers; vomers elongate and separated medially; basipterygoid processes expanded anteroposteriorly, with broad distal articulation, adhering tightly to the body of the basisphenoid and lacking any constriction; crista prootica terminating ventral to facial foramen; cervical and dorsal vertebrae with pseudozygosphenes and low posteriorly arching neural spines with convex dorsal margins.

***VULPESAURUS MAGDALENAE* sp. nov.**

Holotype–RSM P 2622.2 (Figs. 4-1, 4-2), consisting of one cranial block (figured) and three postcranial blocks as well as numerous isolated elements, some embedded in matrix.

Referred material–RSM P 2416.88: posteriorly fractured isolated parietal.

Etymology–"*magdalenae*", named in honor of Magdalena Borsuk-Białynicka, for her contributions to squamate paleontology generally, and her work on cretaceous platynotans of central Asia specifically.

Occurrence–Killdeer Badlands locality, Frenchman Formation (late Maastrichtian), Grasslands National Park (East Block), Southern Saskatchewan, Canada. Referred material from Frenchman River Valley locality, Frenchman Formation, Eastend Saskatchewan.

Diagnosis–As for genus.

DESCRIPTION

Dermal skull roof

Maxilla–Only the posterior-most portion of the left maxilla is preserved and poorly at that, represented by two fragments positioned in a roughly natural linear arrangement and overlying the palatine process of the left pterygoid when viewing the specimen from above (Fig. 4-1). The preserved portion bears positions for approximately nine teeth, three of which are represented by their poorly preserved bases only. The tooth positions extend to the slender posterior terminus and would likely have underlain the orbit to a considerable degree. The teeth are widely spaced, with somewhat expanded bases, and lack resorption pits, characteristic of interdental tooth replacement of the varanoid type. Two dislocated replacement tooth crowns (one attached to the anterior end of the maxillary fragment and underlying the dorsal surface of the parietal ramus of the postfrontal in ventral view, and one lying just ventral to the postorbital, also exposed in ventral view) show a laterally compressed shape. None of the tooth bases are clearly visible in preparation and due to their small size and poor preservation the details of their surfaces are not cleanly resolved when examined through HRXCT. The teeth bear no evidence of plicidentine but instead appear to be quite thin-walled like those of *Colpodontosaurus* and *Provaranosurus*. Like the late Paleocene *Provaranosaurus*, the teeth of *Vulpesaurus* appear to be more trenchant and higher crowned than those of *Colpodontosaurus*. Though the fragments present appear to represent a full 10 mm, the dorsally directed nasal process is not preserved and the proportion of maxilla represented by these fragments is difficult to estimate. Due to its poor preservation an estimate of maxillary length or tooth count is not possible and little else can be said of the maxilla except that its slender posterior tip has a dorsomedial facet for possible articulation with the ectopterygoid and/or jugal.

Prefrontal–Only the left prefrontal is preserved (Fig. 4-4). Its anteromedial surface is visible on the upper surface of the specimen, just beside the anterior portion of the parietal table (Fig. 4-1), while the lateral surface of its frontal process is visible in ventral view (Fig. 4-2). Though some fracturing has occurred, the prefrontal is undistorted and complete except for that anterior-most portion which would have underlain the posterodorsal ramus of the left maxilla. The general shape of the prefrontal is that of a shallow bowl with its concave surface facing anteromedially. The elongate frontal process tapers posteromedially from the body of the prefrontal and its surface as well as the surfaces of the lateral and orbital wall are smooth with no indication of osteodermal ornamentation.

The prefrontal bears clear facets for contact with the maxilla, palatine, frontal and possibly nasal. A broad and somewhat fractured flange extends anteriorly from the dorsal and lateral surfaces to underlie the maxilla suggesting that the posterior tip of the nasal process of the maxilla was medially inflected. The posterior margins of this facet are intact and show the limit of maxillary encroachment onto the prefrontal including a posteriorly emarginated notch on the ventral half of the lateral surface located just anterodorsal to the presumed point of articulation with the lacrimal. The dorsal portion of the maxillary facet continues dorsomedially in a roughly vertical line and meets at an acute angle the medial facet for articulation with the frontal and/or nasal. The lack of any free (non facet bearing) edge of the prefrontal along its anterior and dorsomedial margins indicates clearly its exclusion from the margins of the external bony naris and maxillary-nasal contact is presumed. The medial facet spans the entire anteroposterior length of the element and is undifferentiated suggesting a single facet with the frontal or possibly contact with a confluent frontal and nasal. This facet is dorsoventrally deep covering the entire medial surface of the frontal process as well as the dorsomedial surface of the palatine process of the prefrontal. At the anterior end of the frontal facet, the prefrontal curls under the frontal or nasal forming a short flange similar to that underlying the maxilla. The frontal facet does not continue ventrally along the medial edge of the body of the prefrontal as it would in *Varanus*, suggesting that the subolfactory process is less well developed than in more derived platynotans, and may resemble more that of *Shinisaurus* (Conrad 2004). A large palatine facet is visible in ventral view and is oriented anterolaterally to posteromedially. Just dorsal to this facet is a shallow depression on the posterolateral face of the orbital surface of the prefrontal. A slight crest outlines this depression in a dorsally arched semicircle and is suggestive though not conclusive of an articular surface for the lacrimal. More conclusively, a distinct ovoid depression in the anterodorsal corner of the orbital surface indicates the likely presence of an ossified palpebral though no such element is preserved.

While the dorsal and lateral surfaces of the prefrontal as would be exposed in articulation lack any dermal sculpturing, three features warrant mention. Firstly, there is a prominent and sharp triangular crest projecting posterolaterally above the orbit about half way along the frontal process. Lying just posterior to the palpebral facet this crest may represent a posterior continuation of the supra-orbital shelf created by the palpebral. It is however, more than just a simple buttress but rather a structure quite distinct from the palpebral facet itself. Secondly, in posterolateral view, the point at which the orbital surface and the frontal process meet is the site of a conspicuous and proportionately large semicircular notch suggesting the influence of a large structure of the soft tissue anatomy. Lastly, there are five foramina opening posterodorsally from the dorsal surface of the prefrontal and one foramen opening posterolaterally from the centre of the palpebral facet. The latter structure is easily explained in light of its location relative to the palpebral element while the former are less obvious in their functional significance especially in the absence of evidence for osteodermal ornamentation.

Parietal–(Figs. 4-5, 4-6, 4-7) The parietal is conspicuous in dorsal view (Fig. 4-1) and is all but complete, missing only the left anterolateral most corner of the parietal table and the terminus of the left supratemporal processes. Some fracturing of the parietal has occurred along with a slight axial torsion but the surface texture and articular facets are very well preserved. The fronto-parietal suture is transverse in dorsal view and includes two laterally placed frontal tabs of the parietal projecting anteriorly to underlie the frontal(s). The lateral margins of the parietal decensus are concave though less markedly than those of *Varanus*. The posterior margin is excavated between the supratemporal processes with the parietal notch forming a wide angle of approximately 130 degrees, reminiscent of *Necrosaurus*.

Attachment for the jaw adductors is dorsal with the parietal table constituting less than 50% of dorsal surface area. The parietal table is broadest at its anterior and tapers gently posteriorly with only a slight re-widening occurring before it terminates at the parietal notch. In the degree of constriction of the posterior parietal table, with the narrowest point being only slightly larger than the pineal foramen, the parietal table of *Vulpesaurus* again resembles that of *Necrosaurus* specifically *N. eucarinatus*. However, its dorsal surface is only very slightly rugose, falling within the range of dermal roof texturing seen within *Varanus* (pers. obs.), and is not indicative of the presence of osteodermal ornamentation. The large pineal foramen is completely enclosed in the anterior half of the parietal. Slightly anterior to its midpoint the parietal table bears two laterally projecting bosses which align with the posterior-most extension of the laterally facing facet receiving the parietal ramus of the postfrontal. The table does not contribute significantly to the dorsal surface of the supratemporal processes with the latter forming blade-like structures oriented dorsomedially to ventrolaterally in cross section. A particularly unusual feature of these processes is the absence of any ventrally directed extension toward their posterior ends, a condition very different from other platynotans for which this feature is known possibly suggesting a flattened skull shape.

Facets receiving the postfrontal and supratemporal are visible in lateral view with the latter extending well anterior to the parietal notch. A second narrow facet on the posteroventral surface of the right supratemporal process matches closely that of *Varanus* and suggests that the supratemporal encloses the process both laterally and ventrally, excluding contact with the paraoccipital process or quadrate. The parietal is deepest midway along its decensus parietalis at the point of presumed articulation with the prootics and epipterygoids.

The ventral surface of the parietal is smooth and marked by the anterior pineal foramen and a posterior parietal fossa. The latter is open posteriorly and flanked by two posterolaterally oriented cristae. In occipital view the parietal table is excavated by numerous small pits but is quite thin and bears is no nuchal fossa indicating a possible lack of strong supraoccipital-parietal contact.

Overall the parietal most closely resembles that of *Necrosaurus eucarinatus* Kuhn 1940 in that the parietal table is widest at its anterior and gently tapers posteriorly with only a slight contribution to the dorsal margins of the supratemporal processes. Also resembling *N. eucarinatus* are the length of and degree of angulation between the supratemporal processes, though both these features are difficult to determine in the *N. eucarinatus* material and are inaccurately depicted in Estes 1983. The parietal differs from both *Necrosaurus* and *Shinisaurus* in lacking any dermal sculpturing.

Postfrontal and Postorbital–(Figs. 4-8, 4-9) Visible in dorsal and ventral views (Figs. 4-1, 4-2), the left postfrontal and postorbital are present and well preserved as separate un-fused elements.

The postfrontal is tri-radiate when viewed from above and composed of an anteromedial frontal process, a posteromedial parietal process and a lateral postorbital process. The angle formed by the frontal and parietal processes is approximately 115 degrees and would have cupped the frontal and parietal laterally in articulation. The frontal process is slender in dorsal view with a relatively broad dorsoventral development forming a strap-like extension for articulation with the frontal. In cross section, the long axis of the frontal process is oriented dorsolaterally to ventromedially making the articular facet on the medial side of the frontal process partially visible in dorsal view. The parietal process is equal in length to the frontal process but is dorsoventrally thinner and mediolateraly broader with a triangular, flattened dorsal surface that would be contiguous with the parietal table in articulation. The parietal facet is flat and oriented dorsomedially to ventrolaterally along most of the parietal process with the anterior bearing a horizontally excavated notch where it meets the frontal process; this notch accommodating the anterolateral tab of the parietal table. The laterally projecting postorbital process of the postfrontal is shorter than the others, but much more robust with a ventrally curving distal end. This process bears lateral and posterodorsal facets for articulation with the jugal and postorbital respectively. The jugal facet is crescent shaped with a convex edge facing anterodorsally and a concave edge facing posteroventrally. This facet forms the anterior one third of the articulation with the jugal (the other two thirds being formed by the postorbital) and is posteriorly bordered by another longer crescent shaped facet, with its convex edge facing dorsolaterally, articulating with the postorbital. The dorsal border of the postorbital facet is gently s-shaped in dorsolateral view, the medial curvature of the 's' accommodating an anteriorly projecting dorsomedial tab of the postorbital, and the lateral curve outlining a posteriorly projecting dorsolateral tab of the postfrontal. The postorbital facet does not extend the entire posterolateral length of the parietal process and as such the postfrontal does contribute to the anteromedial margin of the upper temporal fenestra.

The anterodorsal surface of the postorbital process bears a small tubercle in a position equivalent to that of the anterior postorbital prong observed in *Shinisaurus* (Conrad 2004). Much smaller than the structure described for *Shinisaurus* this feature more closely resembles similarly sized anterior projections present on the postfrontal of some anguid taxa such as *Elgaria* (pers. obs.). The dorsal surface of the postfrontal, like that of the prefrontal, bears numerous foramina as does the ventral surface.

The general shape of the postorbital in dorsal view is that of an elongate triangle pointing posteriorly. In lateral view it is roughly L-shaped with the long branch of the L directed posteriorly and the short branch pointing ventrally. The squamosal process makes up the bulk of the element and includes a medially directed lamina that would have roofed the supratemporal fenestra to some considerable degree when compared to more derived platynotans. Despite this there is no evidence that the postorbital contacted the parietal as occurs in some anguids. A fracture is present near the end of the squamosal process but the natural outline of the element appears unaffected. Facets for articulation with the postfrontal, jugal and squamosal are visible and clearly defined.

The postfrontal facet of the postorbital is visible in anterior view. It covers the anterior surface, is crescent shaped with the convex surface facing dorsolaterally, and bears a tongue-like process near the midline of the facet which fits a corresponding groove on the posterior of the postorbital process of the postfrontal. The dorsal margin of this facet is curvilinear when viewed dorsally and matches the s-shaped curve described on the posterodorsal surface of the postfrontal. The laterally facing jugal facet is extensive and in combination with the somewhat smaller jugal facet on the postorbital process of the postfrontal provides a broad and deep lateral contact for the jugal. The ventrolateral facet for contact with the squamosal runs the posterior two thirds of the postorbital and is lightly convex. The facets for the jugal and squamosal approach each other but are not contiguous indicating a lack of contact between their corresponding elements.

The dorsal surface of the postorbital is smooth with five foramina visible, while the ventral surface of the squamosal process bears an ovoid concavity centered on its anterior half.

Jugal–A relatively large and block-like fragment of bone is visible in dorsal view lying adjacent to the toothed portion of the left pterygoid (Fig. 4-1). This fragment is interpreted as the anterior portion of the left jugal (Fig. 4-10). Its identification is based on the preservation of the anteroventral facet for receipt of the posterior tip of the maxilla. This facet is quite large and also likely overlaid the anterior process of the left ectopterygoid where it contacted the maxilla and palatine. The lateral margin of the facet continues posterior to it in the form of a posteroventrally directed crest, much like the ventral crest seen on the jugal of *Heloderma* and *Shinisaurus* (Conrad, 2004). Like those taxa, this crest may mark the ventral edge of a posteriorly expanding flattened lateral surface of the jugal though the presence of a posterior process of the jugal cannot be confirmed. The lateral surface of the jugal is fairly smooth matching the surface texture observed on the parietal, prefrontal and maxilla.

Directly opposite the maxillary facet, on the dorsal surface of the jugal there is an equally long sulcus created by the presence of a dorsomedial process. Conrad (2004) describes such a process in *Shinisaurus* (medial process in his text) and illustrated the posterior portion of the lacrimal lying in the facet created between this process and the lateral surface of the jugal. The dorsal sulcus on the jugal may have received the posterior tip of the lacrimal but it is unlikely that the lacrimal possessed a posterior process long enough to fill the entire sulcus.

In general shape and proportion, as well as in having a flattened lateral surface, the jugal of *Vulpesaurus* more closely resembles that of platynotans in which the jugal is robust, and is made up of distinct anterior and dorsal rami. This in contrast to that of *Varanus*, where it forms a more gracile element that gently curves posterodorsally and fails to make any broad contact with the postorbital or postfrontal. As was described above, the postfrontal and postorbital of both bear facets showing broad contact with the jugal.

Squamosal–The left squamosal is visible in dorsal view lying immediately beside the parietal (Fig. 4-1). The visible anterior half is well preserved though fractured while the posteriormost portion is obscured from view underlying the left supratemporal process of the parietal. Unlike the postorbital the squamosal is relatively narrow in dorsal view with no medial expansion contributing to a supratemporal roof. The anterior half gradually tapers to a thin blade-like point articulating laterally and slightly ventrally to the postorbital via the lengthy trough-like postorbital facet. The posterior end widens slightly along an oblique axis at the point of articulation with the supratemporal. The supratemporal articulation, appearing as an abutment whose face is directed posteromedially, is difficult to resolve when isolated using HRXCT due to its intimate contact with numerous bone fragments. Despite this, the posterior terminus is complete and the overall length and shape of the squamosal can be reconstructed though the presence or absence of a facet articulating with the quadrate cannot be determined.

In lateral view, the squamosal is relatively flat, mirroring the posterior parietal table in its profile. Unlike that of most other anguimorphs where the posterior end bears a considerable ventral curvature, this squamosal curves only slightly downward upon reaching the supratemporal. As noted for the parietal, this lack of dorsoventral depth in the supratemporal processes of the parietal and accompanying suspensorium is an unusual feature for an anguimorphan and perhaps most comparable to *Aigialosaurus* (Dutchak and Caldwell 2006, 2009), *Pontosaurus* (Pierce and Caldwell 2004; Caldwell 2006) and the basal russellosaurine mosasaurs *Russellosaurus* (Polcyn and Bell, 2005), *Tethysaurus* (Bardet et al, 2003) and *Yaguarasaurus* (Paramo 1994).

Supratemporal–The right supratemporal is visible in dorsal view lying next to the supratemporal process of the parietal (Fig. 4-1). It is well preserved though missing the long lamella of bone that would have articulated medially with the parietal as evidenced by the distinct facet present on the posterolateral surface of the latter element. The remaining portion is a roughly rectangular block of bone, longer than wide, with articular facets for the parietal, squamosal, otooccipital and quadrate.

The lateral surface of the posterior end of the supratemporal is entirely covered by the relatively flat facet articulating in a butt joint with the posterior tip of the squamosal. Medially, two facets are visible, one anteromedial, and one posteromedial. The anteromedial facet is a groove oriented anteroventrally to posterodorsally and receives the posterior edge of the supratemporal process of the parietal while the larger posteromedial facet forms a crescentic depression for articulation with the paraoccipital process of the otooccipital. Lastly, the posteroventral tip of the supratemporal bears a facet for articulation with the posterodorsal surface of the quadrate.

The dorsoventral depth of the posterior supratemporal matches perfectly that of the squamosal and also lacks the strong downward curvature typical of terrestrial anguimorphans.

Palate

Pterygoid–The left pterygoid is complete and clearly visible in dorsal view lying to the left of the parietal with its ventral surface facing upward (Fig. 4-1). The main block also contains the distal tip of the right ectopterygoid process with its broken shaft visible to the right of the right decensus parietalis (Fig. 4-1) as well as the right palatine process underlying the anterior of the parietal and visible in ventral view (Fig 4-2). Separated from the main block, there is also a fragment representing the region of the right pterygoid around the columellar fossa.

Though some fracturing has occurred, the left pterygoid is complete (Figs. 4-11, 4-12) and relatively undistorted. It is a triradiate bone consisting of an anterior palatine process, an anterolateral ectopterygoid process and a posterolateral quadrate process. The Palatine process is very long, slender and dorsoventrally flattened, tapering to a thin, delicate lamella of bone for its anterior one third. The ventral surface of the palatine process bears a prominent row of approximately eighteen teeth (damage to the anterior half rendering a precise count impossible) beginning at the ventromedial edge where the quadrate and palatine processes meet. The tooth row then curves laterally, reaching the lateral edge of the palatine process before passing anterior to the suborbital lamina joining the palatine and ectopterygoid processes. The anterior half of this tooth row is heavily damaged though one tooth remains intact and shows a conical, recurved shape. The palatine process fragment of the right pterygoid also retains several teeth of this shape. The posterior half of the tooth row on the left pterygoid is better preserved, though the tooth crowns have all been sheared away, and clearly shows deeply socketed, conical tooth bases.

The ectopterygoid process projects anterolaterally at an angle of approximately 60 degrees from the central axis of the palatine process. It expands dorsoventrally towards its distal tip resulting in a proportionately large and spatulate process oriented along an anterodorsal to posteroventral axis. The anteromedial surface of the ectopterygoid process of the pterygoid bears two facets for dorsal and ventral pterygoid processes of the ectopterygoid. These facets are separated by a low ridge of bone that is contiguous with the suborbital lamina connecting the ectopterygoid and palatine processes. The dorsal surface of this lamina has a conspicuous foramen housed within an anterodorsally directed fossa visible in dorsal view just anterior to the columellar fossa. The foramen communicates with the ventral surface of the pterygoid through a pit located just lateral to the tooth row and anterior to the beginning of the quadrate process. The presence of a similarly located foramen is observed in other platynotans, specifically *Varanus,* though its presence/absence is highly variable with some individuals possessing such a foramen only in one of the two pterygoids. Unlike other taxa observed however, the foramen exiting from the suborbital lamina of *Vulpesaurus* is proportionately very large and immediately apparent while in other taxa it is typically overlooked due to its tiny size. A similar, slightly smaller fossa is also present on the ventral surface of the suborbital lamina but, while deep, it does not appear to pass completely through the pterygoid.

The quadrate process is just over one half the length of the palatine process and roughly twice the length of the ectopterygoid process. At its origin, a large columellar fossa opens dorsally for articulation with the epipterygoid. The medial surface lying adjacent to this fossa is deeply excavated and buttressed by a posteromedially projecting shelf of bone ventrally forming a medial notch for receipt of the pterygoid process of the basisphenoid. This notch is discrete being restricted to the region immediately adjacent the columellar fossa while a separate and elongate sulcus, site of attachment for the pterygoideus internus muscle, dominates the posteromedial surface of the posterior two thirds of the quadrate process coinciding with a dorsoventral expansion of the same. The lateral surface of the quadrate process is concomitantly convex with a large flattened facet taking up the posterior one third where contact is made with the quadrate. The dorsal surface of the quadrate process anterior to the presumed contact with the quadrate is also gently convex and would have received the protractor pterygoideus muscle. The lateral inflection of the quadrate process relative to the axis of the palatine process is more marked than in other platynotans creating a roughly 90 degree angle between it and the ectopterygoid process suggesting a relatively wide posterior region of the skull.

In general shape and proportions the pterygoid of *Vulpesaurus* resembles most that of *Shinisaurus* when compared to terrestrial platynotans for which the element is known. Conrad (2004) notes in *Shinisaurus* a suborbital lamina much less extensive than that of other anguimorphs; a character here shared by *Vulpesaurus*. Also shared with *Shinisaurus* are the elongate palatine processes and the single row arrangement of the pterygoid teeth. It should be noted that these are also all characteristics seen in the pterygoids of mosasaurs (Russell, 1967). Indeed, *Vulpesaurus* differs from *Shinisaurus* and resembles more the mosasauroid condition in the extreme length of the palatine process of the pterygoid and in the orientation and extent of its pterygoid dentition. Like *Vulpesaurus*, mosasaurs generally possess pterygoid teeth that extend posteriorly to the point where the pterygoid contacts the basisphenoid, a condition unknown in other terrestrial platynotans except *Eosaniwa* (Rieppel et al. 2007 and pers. obs.). The pterygoid tooth row of *Vulpesaurus* is also far more extensive than is seen in other terrestrial platynotans, with the anterior- most pterygoid teeth likely existing in broad overlap with the posterior-most maxillary teeth (presumed due to the fact that their anterior extent is level with the anterior tip of the articulated ectopterygoid and that the maxilla bears teeth on its posterior terminus where actual or near contact with the ectopterygoid is likely). The arrangement of the pterygoid teeth also resembles that of mosasaurs (Russell 1967; Konishi & Caldwell 2007) in that it migrates from a medial position at its posterior end reaching a lateral position by the time it comes level to the ectopterygoid process and then proceeds along the lateral edge of the palatine process until it terminates. The pterygoid teeth themselves differ from those of mosasaurs in that they are both more numerous and proportionately much smaller.

Ectopterygoid–The right ectopterygoid (Fig. 4-13) is well preserved, complete and visible in ventral view lying below the ectopterygoid process of the left pterygoid with its anterior process pointing toward the palatine process of the same (Fig.5-2). The shape of the ectopterygoid is very like that of *Heloderma* with anterior and pterygoid processes of approximately equal length meeting at an angle of 130 degrees and tapering toward their ends. The anteromedial surface of the resulting angle forms a gentle curve while the posterolateral corner projects somewhat creating a more sharply angled surface.

The anterior process of the ectopterygoid forms an acute triangle in cross section with a sharp peak pointing dorsally for most of its length. This peak is flanked both dorsomedially and laterally by facets; the dorsomedial facet taking the form of an ovate concavity while the lateral facet forms a broad, shallow and flat indentation. As was indicated by the presence of substantial facets on the postfrontal and postorbital for receipt of the jugal, a robust jugal was likely present and probably contacted broadly, along with the maxilla, the lateral facet of the ectopterygoid. The dorsomedial facet, while not entirely congruent with that resulting from contact with the palatine in taxa that show palatine/ectopterygoid contact (*Lanthanotus*, *Heloderma*, *Varanus*), is here interpreted as evidence for just such a contact in *Vulpesaurus*. In extant varanoids, the dorsomedial facet of the anterior process of the ectopterygoid is nearly horizontally oriented with the articular surface facing more dorsally than medially. In contrast to this, *Vulpesaurus* displays a more vertically oriented facet. However, if viewed ventrally in articulation, the skull of *Vulpesaurus* would show distinctly the palatine contacting the medial edge of the anterior process of the ectopterygoid with the ventral surface of the ectopterygoid clearly excluding the maxilla from the border of the suborbital fenestra, much as it appears in known varanoids regardless of the orientation of the plane of contact.

Vomer–The left vomer can be seen lying just lateral to the palatine process of the left pterygoid when viewed from above (Fig. 4-1). As with the pterygoid, the vomer has suffered fracturing along its length, though the anterior two thirds remain largely intact and display several distinct features.

A long, thin, strap-like bone, the vomer (Fig. 4-14) tapers toward its anterior ending in a rounded point. Midway along its fractured lateral edge there is an ovoid embayment oriented anteromedially to posterolaterally which is here interpreted as the fenestra vomeronasalis externa. The dorsal surface of the vomer is flat and quite smooth while the ventral surface is marked by three independent and longitudinally oriented crests of varying length.

As mentioned above, the lateral edge of the vomer is fractured from just anterior to the foramen vomeronasalis externa to its posterior tip. Anterior to this fracture is a facet for articulation with the maxilla. This long, concave facet is approximately one third the length of the vomer as preserved and somewhat dorsoventrally expanded, its ventral edge forming a crest on the underside of the vomer. The length of this facet represents both a significant degree of vomer-maxilla contact as well as a posteriorly placed septomaxilla relative to the tip of the rostrum. The nature of any possible contact between the vomer and maxilla posterior to the vomeronasalis externa cannot be determined directly due to the fractured condition of the posterior half of the lateral edge of the vomer. However, the close proximity of the lateral margin of the fenestra vomeronasalis externa relative to the medial margin of the maxilla as estimated by the posterior extension of its anterior articulation with the vomer, would suggest that even a modest palatal shelf of the maxilla would be able to bridge the gap creating a 'neochoanate' condition sensu Lakjer (1927) in *Vulpesaurus*.

A second ventrally projecting crest dominates the medial margin of the vomer along most of its length, gently tapering anteriorly and disappearing entirely before reaching the anterior tip. This crest is formed by a ventrally inflected curvature of the smooth dorsal surface of the vomer and is confluent with that surface. The depth of this curled crest increases posteriorly while simultaneously becoming thinner.

A third crest running lengthwise through the center of the vomer starts at the very tip, and becomes ventrally and laterally expanded forming an L shape with the horizontal portion directed laterally. Together with the main horizontal splint of the vomer this crest houses a deep ventrolaterally open channel anterior to the fenestra vomeronasalis externa. Posterior to this fenestra the crest continues laterally at an oblique angle as a simple crest without the lateral expansion (possibly due to damage).

The arrangement of the aforementioned crests, and the broad concave depressions between them, are reminiscent of the vomer of *Varanus*, though a direct comparison cannot be made due in part to the position of the fenestra vomeronasalis externa. In *Varanus* this opening would be positioned within the anterior third or even one quarter of the vomer while in *Vulpesaurus* it is positioned almost exactly at the mid-point along the element's preserved length. The vomer is presumed to be nearly complete despite the posterior breakage due to its length already exceeding that of *Varanus* proportionately. In *Varanus* the vomer is typically equal to the length of the quadrate process of the pterygoid (pers. obs.) while in *Vulpesaurus* it is at least thirty percent longer.

The vomer of *Vulpesaurus* resembles closely those of *Mosasaurus hoffmani* Conybeare 1822 (Lingham-Soliar 1995) and *Platecarpus* (Williston 1898; Russell 1967) in the length, general shape and degree of maxillary contact; the placement and orientation of the fenestra vomeronasalis externa; the absence of an apparent medial contact between vomers; and in the presence of an obliquely oriented, ventrally directed crest running from the tip of the vomer, medial to the fenestra vomeronasalis externa, and terminating on the lateral edge before reaching the posterior tip of the element. The proportional length of the vomer of mosasaurs very likely exceeds that of *Vulpesaurus* though the point of contact with the vomerine process of the palatine in those taxa is difficult to determine (Russell 1967; though see Konishi and Caldwell 2007). It is tempting to assume, given the fractured condition of the posterior third of the vomer here described, that the element was much longer in life than preserved and thus bore an even more remarkable resemblance to that of the mosasaurs discussed above. However, as previously noted the length of the vomer as preserved already exceeds that which is typical of terrestrial playtynotans apart from *Eosaniwa koehni* (Rieppel et al. 2007) and when combined with the length of the palatine process of the pterygoid and the presumption of little or no overlap between these two elements, results in a reconstructed rostrum of considerable length (see discussion below on palatal reconstruction).

Braincase

The braincase of *Vulpesaurus* is represented by well-preserved elements of the basioccipital, the right otoocipital, the basisphenoid and fractured portions of both the left and right prootics. These elements are quite cleanly disarticulated, showing a lack of complete fusion of the braincase and indicating the possibility that the specimen is a sub-adult. It should be noted however, that other features of the braincase indicate an adult level of maturation, most notably, the complete closure of the basicranial fontanelle as well as the strong development of the paraoccipital processes of the otoocipitals, the alar processes of the prootics and the parasphenoid rostrum (Romer 1956; Bever et al. 2005).

Basioccipital–When viewing the specimen dorsally, the basioccipital is visible, its contribution to the occipital condyle directed dorsally and lying just ventral and posterior to the right supratemporal process of the parietal (Fig. 4-1).

The basioccipital (Figs. 4-15, 4-16) bears two prominent basal tubercles (the spheno-occipital tubercles of Oelrich 1956; spenoccipital tubercles of

Borsuk-Białynicka 1984) which provide an attachment site for the *longus coli* (Rieppel and Zaher 2000). These tubercles are substantial in size, directed ventrolaterally and joined along their ventral surface via posterolaterally directed crests (sphenoccipital torus of Borsuk-Białynicka 1984) to the large posteriorly projecting occipital condyle. The body of the basioccipital is a horizontal plate of bone of an irregular hexagonal shape, tapering both anteriorly and posteriorly and widest at the point where it extends into the basal tubercles.

In ventral view, the region of the basioccipital immediately anterior and medial to the basal tubercles forms a deep crescent shaped concavity. From the posterior end of this concavity there rises a median ridge of bone that expands anteriorly to form a sub-triangular plateau where the basioccipital meets the basisphenoid. Depressions in the ventral surface of the basioccipital, anteromedial to the basal tubercles, are present in *Estesia* (Norrell and Gao 1997), *Shinisaurus* (Bever et al., 2005), *Telmasaurus grangeri* (ZPAL MgR-I/65) as well as some anguids (*Elgaria, Ophisaurus, Anguis*), though to a much lesser extent. In the above taxa, these depressions are typically shallow elongate ovals running anterior to and in parallel with the ventral ridges of the basal tubercles, and are separated medially in all but *Telmasaurus* by a ventrally contiguous surface running from the occipital condyle to the basisphenoid articulation. The condition in *Telmasaurus* is very similar to that seen in *Vulpesaurus* including the presence of the anteroventral eminence where the basioccipital meets the basisphenoid. It should be noted that the presence of these depressions in all taxa mentioned above coincides with the relatively posterior placement of the basal tubercles. Borsuk-Białynicka (1984) outlined a 'primitive type' of anguimorphan braincase which included basal tubercles located posteriorly, closer to the occipital condyle than to the base of the basipterygoid processes of the basisphenoid. Contrast this with more derived platynotans where the tubercles are roughly halfway between the occipital condyle and the basiptyerygoid processes, and in some cases, such as *Varanus* and *Lanthanotus*, where the tubercles abut the transverse contact with the basisphenoid. In the advanced condition, the absence of any ventral depressions anterior to the basal tubercles may be a direct result of the anterior migration of the latter. Borsuk-Białynicka (1984) noted and Bever et al. (2005) confirmed the presence of calcified cartilages associated with the distal surfaces of the basal tubercles. The texture of these surfaces on the basal tubercles of *Vulpesaurus* suggests a similar condition.

In dorsal view, the basioccipital is dominated by a central concavity forming the posterior floor of the braincase. Posterior to this lies the basioccipital portion of the foramen magnum flanked on either side by the dorsolaterally directed facets for contacting the otooccipitals which run anteriorly to a point just in front of the basal tubercles. At this point a second pair of facets, facing anterodorsally, receive the prootics. The dorsal surfaces of the basal tubercles are again hollowed out this time forming the ventral pockets of the occipital recesses, the posterior and anterior margins of which are not bounded by contact with the otooccipital or prootic. Contrast this with *Varanus*, *Heloderma*, *Lanthanotus*, and *Shinisaurus* (Conrad 2004; Bever et al. 2005) in which a prominent posterolateral crest (the crista tuberalis) as well as an anterior crest (crista interfenestralis of Säve-Söderbergh 1947) of the exoccipital attach to and contribute considerably to the posterodorsal surface of the basal tubercle and the anterior margin of the occipital recess respectively. As already mentioned, the sutural contact between the basioccipital and the otooccipital and prootic in *Vulpesaurus* is anteroposteriorly quite linear with only a modest lateral projection posterior to the occipital recess suggesting a reduced crista tuberalis of the otooccipital. The size and shape of the occipital recess is comparable with that of *Estesia* (Norrell and Gao 1997), though otooccipital-basioccipital contact in that taxon seems to show a greater contribution of the otooccipital to the dorsal surface of the basal tubercle. The basal tubercles of *Estesia* are also posterolaterally directed though much less ventrally inflected than in *Vulpesaurus*. In posterior view, the basioccipital can be seen to contribute the bulk of the articular surface (greater than one half) of the occipital condyle.

Otooccipital–The early ontogenetic fusion of the exoccipital and opisthotic result in a compound element here referred to as the otooccipital. This follows terminology used by Maisano (2001) and Conrad (2004) as opposed to the usage of the term exoccipital by Olerich (1956) and Norrell and Gao (1997). The anterolateral surface of the right otooccipital is visible lying lateral to the right supratemporal process of the parietal when viewed from above (Fig. 4-1). This element is nearly complete, missing only the ventrolateral extensions of the cristae tuberalis and interfenestralis, as well as the flange of bone that partially divides the vestibule from the lagenar recess and encompasses the perilymphatic foramen. Though damaged, the extent of the cristae tuberalis and interfenestralis can be assumed to have been rather small given the modest size of the facets where they contacted the basioccipital.

In posterior view (Fig. 4-17) the otooccipital contributes approximately one quarter of the occipital condyle and forms a substantial portion of the lateral margin of the foramen magnum. The large posterolaterally oriented paraoccipital process projects dorsolaterally from the foramen magnum and expands dorsoventrally toward its distal end. A flange of bone ascends anterodorsally from the paraoccipital process to contact the supraoccipital dorsomedially and the prootic dorsolaterally. A similar flange extends ventrally to form the crista tuberalis. Posterior to the crista tuberalis and near the base of the paraoccipital process there are three conspicuous foramina (Fig. 4-18). The uppermost foramen is the vagus foramen (cranial nerves X and XI) and is the largest of the three. Internally the vagus foramen forms a vertical slit that exits on the medial surface of the foramen magnum just posterior to the otic capsule. The two lower foramina are the hypoglossal foramina. The anterior hypoglossal foramen is bifurcated, as is not uncommon (Gao and Norrell 1998), while the posterior hypoglossal foramen is singular. All three branches of this nerve enter the braincase on the medial wall of the foramen magnum, below the vagus foramen.

In ventral view, the crista tuberalis is joined at an acute angle by the crista interfenestralis about midway along its length. The thin triangular space formed between them marks the posterolateral margin of the occipital recess (following the terminology of Norrell and Gao 1997; = recessus scala tympani of

Conrad 2004 and Bever et al. 2005), the base of which is formed by the basioccipital. The foramen rotundum is conspicuously absent from the preserved portion of the occipital recess. As such it can be presumed to have been located relatively far anterior within the otic recess as opposed to being near the apex of the triangular space formed by the cristae tuberalis and interfenestralis as is noted for *Shinisaurus* by Bever et al. (2005) and figured by Conrad (2004). Immediately ventral to the lagenar recess, the posterior margin of the perilymphatic foramen is preserved. Dorsal to the crista interfenestralis, a shallow depression covers the anterolateral surface of most of the paraoccipital process. Anteromedial to this depression lies a second smaller depression incorporating the posterior margin of the foramen ovalis.

In anterior view, the osseous capsule which would have housed the inner ear is clearly visible and bordered dorsomedially by a sutural facet for contact with the supraoccipital, and posterolaterally and anteromedially by facets for the contact with the right prootic. The vertically oriented flange of bone that would have partially separated the capsule into a dorsomedial vestibule and ventrolateral lagena has been broken away. A dorsally directed opening pierces the supraoccipital facet where the posterior semicircular canal passes through it into the body of the otoocipital. A second opening, for the passage of the horizontal semicircular canal, lies within the posterolateral facet for the prootic, just posterior to the vestibule. These two canals merge in the posterior ampullar recess, visible on the posterior wall of the vestibule interior.

Prootic–Both prootics are present though heavily damaged and lying beneath the posterior half of the parietal (Fig. 4-1). The right prootic has undergone less fracturing and is basically complete though its medial surface is too occluded by other fractured bone and matrix to be effectively isolated with HRXCT. In lateral view (Fig. 4-19), the right prootic presents the tri-radiate outline typical of scleroglossans with a considerably well-developed alar process (= crista alaris prootica of Conrad 2004), an equally large posterior process (= paroccipital process of Jollie 1960) and a less well-developed anterior inferior process. The alar and inferior processes outline the trigeminal notch, just posterior to which lies the bulbous swelling of the anterior ampullary recess located at the base of the alar process. A modest crista prootica runs anteroventrally, from the posteroventral tip of the posterior process, to about the midpoint of the prootic where it becomes confluent with the body of the element. Medial to the ventral terminus of this crest lies a single large facial foramen.

As already noted, the preserved braincase elements of *Vulpesaurus* are completely disarticulated, and though facets showing sutural contact with other elements are largely preserved, the posteroventral edges of the right prootic, where it would have contacted the right otooccipital and the basioccipital, appear to have been eroded somewhat. Despite this, the anterodorsal border of the fenestra ovalis is preserved lying along this margin, posteroventral to the crista prootica and at about the same level as the anterior ampullary recess. Additional damage includes two fractures: one through the main body of the prootic, starting midway along the dorsal margin and crossing the crista prootica just anterior to the fenestra ovalis, and one cleaving the base of the alar process and running through the middle of the anterior ampullary recess. Only the later fracture causes distortion in the form of a slight torsional displacement of the alar process.

The prootic is typically anguimorph, with a robust, laterally compressed and anterodorsally projecting alar process, formed by a vertical flange of membrane bone that would have buttressed medially the dorsal tip of the epipterygoid and closely approached the descensus parietalis. The base of the alar process is not offset from the trigeminal notch by a supratrigeminal process though the damaged anterolateral surface of the anterior ampullary recess suggests the rudiments of such a structure. The crista prootica is oriented in a posterodorsal to anteroventral direction and is modestly developed in comparison to *Varanus*, though comparable with that of other platynotans. Unlike other platynotans observed, the crista prootica terminates immediately anterior to the facial foramen, leaving the lower lateral surface of the prootic smooth. As such, the lower portion of the recessus vena jugularis is indistinct and the ‘carotid fossa’ of Norell and Gao (1997), cited by those authors as present in anguids, reduced in xenosaurs, *Shinisaurus*, and *Heloderma*, and lost in *Varanus*, is completely absent here. Conrad (2004, pg.423) reported a similar state for *Shinisaurus*: “The crista prootica becomes confluent with the main body of the prootic as [sic] the anterior margin of the facial foramen”, though figure 14.A of the same paper clearly illustrates the crest continuing anteroventrally to the level of the posterior Vidian canal located in the basisphenoid. Bever et al.

(2005) confirm that the crista prootica of *Shinisaurus* does indeed span the length of the prootic, reaching the clinoid process of the sphenoid, though they also point out its relatively lesser development in the region below the facial foramen. Loss of the crista prootica below the level of the facial foramen results in a somewhat simplified articulation with the basisphenoid. In all other anguimorphans observed, the lowest anterior tip of the prootic, includes a ventrally directed spur of bone that laterally overlaps a portion of the clinoid process of the basisphenoid. This spur is typically located at the anteroventral terminus of the crista prootica. In *Vulpesaurus*, where no lower extension of the crista prootica exists, there remains only a weakly developed spur located on the ventrolateral edge of the inferior process of the prootic.

Borsuk-Białynicka (1984) cited the extension of the posterior process of the prootic toward the dorsal tip of the paroccipital process in combination with a well-developed anterodorsally directed alar process, as plesiomorphic for anguimorphs, though with an increasingly steep angle of the recessus vena jugularis, and larger and more dorsally directed alar processes, being indicative of more derived platynotans. Orientation of these features is problematic when dealing with isolated elements as the natural position of the feature is unknown, and the clinal nature of the character being examined allows for a mere tilt of the head to alter ones perception of that orientation from sub-vertical to sub-horizontal. However, the relative angulation created between the crista prootica and the alar process is unaffected by orientation and does appear to become increasingly acute within Platynota, when compared to anguids and xenosaurs, with *Varanus* displaying the most advanced (acute) state. The condition of these features in *Vulpesaurus* suggest its platynotan affinity, with the overall morphology of the prootic resembling most that of *Shinisaurus*.

Basisphenoid–The ventral surface of the basisphenoid of *Vulpesaurus* (Fig. 4-21) is visible on the ventral side of the prepared specimen (Fig. 4-2). Though there is some damage to both the posterior basioccipital processes, those elements are present, and the entire basisphenoid is intact including a well-developed and ossified parasphenoid rostrum.

Immediately apparent in the prepared specimen, is the unique nature of the basipterygoid processes, with their broadly rounded distal surfaces spanning the entire flank of the basisphenoid, and their tight association to the sphenoid body, lacking any discernable, constriction or neck (Fig. 4-20). The distal surfaces of these processes are comprised of cancellous bone in keeping with the presence of cartilaginous pads that would have mediated a synovial joint between the braincase and the pterygoids of the dermal palate. Typical of lepidosaurs (Romer 1956), the basipterygoid processes project ventrolaterally to the point of pterygoid articulation. However, in most squamates that possess them, the basipterygoid processes pass through a constricted ‘neck’ region as they project away from the base of the sphenoid, before expanding at their distal tip where contact with the pterygoids occurs. No such constriction exists on the basipterygoid processes of *Vulpesaurus*. Rather, the basipterygoid processes expand nearly equally in anterior, lateral and even posterior directions, fanning out from the otherwise triangular base of the basisphenoid combining to create a sub-circular shape in ventral view. In this way, excluding the parasphenoid rostrum and the basioccipital processes, the basipterygoid processes are anteroposteriorly longer than the base of the basisphenoid itself. The ventral surfaces of the basipterygoid processes and that of the basisphenoid proper are contiguous and concave; gently so in the processes, and more greatly so in the body, forming a trough that tapers anteriorly where the base of the parasphenoid rostrum curves dorsally. On either side, ventral to the sutural contact with the basioccipital, there are two triangular tongues of bone, each partially separated from the posterior tips of the basipterygoid processes by a sharp sulcus. Much thinner than the basipterygoid processes, these projections appear not to articulate with any portion of the basioccipital, but rather, project posteroventrally, filling in the space between the basioccipital facet and the posterior tips of the basipterygoid processes.

In lateral view, the ovate articular surface of the basipterygoid process thickens considerably in its anterior half. The upper half of the thickened articular surface also inclines, sloping posteromedially toward the lateral wall of the basisphenoid. With the floor of the braincase horizontal, and the parasphenoid rostrum directed anteriorly, the ventral surface of the basipterygoid process slopes anteroventrally, but only slightly. From the curved upper margin of its distal tip, the dorsal surface of the basipterygoid process proceeds medially to the base of the lateral wall (or alar process) of the basisphenoid where it curls dorsally and laterally, creating a deep sulcus. Anterodorsally, this ala forms a distinct but weakly developed clinoid process, while the posterior portion tapers into a ventrolaterally curving and posteriorly directed basioccipital process. This process is of considerable length and would have sutured onto the anterolateral surface of the basal tubercle of the basioccipital, nearly reaching the tip of the tubercle. Such basioccipital processes occur in all known anguimorphans though they are much less extensive in *Lanthanotus* and *Varanus*, likely as a result of the anterior migration of the basal tubera in those taxa.

The posterior opening for the vidian canal lies within a fossa formed between the basioccipital process above, and the posterior end of the basipterygoid process below, and is obscured from lateral view. The medial wall of this fossa is formed by a vertical strut of bone that joins the dorsal surface of the posterolaterally projecting tongue that adjoins the basipterygoid process, to the ventromedial surface of the base of the basioccipital process. Medial to this strut, and lateral to the posterior end of the body of the basisphenoid, a deep pocket exists, similar in size and orientation to the fossa that bears the posterior opening of the vidian canal, but housing no such foramen itself. The presence of a blind pocket, medial to the posterior opening of the vidian canal is not observed in other platynotans. The anterior opening of the vidian canal emerges where the bases of the basipterygoid process and the parasphenoid rostrum meet, with a distinct sulcus running anterior to the opening along the ventrolateral edge of the crista trabecularis. Dorsal and medial to the anterior openings of the vidian canals, and lying within the pituitary fossa, are the openings for the internal carotid arteries. These lie along the lateral wall of the pituitary fossa and are not widely separated from the common carotid/vidian canal. The pituitary fossa itself, its margins clearly defined, is relatively deep and quite cylindrical compared to that of other platynotans. The cristae trabeculae are tall, forming the ventral and lateral walls of this cylinder, and in their posterior reaches are met dorsally by the overhanging dorsum sella. The latter is weakly developed and forms an anteriorly projecting point at its center. The anterior extension of the parasphenoid rostrum is considerable, its anterior tip exceeding those of the basipterygoid processes. The dorsum sella is pierced on either side by short canals transmitting the abducens nerve (cranial nerve VI) from the lateral interior floor of the braincase. The anterior openings of these canals lie dorsal to the anterior openings of the vidian canals, lateral to the pituitary fossa and ventral to the clinoid processes. The interior floor of the braincase is typically concave and bordered anterolaterally by the prootic facets and posterolaterally and posteriorly by the occipital facet. The latter is complete and transverse across the posterior midline indicating the closure of the basicranial fontanelle.

Mandible

Surangular–The mandible of *Vulpesaurus* is represented by two preserved elements, the right surangular and splenial (Fig. 4-22). Separated from the cranial block, the right surangular is free of matrix, visible on all surfaces and complete save for the anterior most portion that would have articulated medial to the posterolateral wall of the right dentary. The surangular is typically platynotan in that in that the exposed lateral surface is rounded at its anterior tip with clear articular surfaces for posteriorly projecting angular and surangular processes of the dentary. Overlap between the two elements appears limited though the broken anterior tip of the surangular makes interpretation of the presence or absence of intramandibular mobility difficult to assess. A dorsal ridge positioned at approximately one quarter of the total length from the anterior tip marks the point at which the posterior ramus of the coronoid descends posteromedially to attach to the medial side of the surangular just anterior to the adductor fossa. The anterior position of the coronoid relative to the anterior tip of the lateral surface of the surangular visible in articulation indicates a primitive condition in which the surangular does not extend well past the coronoid eminence. Long ventromedial and ventrolateral facets receive the prearticular and angular, respectively, a sharp uninterrupted ventral crest separating them for their entire length. This arrangement resembles that of *Varanus* and *Lanthanotus* where the prearticular is largely excluded from the lateral surface of the mandible being visible only on the posteroventral border. The anterior surangular foramen lies on the lateral surface just ventral to the coronoid crest much as it does in *Heloderma*, with the surangular forming all but its anteriormost border which would be formed by the coronoid. The posterior half of the dorsomedial edge of the surangular, together with the facets for the prearticular and coronoid, outlines the elongate adductor fossa typical of platynotans. A large posterior surangular foramen lies within the adductor fossa halfway between the articular facet and coronoid facet. The width of the adductor fossa, and any possible medial expansion of same, cannot be established with certainty but the degree of dorsal overhang contributed by the surangular strongly suggests it was narrow in dorsal view. The posterior half of the surangular gently curves medially and its lateral surface bears a posterolateral process while its medial surface turns abruptly inward. These two processes form a buttressing facet cupping the anterior and lateral surfaces of the articular and its glenoid surface. The posterodorsal margin of the glenoid buttress is raised only slightly, and closely resembles *Varanus* and *Heloderma* in this respect. In general shape and proportion, the surangular of *Vulpesaurus* appears primitively platynotan in possessing reduced surangular-dentary overlap with an anteriorly displaced coronoid eminence.

Splenial–The right splenial (Fig. 4-23) can be seen in ventral view (Fig. 4-2) lying transversely beneath the parietal just posterior to the pineal foramen. A thin and delicate sheet of bone, its dorsal and ventral margins are largely intact indicating a loose cartilaginous connection with the dentary. The splenial is approximately 75% the length of the surangular and the two elements combined with a small amount of pre-coronoid overlap assumed would measure approximately 30 mm; this then, is the minimum mandibular length anterior to the glenoid articulation with the quadrate. However, as is the case with other anguimorphans, the splenial of *Vulpesaurus* would likely not have extended far beyond the mid-point of the dentary and a total mandibular length (excluding the retroarticular process) of 35-40 mm may safely be assumed. Although long, this estimate correlates favorably with the elongation of the palate indicated by the length of the palatine process of the pterygoid and the vomer described above.

Axial Skeleton

Cervical Vertebrae–The right half of the neural arch of the atlas is preserved, lying beneath the right otoocipital just lateral to the right supratemporal process of the parietal (Fig. 4-2). It resembles that of other anguimorphans in having a large dorsomedially projecting fan-like plate attached to a block of bone with anteromedial and posteromedial facets for articulation with the occipital condyle of the skull and the odontoid process of the axis respectively. Like other anguimorphs there are two posterolateral processes, one projecting from the posteroventral margin of the dorsal fan-like process and one from the posterior margin of the body of the atlas just posterolateral to the odontoid facet. The second of these is larger and proportionately resembles more the condition seen in varanoids than anguids (Rieppel 1980a).

The axis of RSM P 2622.2 is not preserved but the third and fourth cervicals are present and well preserved in the cranial block just posterior to the basioccipital. (Fig. 4-1). Of the two, C3 (Fig. 4-24) is better preserved its dorsal surface and anterior cotyle visible in dorsal view. Both cervical centra are quite short in comparison to the dorsal vertebrae and to the cervicals of other basal *Shinisaurus*, resembling more the proportions of anguids (specifically *Gerrhonotus*), *Lanthanotus* (Rieppel 1980b) and *Heloderma*. Despite this, they appear otherwise platynotan, with a large and posteriorly located ventral hypapophysis bearing a facet for the cervical intercentrum covering more than half of the ventral surface. The lack of fusion of the cervical intercentrum is shared with crown varanoids and *Necrosaurus* though the state of this character is not known for other platynotans. Also similar to *Necrosaurus* is the presence of pseudozygosphenes, a character shared with *Saniwa* though lost in *Varanus*. The neural spine is broadly based, tapers posterodorsally to overhang the condyle and is not particularly elongate. There is some anteroposterior expansion of the neural spine, its anterior margin being broadly convex as opposed to concave as is the case in *Shinisaurus*, *Lanthanotus* and *Heloderma*. Anteroposterior expansion of neural spines is found in *Saniwa* and *Varanus*, though in those taxa the dorsal apex of the spine remains expanded and does not taper nor does it project posteriorly to overhang the condyle as is the condition in *Vulpesaurus*. The pre- and postzygapophyses are deep and elevated from the horizontal plane at about 45 degrees. The synapophyses is large and broad on its distal tip which is oriented slightly oblique to the horizontal plane. The condyle and cotyle are modestly dorsoventrally depressed and show only slight obliquity. The condyle lacks any expansion or flare and a precondylar constriction is absent.

Dorsal Vertebrae–The dorsal vertebrae are somewhat more elongate than the cervicals and are slightly concave on their ventral surface. The pre- and postzygapophyses are less inclined than in the cervical vertebrae and pseudozygosphenes remain present. The neural crest follows the pattern seen in the cervical region, forming a low convex arch in lateral view with its apex placed at the posterior tip. The centrum shape in ventral view is columnar with a slight lateral flare occurring below the vertically oriented synapophyses, and appears primitive relative to the more broadly triangular form seen in

Necrosaurus. Apart from the pseudozygosphenes and unique neural crest morphology, the dorsal vertebrae appear very similar to *Shinisaurus*.

DISCUSSION

Like most basal platynotans *Vulpesaurus magdalenae* exhibits a mixture of primitive and derived platynotan characters. It bears no clear resemblance to any of the crown varanoids and likely lies on the platynotan stem leading to Varanoidea. Some similarities it shares with *Necrosaurus* support this placement and include: cervical hypapophyses with free epiphyses; pseudozygosphenes and an anteroposteriorly expanded neural spine base; toothed pterygoids and dorsally attached adductor musculature; and varanoid features of the dentition such as interdental tooth replacement, trenchant teeth with expanded bases and lack of resorption pits. Also shared with *Necrosaurus* (and *Bahndwivici* as well) is the general shape of the parietal and posterior constriction of the parietal table. *Vulpesaurus* differs from *Necrosaurus* and all other basal platynotans from North America in the total absence of any evidence for osteodermal ornamentation.

The dentition of *Vulpesaurus*, insofar as it can be examined, shares some features with the late Cretaceous form *Colpodontosaurus*, and the late Paleocene *Provaranosaurus*. This is important to consider as both of these taxa are known exclusively from maxillary and dentary material, elements lacking adequate representation in *Vulpesaurus*, and in light of the temporal and geographical overlap between *Colpodontosaurus* and *Vulpesaurus.* The latter may be distinguished from the former based on the size of the teeth, being larger and more widely spaced, and on presence of higher, clearly trenchant, tooth crowns (Estes 1983; Gao and Fox 1997). These last two features are shared with *Provaranosaurus* though the crowns of *Vulpesaurus* are again much larger and not needle-like as in the Paleocene form (Estes 1983). Thus assignment of RSMP P 2622.2 to either of these taxa can be ruled out but a close relationship may be considered on the basis of the very thin tooth walls and the apparent lack of plicidentine. Without further evidence, either in the form of tooth-bearing elements of *Vulpesaurus* or palatal, skull roofing, or braincase elements of *Colpodontosaurus* and *Provaranosaurs*, little can be said of the specific interrelationships of these three North American basal platynotans other than that they may be distinguished from one another at the level of species.

One other major aspect of *Vulpesaurus'* cranial anatomy differing markedly from the pattern seen in most basal platynotans warrants discussion and requires some degree of interpretive reconstruction.

Palatal reconstruction and a narrow elongate skull–As noted in the description given for *Vulpesaurus* above, the palatine process of the pterygoid is very elongate and forms a thin lamella of bone in its anterior one third. A similar condition is observed in *Platecarpus planifrons* Cope, 1874 whereby thin anterior processes of the palatine and pterygoid overlap the vomer from its posterolateral side (Konishi and Caldwell 2007) indicating a pterygoid-vomer contact. As pointed out by Konishi and Caldwell (2007), a vomerine-pterygoid contact is otherwise unknown for Squamata (see Romer 1956). However, given the extreme length and thin lamellar structure of the palatine process of the ptyerygoid observed in *Vulpesaurus,* as well as the considerable length of the accompanying vomer, some degree of overlap between these two elements might be presumed. Alternatively, if aligned tip to tip with no overlap, the combined length of the pterygoid and vomer would reconstruct an antorbital palate of roughly 50% total skull length; a condition seen only in some species *Varanus* (Mertens 1942), within Mosasauroidea, and in *Eosaniwa koehni* Haubold 1977, an enigmatic platynotan from the mid-Eocene of Germany (Geiseltal) known to possess an extremely elongate rostral region (Rieppel et al. 2007). While the possession of such an elongated rostrum in *Vulpesaurus* cannot be ruled out, the close resemblance of the palatine process of the pterygoid with that of *Platecarpus planifrons*, in respect not only to its length but also in the thin lamellar structure of its anterior extension, leads the author to conclude that a vomerine-pterygoid contact was likely present in *Vulpesaurus*.

A second aspect of palatal reconstruction that needs to be addressed is the nature of the palatobasal articulation between the pterygoids and the basisphenoid. The distal (potentially articular) surfaces of the basipterygoid processes of the basisphenoid are anteroposteriorly elongate, covering the entire length of the basisphenoid. As preserved, the corresponding surface of the pterygoid notch appears typically platynotan with a discrete posteromedially facing sulcus, bordered anteromedially by a medial projection preventing anterior dislocation of the sphenoid relative to the pterygoid. As such, the pterygoids would appear to articulate only with the anterolateral most surfaces of the basipterygoid. The anterior tip of the basipterygoid processes is thickened at the point of presumed contact and the articular surface curves posterodorsally conforming to the interior surface of the pterygoid notch. As a consequence of the lack of anteroventral extension of basipterygoid processes, the pterygoids are placed more medially than is typical and the interpterygoid vacuity (pyriform recess) is significantly narrowed. This is corroborated by the increased lateral inflection seen in the quadrate processes of the pterygoids as they angle more sharply to achieve the width required to abut the quadrates, and by the relatively narrow shape of the parietal. Thus the interpretation of the skull of *Vulpesaurus* as relatively long and narrow seems well supported.

Even under the presumption of vomerine-pterygoid overlap, the rostrum of *Vulpesaurus* could be considered elongate for a basal platynotan. Both the palatal reconstruction and the estimated (pre-glenoid) mandibular length of 35-40 mm suggest that *Vulpesaurus* possessed a rostral extension similar to *Varanus* and proportionately longer than any other North American platynotan. A total skull length is estimated at approximately 45-50 mm.

CONCLUSIONS

Beyond possessing a suite of dental characters common within Platynota and suggesting a predaceous habit, little can be said of the life history of *Vulpesaurus magdalenae*. Some features of the braincase and palate of *Vulpesaurus* are unique among terrestrial platynotans but resemble closely those of mosasaurs. Lee (1997) constructed characters relating to the basipterygoid processes of the basisphenoid in mosasaurs, that describe these processes in *Vulpesaurus* equally well. The broad fan-like shape of the basipterygoid processes, lacking basal constriction or anteroventral extension away from the body of the basisphenoid, are characteristic of mosasaurs and ophidians and are otherwise unknown in terrestrial platynotans. Also the general shape of the pterygoid and the topological relationships of the surrounding elements as interpreted above match closely those reported for *Platecarpus* (Konishi and Caldwell 2007). Phylogenetic hypotheses placing mosasaurs within Platynota have a long history (Baur 1890; Camp 1923; McDowell and Bogert 1954; Rieppel 1980a; Lee 1997; Rieppel et al. 2007; Conrad 2008, Conrad et al. 2010), though the inclusion of Mosasauroidea within Platynota is far from universally accepted (Gauthier 1982; Pregill et al. 1986; Caldwell 1999, 2000, 2012; Gauthier et al 2012). In light of this and the characters discussed above, an analysis of the phylogenetic position of *Vulpesaurus magdalenae* in the context of an Anguimorpha inclusive of the mosasauroid genus *Aigialosaurus* Kramberger 1892 (Dutchak and Caldwell 2006, 2009) and the closely related *Pontosaurus* Kramberger 1892 (Pierce and Caldwell 2004; Caldwell 2006) will be undertaken in the following chapter.

FIGURE 4-1. 3D Volume rendering of the cranial block of RSMP P2622.2 in dorsal view. Scale bar = 10mm.

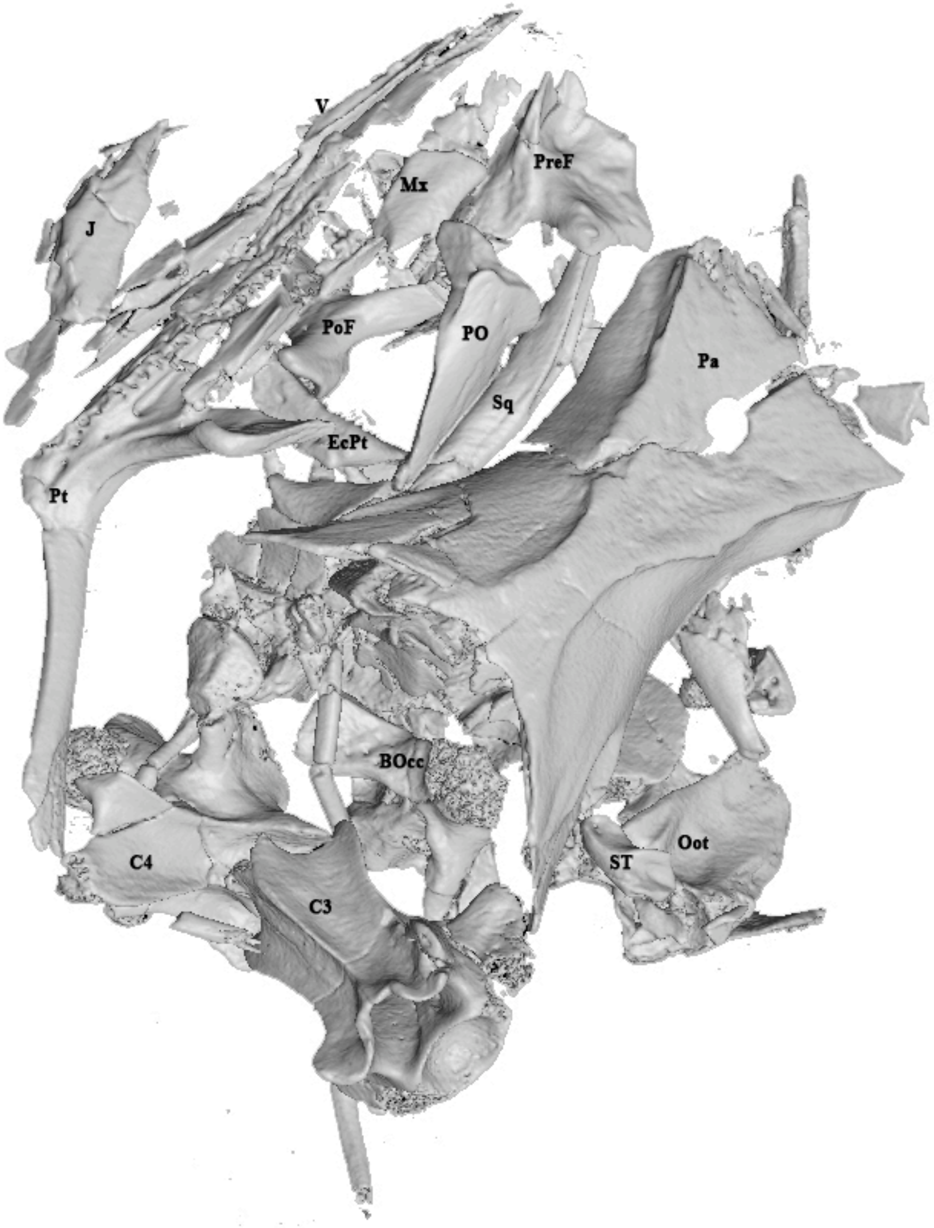

V
PreF
Mx
J
PoF
PO
Pa
Sq
EcPt
Pt
BOcc
Oot
ST
C4
C3

FIGURE 4-2. 3D Volume rendering of the cranial block of RSMP P2622.2 in ventral view. Scale bar = 10mm.

PreF
Mx
V
J
Pa
Sq
PO
PoF
EcPt
Pt
Spl
Sph
Pro
C4
Oot
Atl
BOcc
C3

FIGURE 4-3. Map inset showing the location of the Killdeer Badlands Locality within the East Bloch of Grasslands National Park, Saskatchewan where RSMP P2622.2 was collected.

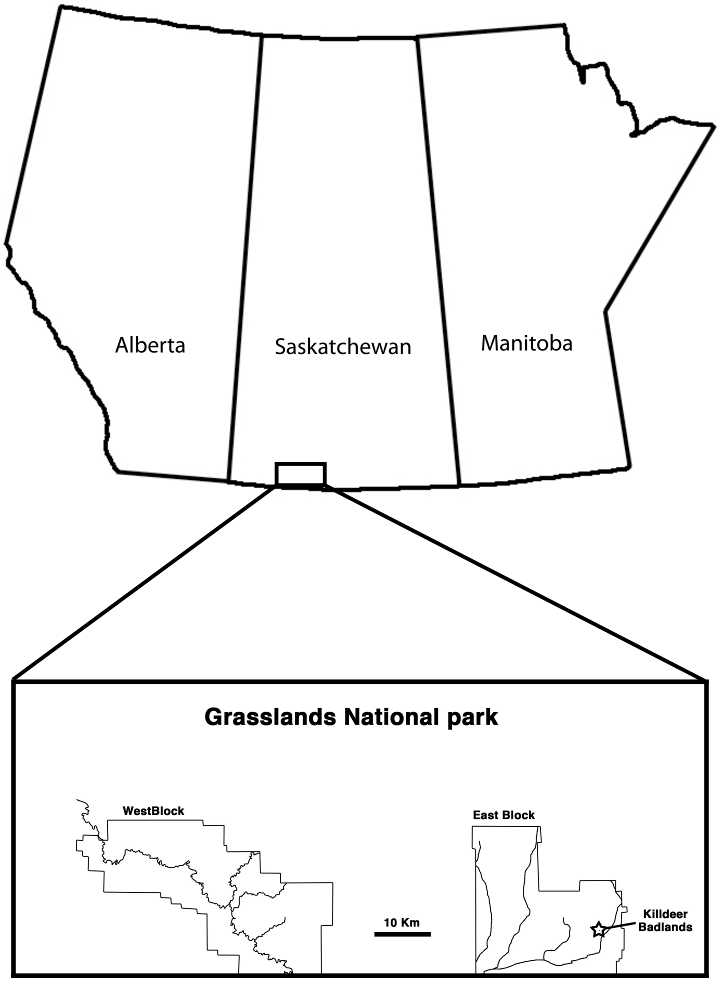
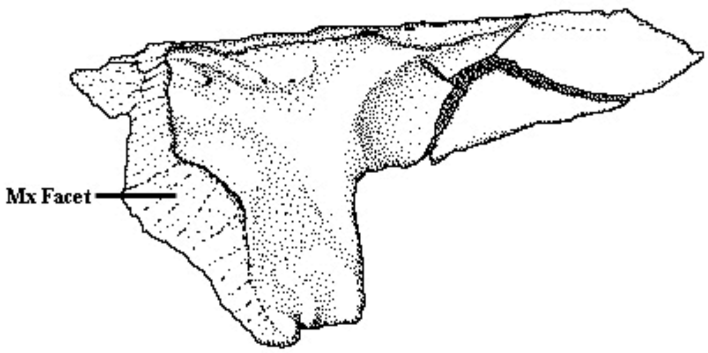
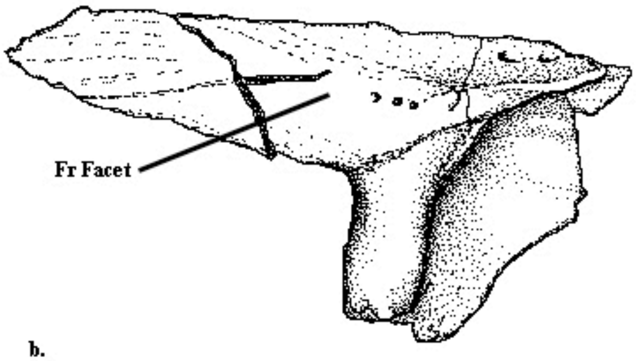

Alberta
Saskatchewan
Manitoba
Grasslands National park
WestBlock
East Block
10 Km
Killdeer Badlands

FIGURE 4-4. Left prefrontal in a. lateral view and b. medial view. Scale bar = 10mm.



a.



b.

FIGURE 4-5. Parietal in dorsal view. Scale bar = 10mm.

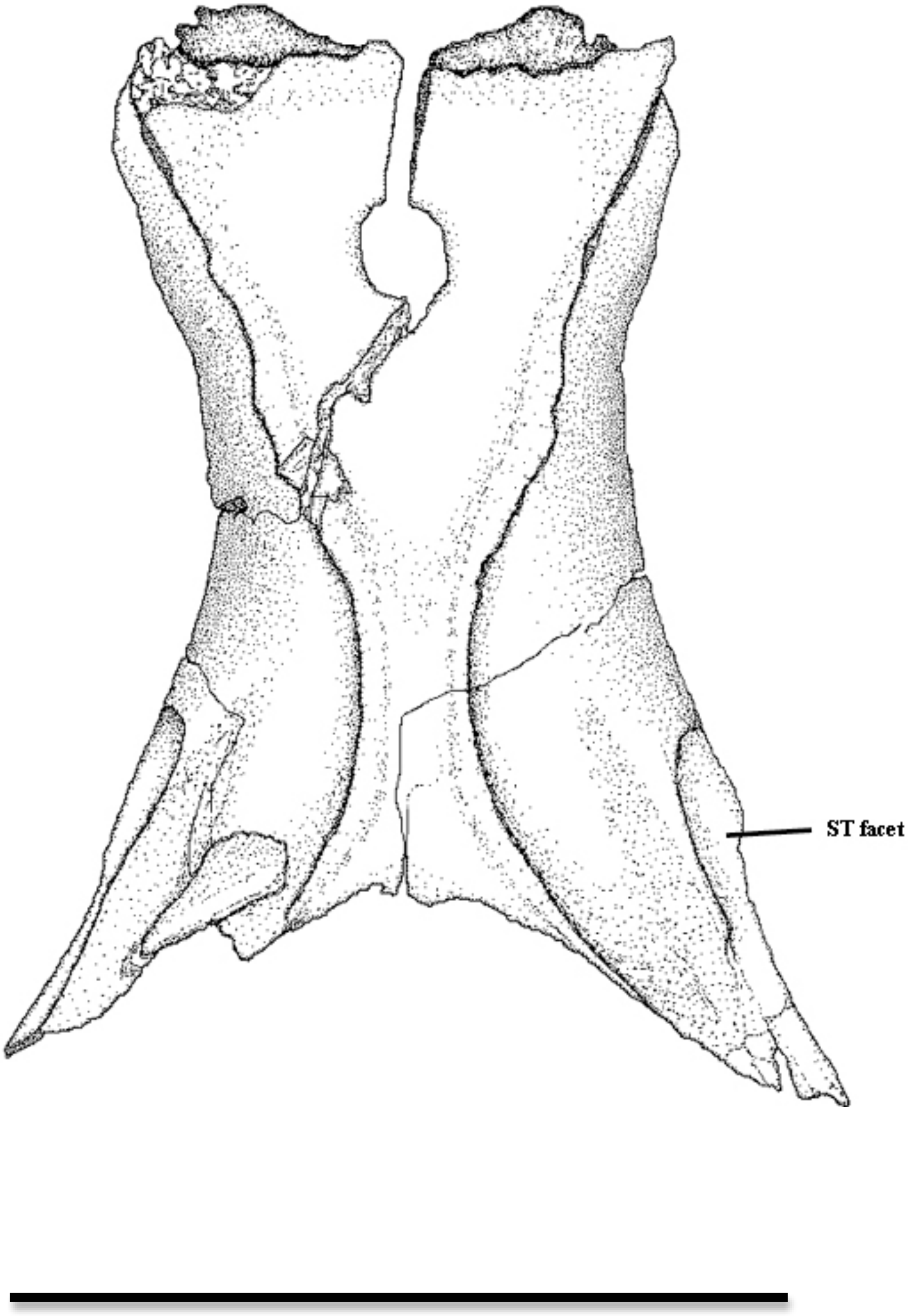

ST facet

FIGURE 4-6. Parietal in ventral view. Scale bar = 10mm.

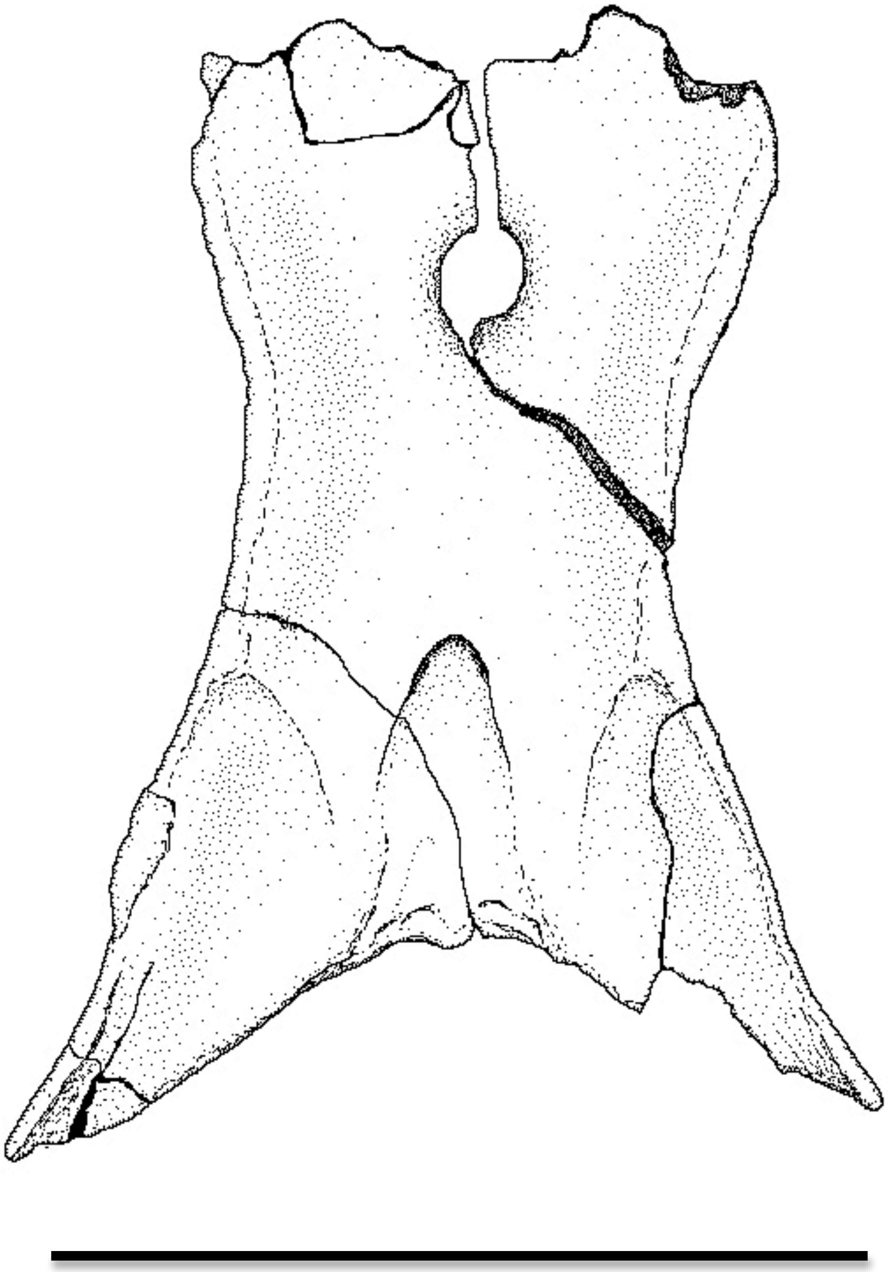


FIGURE 4-7. Parietal in right lateral view. Scale bar = 10 mm.

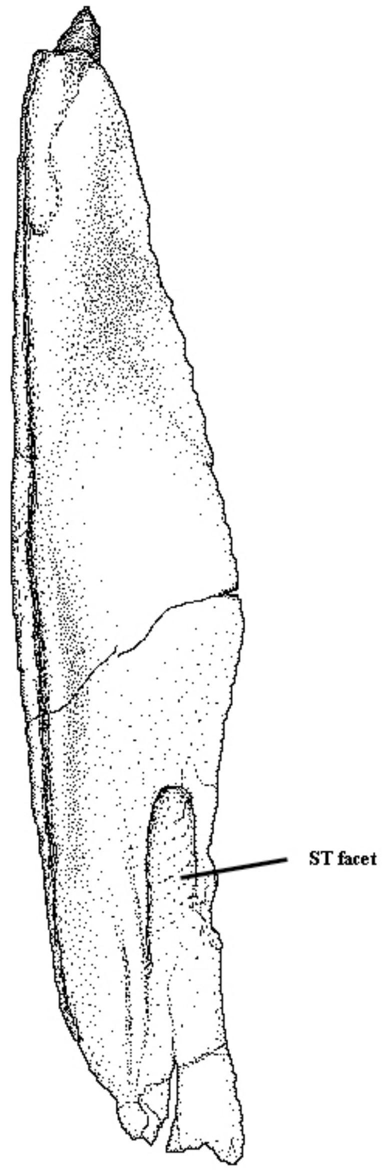
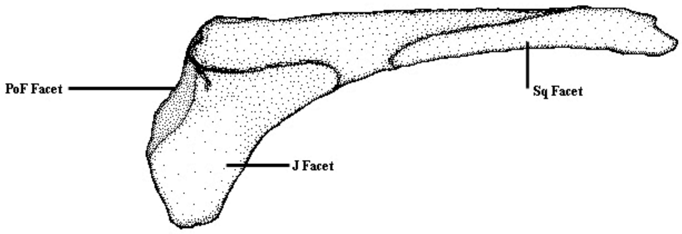
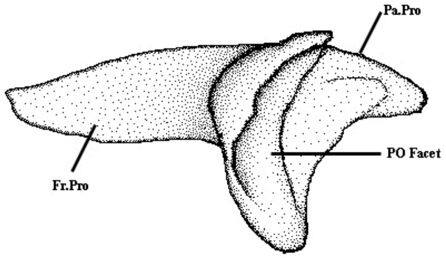

ST facet

FIGURE 4-8. Lateral views of a. left postorbital and b. left postfrontal. Scale bar = 10mm.

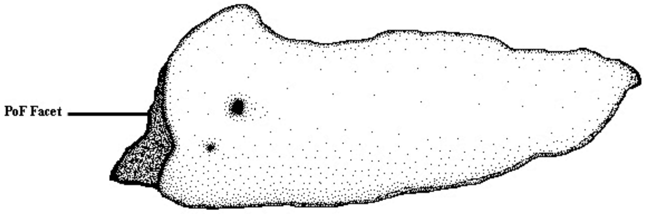


a.

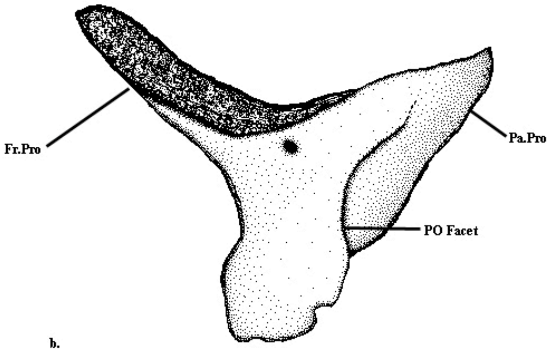


b.

FIGURE 4-9. Dorsal views of a. left postorbital and b. left postfrontal. Scale bar = 10mm.



a.



b.

FIGURE 4-10. Anterior tip of left jugal. Scale bar = 10mm.

FIGURE 4-11. Left pterygoid in ventral view. Scale bar = 10mm.

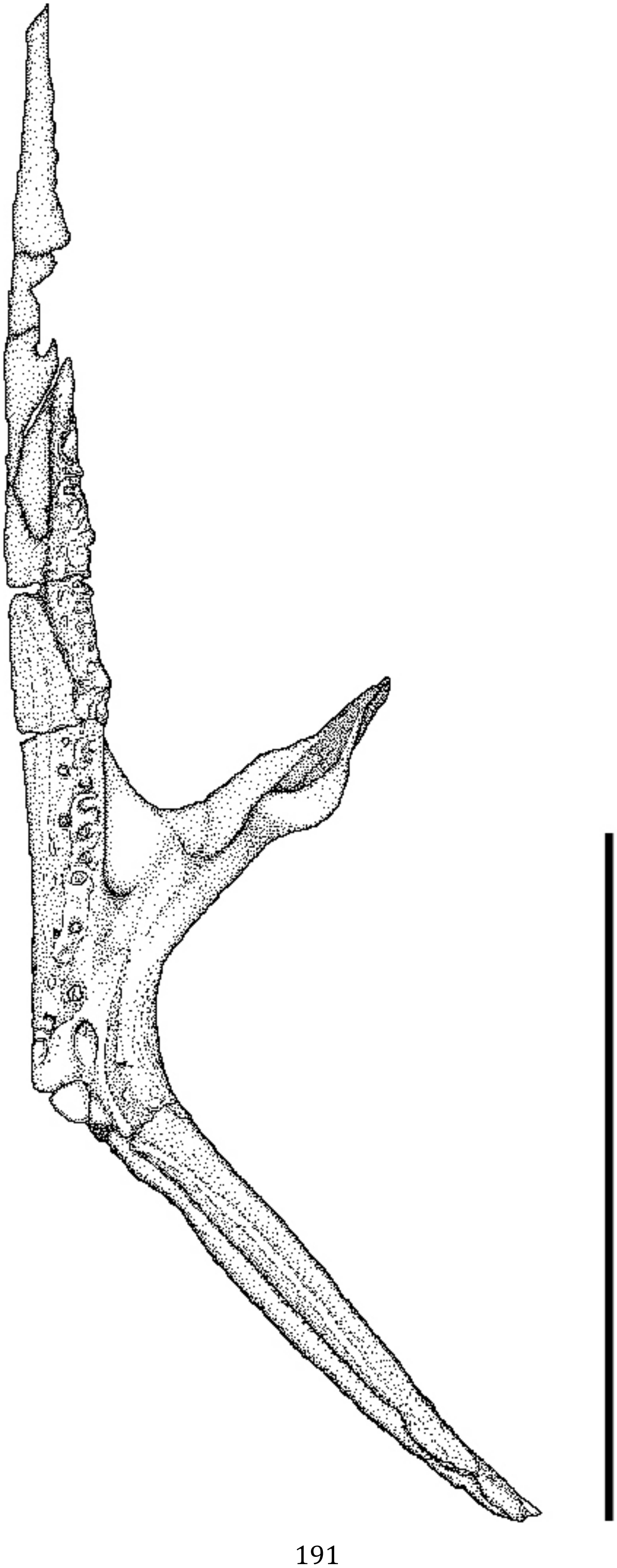


FIGURE 4-12. Left pterygoid in dorsal view. Scale bar = 10mm.

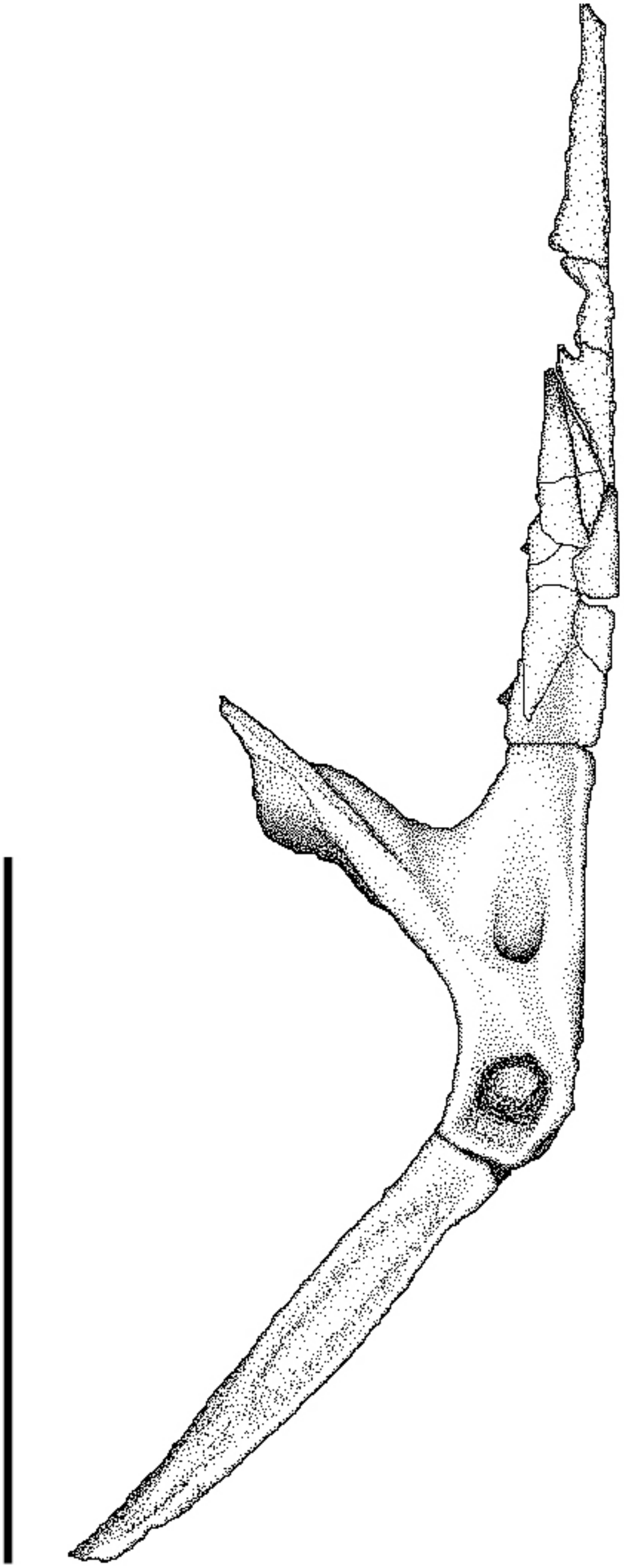
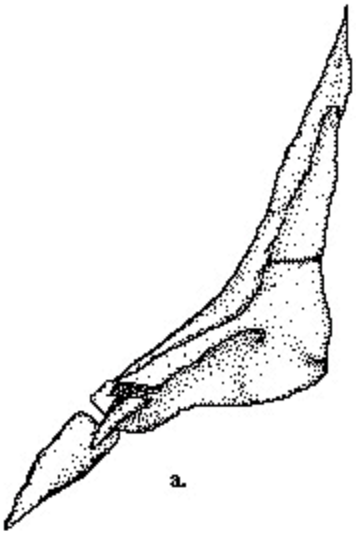
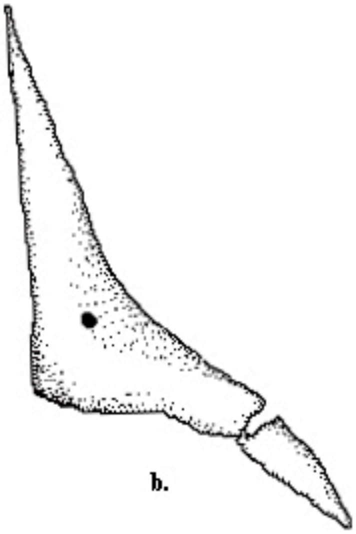


FIGURE 4-13. Right ectopterygoid in a. dorsal view and b. ventral view. Scale bar = 10mm.



a.



b.

FIGURE 4-14. Left vomer in a. dorsal view and b. ventral view. Scale bar = 10mm.

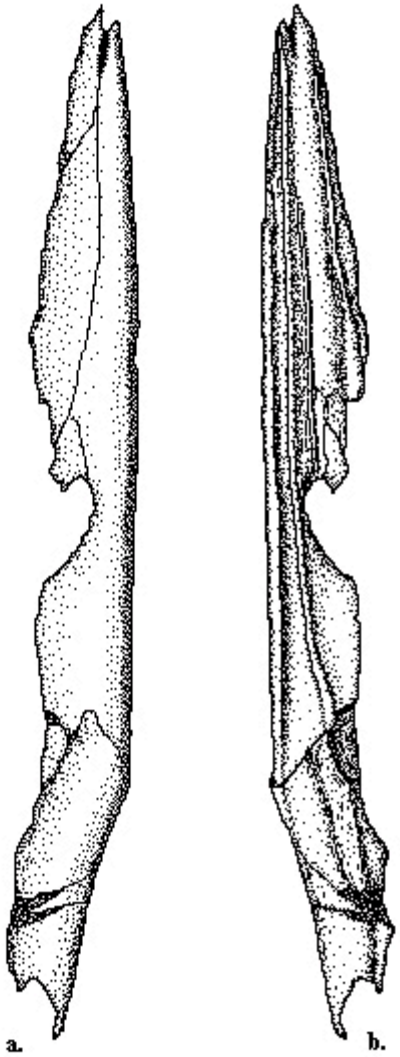
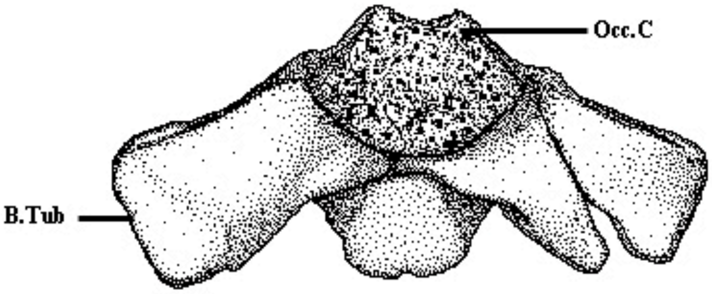
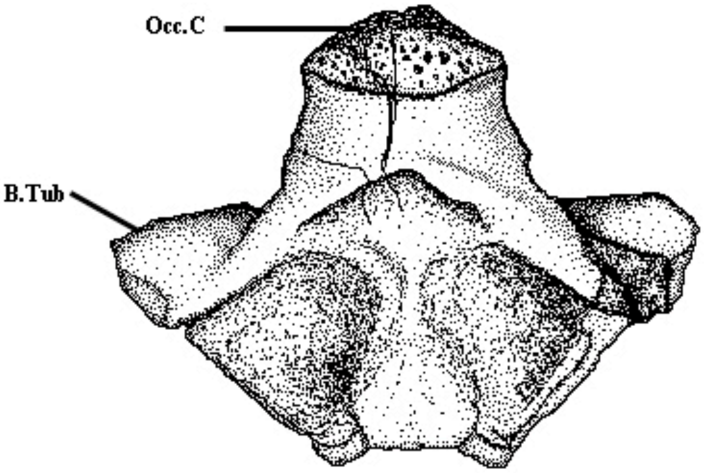

a.
b.

FIGURE 4-15. Basioccipital in a. posterior view and b. ventral view. Scale bar = 10mm.

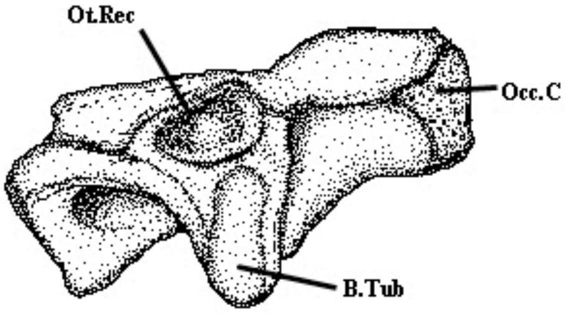


a.

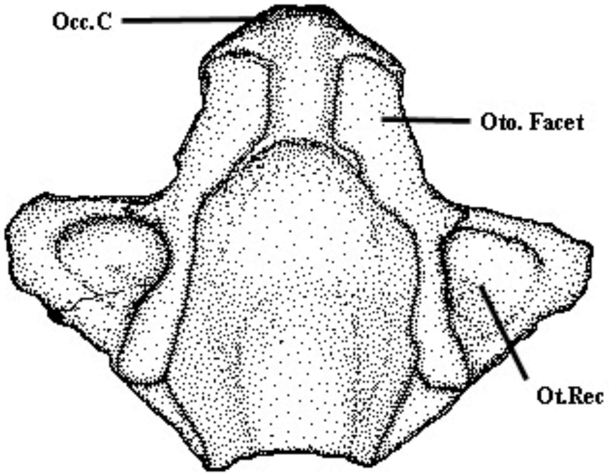


b.

FIGURE 4-16. Basioccipital in a. left lateral and b. dorsal view. Scale bar = 10mm.

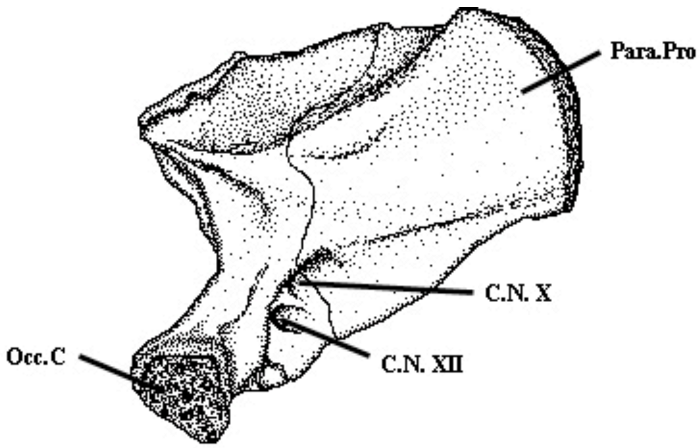


a.

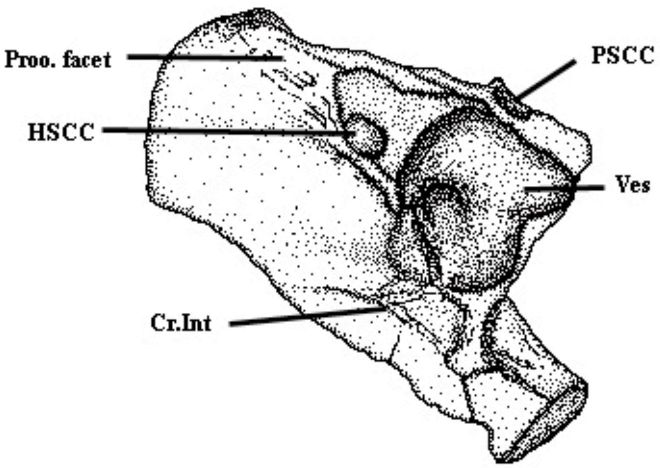


b.

FIGURE 4-17. Right otooccipital in a. posterior view and b. anterior view. Scale bar = 10mm.



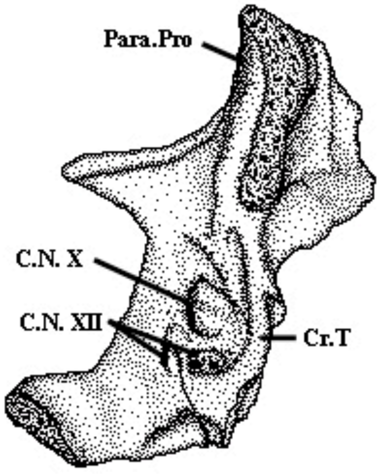
a.



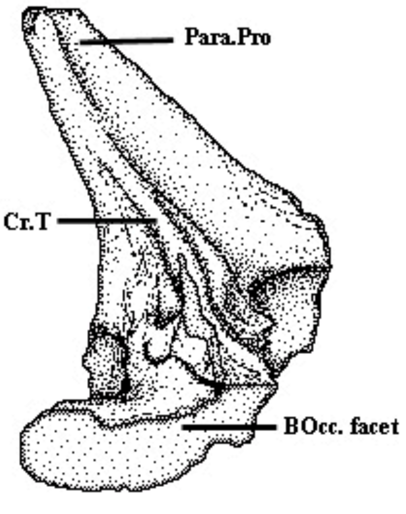
b.

FIGURE 4-18. Right otooccipital in a. oblique lateral view and b. ventral view.

Scale bar = 10mm.



a.



b.

FIGURE 4-19. Right prootic in lateral view. Scale bar = 10mm.

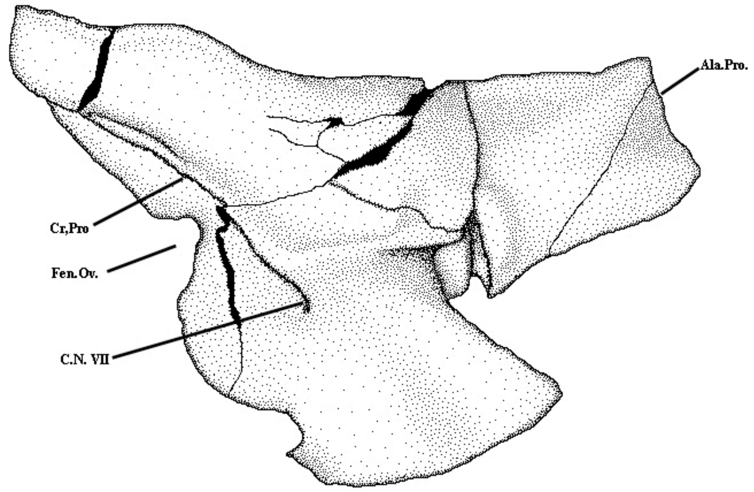
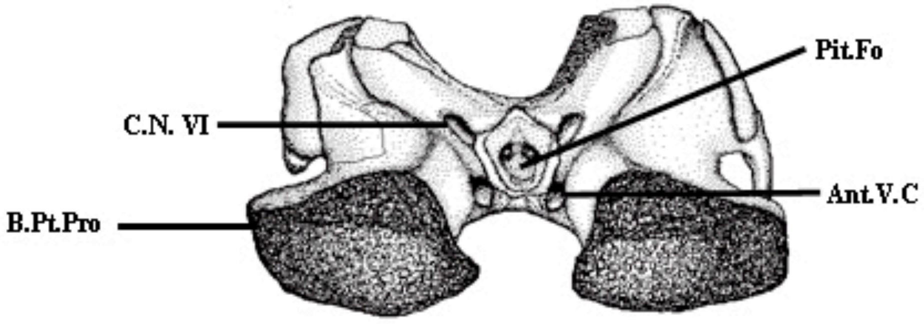
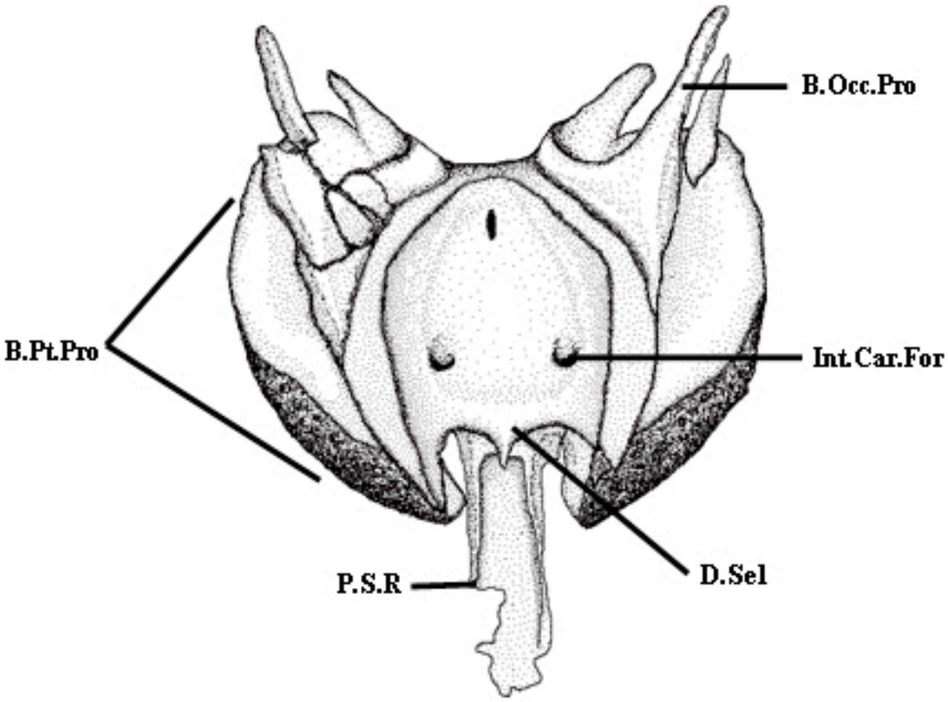

Ala.Pro.
Cr,Pro
Fen. Ov.
C.N. VII

FIGURE 4-20. Basisphenoid in a. anterior view and b. dorsal view. Scale bar = 10mm.



a.



b.

FIGURE 4-21. Basisphenoid in ventral view. Scale bar = 10mm.

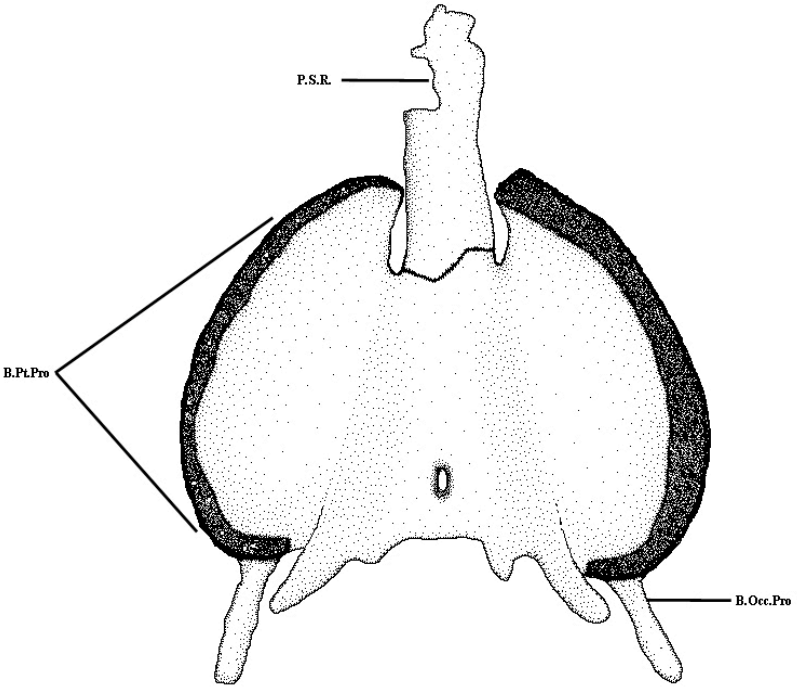

P.S.R.
B.Pt.Pro
B.Occ.Pro

FIGURE 4-22. Right surangular in a. lateral view and b. medial view. Scale bar = 10mm.

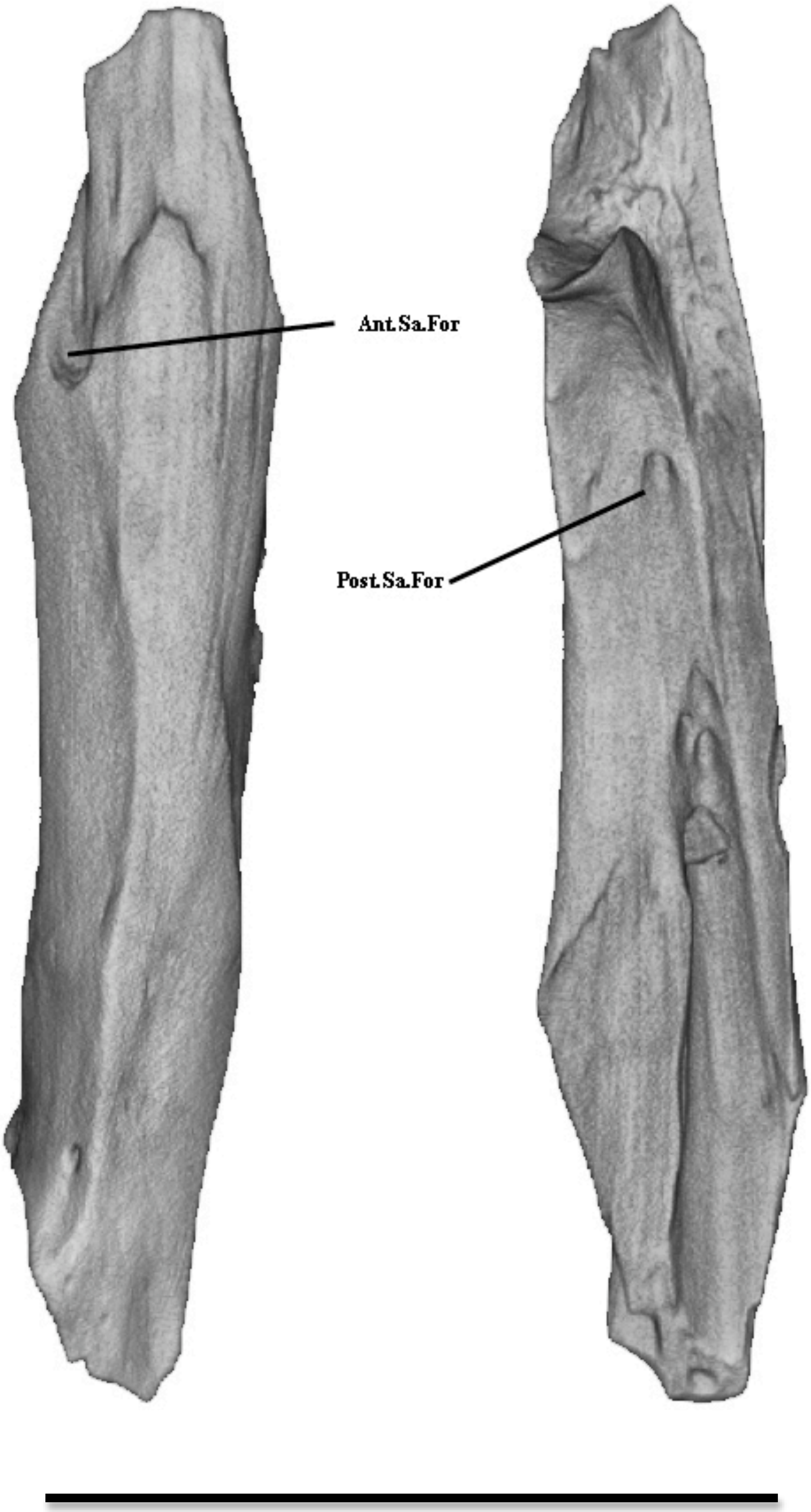

Ant.Sa.For
Post.Sa.For

FIGURE 4-23. Right splenial in lateral view. Scale bar = 10mm.

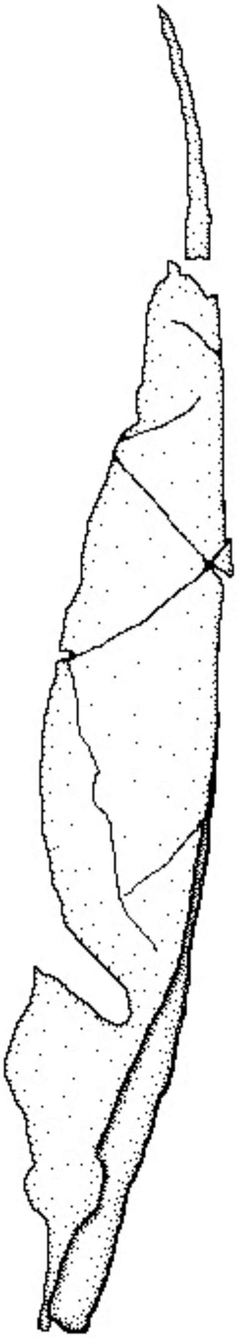
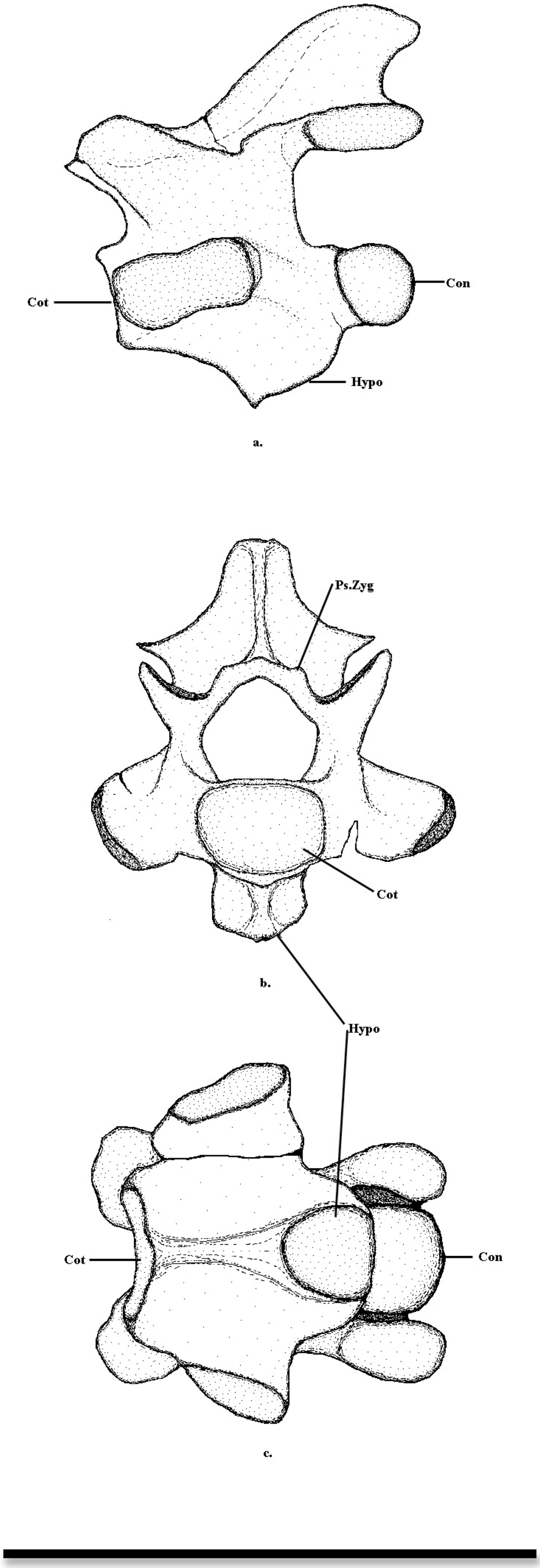


FIGURE 4-24. Third cervical vertebra in a. left lateral view, b. anterior view and c. ventral view. Scale bar = 10mm.


Cot
Con
Hypo
a.
Ps.Zyg
Cot
b.
Hypo
Cot
Con
c.

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CHAPTER FIVE

PHYLOGENETIC REVISION OF ANGUIMORPHA WITH AN EMPHASIS ON BASAL PLATYNOTAN RELATIONSHIPS

INTRODUCTION

A ‘stem-based’ taxon as commonly used and defined by Lee (1997), Platynota includes all anguimorphs more closely related to crown varanoids (*Varanus, Heloderma and Lanthanotus*) than to the Anguidae and Xenosauridae. The consistency with which this term is applied (McDowell and Bogert 1954; Rieppel 1980; Borsuk-Białynicka 1984; Pregill et al. 1986; Lee 1997; Balsai 2001; Conrad 2006; Rieppel et al. 2007; Norell et al. 2008; Conrad 2008; Conrad et al. 2010), though not universal (Estes 1983; Gao and Norell 1998), is based on need, as several fossil forms are consistently found to lie on the stem leading to Varanoidea with little or no evidence to suggest a special relationship with any one crown clade. Traditionally, the study of platynotan relationships within the broader context of Anguimorpha, has taken two forms: broad taxonomic works like those of Cope (1964), Siebenrock (1892), Camp (1923), Lakjer (1927), and Estes et al. (1988), which sought to place anguimorphans and some specific constituents thereof into the broader context of Squamata; and other works with the more exclusive aim of understanding relationships between the living representatives found within Anguimorpha (Mertens 1942; Barrows and Smith 1943; McDowell and Bogert 1954; Rieppel 1980; Lee 1997). Fossil anguimorphans have not been completely overlooked (Gilmore 1922, 1928, 1943; Fejérváry 1935; Kuhn 1940; Hoffstetter 1943, 1954; Estes 1964; Meszoely 1970; Sullivan 1977; Haubold 1977; Estes 1983; Gao and Fox 1997) but prior to the last twenty years the majority of the work done on fossil forms was alpha-taxonomic and attempts to rigorously test theories of relationship between fossil and extant forms were relatively rare and often narrow in taxonomic scope, Gauthier (1982), and Borsuk-Białynicka (1984) being notable, exceptions. This is understandable in light of the fragmentary nature of most of the fossil material available and the inclination to append a phylogenetic analysis to the description of a single fossil taxon all too often results in an ingroup composition biased toward presumed relationships of the taxon being described (Norell and Gao 1997).

Beginning with Borsuk-Białynicka (1984), the record of fossil platynotans has been steadily increasing over the past thirty years, as has the quality of numerous specimens, especially those collected in central Asia (Borsuk-Białynicka 1984; Norell and Gao 1992; Gao and Norell 2000; Norell et al. 2008). Phylogenetic studies incorporating fossil platynotans in a broad sense have also become more common (Gao and Norell 1998; Nydam 2000; Balsai 2001; Rieppel et al 2007; Norell et al. 2008; Conrad 2008; Conrad et al. 2010), though others remain unnecessarily taxonomically restricted (Conrad 2006). Despite this, the relationships between fossil platynotans and extant varanoid anguimorphs remain largely unresolved with considerable discrepancies existing between proposed phylogenies (Gao and Norell 1998; Norell et al. 2008 Conrad 2008; Conrad et al. 2010), especially near the base of the platynotan stem.

Part of the problem is historical. As noted above, extensive analyses of anguimorphan relationships prior to Gauthier (1982), focused on variability in characteristics observed in reasonably abundant and complete specimens of extant species. As pragmatic as this may seem, and in fact be, it must not circumscribe the approach to phylogenetic reconstruction of broader taxonomic groups where rare or extinct species are included. Prior to the lengthy discussion of the enigmatic earless water monitor of Borneo (*Lanthanotus*) by McDowell and Bogert (1954), the classification by Camp (1923) of *Heloderma* as an anguid was widely accepted. Features of *Lanthanotus*, intermediate between *Heloderma* and *Varanus*, helped to redefine the characters that unite the modern concept of Varanoidea. Previously thought to be allied with *Heloderma* based on superficial appearance, the examination of the anatomy of *Lanthanotus* by McDowell and Bogert (1954) provided crucial information that added to and illuminated the broader discussion of anguimorphan relationships. The same problem that once saw the shoe-horning of *Lanthanotus* and *Heloderma* into Anguidae, lack of reliable data about one or more taxa, currently plagues fossil platynotans. Geographically widespread and disparate in their morphology, basal platytnotans are often coded from the literature (Norell and Gao 1997; Gao and Norell 1998; Rieppel et al. 2007; Conrad 2008) and variable coding is not uncommon (See coding of plicidentine in *Paravaranus* in the previously cited studies).

A good example of the problems surrounding basal platynotan relationships can be found in the Necrosauridae (sensu. Estes 1983; Borsuk-Białynicka 1984; Gao and Fox 1997) described by Estes (1983) as having "...always been characterized as having character states of both Anguioidea and Varanoidea…". Indeed, the characters and character states traditionally used to describe 'necrosaurs' are almost exclusively based on similarities they share with either anguids or varanoids, i.e. anguid and varanoid characters. This is both natural and necessary and is not argued against here, but the fact that ‘necrosaurs’ are rarely if ever discussed in terms of potential ‘necrosaur’ characters is problematic. The recovery of a monophyletic clade of taxa, represented by fragmentary specimens, and for which no unique characters are hypothesized/constructed/coded seems incredibly unlikely. In short, the paraphyly attributed to Necrosauridae (Estes 1983; Borsuk-Białynicka 1984; Gao and Fox 1997) is the direct consequence of the absence of any attempt to formulate hypotheses of necrosaurid synapomorphies.

The recovery of basal polytomies and paraphyletic assemblages in morphological analyses is by no means unusual and has often been attributed to a lack of data for the fossil taxa involved (Gauthier 1986; Novacek 1992; Wilkinson and Benton 1995; Gao and Norell 1998). Morphological data sets can be amplified in one of two ways: by the inclusion of greater numbers of taxa, or by an increase in the number of characters for which taxa can be scored. The first of these has been facilitated through the recent increase in described fossil platynotans, but an increase in this kind of data is necessarily dependant on discovery and is beyond any one researcher’s control. However, the second approach, the construction and addition of new characters potentially relevant to the understanding of poorly resolved taxa, may be actively pursued through careful observation of similarity, variation and potential covariance of morphology among fossil groups. As fossil platynotan specimens increase in number and kind, opportunities for the construction of characters specifically relevant to examining the relationships of fossil taxa increase as well. Wiens

(2003, 2006) has pointed out that the addition of a single character can often mean the difference between a problematic or poorly resolved taxon placement and the formation of a relatively robust sister-group relationship. As such, a modest increase in the number of characters directly addressing morphological variations observable in and among fossil platynotans and their extant relatives, may help resolve the persistent problem of 'necrosaur' paraphyly.

The focus of the present analysis is to test the potential phylogenetic position of *Vulpesaurus magdalenae* gen. et sp. nov. as described in Chapter 4 of this thesis within Anguimorpha generally and Platynota specifically. Additionally, an explicit effort has been made to construct primary hypotheses of homology for taxa traditionally classed as 'necrosaurs'; these being based on the revised generic and familial diagnoses of *Necrosaurus* and Necrosauridae as presented in Chapter 3. of this thesis. A secondary aim of the present study is to test these hypotheses of monophyly in *Necrosaurus* and Necrosauridae, within the broader context of anguimorphan phylogeny.

PHYLOGENETIC ANALYSIS

A data set containing 42 taxa (3 outgroup and 39 ingroup) scored for 110 characters was constructed (Appendix 3) using Mesquite V2.72 (Maddison and Maddison 2009) and was analyzed using PAUP 4.0b10 (Swofford 2002). Characters used in the analysis are derived from several sources (Rieppel 1980; Pregill et al. 1986; Estes et al 1988; Norell et al 1992; Lee 1997; Norell and Gao 1997; Gao and Norell 1998; Conrad 2008) with modifications being made to some character descriptions as well as the addition of 13 new ones (Appendix 2). In addition to *Vulpesaurus magdalenae* gen. et sp. novum, 21 fossil and 3 extant platynotans were included in the initial ingroup analysis as well as 5 anguids (1 fossil) and 4 xenosaurs (2 fossil). The putative basal anguimorphan *Dorsetisaurus purbeckensis* Hoffstetter 1967, and putative basal platynotan *Parviraptor estesi* Evans 1994, were also included. Scincomorpha, Gekkota and Iguania were chosen as successive outgroups for polarizing characters based on similar studies (Gao and Norell 1998; Nydam 2000) and on the phylogenetic hypothesis presented by Estes et al. (1988). In order to test the potential relationships between *Vulpesaurus magdalenae* gen. et sp. nov. and mosasaurs, two pythonomorph genera (*Aigialosaurus* Kramberger 1892 and *Pontosaurus* Kramberger 1892) were also constrained as ingroup taxa. All ingroup character scoring was made through direct observation (see Appendix 1 for a list of specimens examined) and supplemented with literature reviews except for the following which were coded based on published descriptions: *Aigiolsaurus* (Dutchak and Caldwell 2006, 2009)*; Pontosaurus* (Pierce and Caldwell 2004; Caldwell 2006)*; Estesia* (Norell et al. 1992; Norell and Gao 1997)*; Ovoo* (Norell et al. 2008)*; Parviraptor* (Evans 1994)*; Restes* (Gauthier 1982); *and 'Saniwa' feisti* (Stritzke 1983). Coding of *Necrosaurus cayluxi, Necrosaurus eucarinatus* and *'Saniwa' feisti* was facilitated additionally by the provision of numerous photographs of specimens provided by M. Caldwell and R. Nydam. Coding for soft tissue characters follows that of Gao and Norell (1998). Due to the large size of the data set, a Heuristic search was performed in PAUP; all characters were unordered and unweighted, multistate characters were treated as polymorphic, and character state reconstructions at ancestral nodes were optimized using DELTRAN. Four separate analyses were made (A-D discussed below), beginning with the complete data set of 42 taxa. Successive analyses involved the cumulative removal of taxa based on the reasoning presented for each discussion.

Analysis A–Analysis of the complete data set recovered 50,000 (the pre-set maximum) most parsimonious trees (MPT's) with a tree-length of 392 steps with a Consistency Index (CI) of 0.518 and Retention Index (RI) of 0.714. A strict consensus of these trees reveals two large polytomies, one at the base of Anguimorpha and one at the base of Platynota (Fig. 5-1). Despite this lack of resolution there are a few relationships worth noting. The traditional concepts of separate clades containing Anguidae and Platynota as well as the basal anguimorphan placement of the xenosaurs (*Xenosaurus, Shinisaurus, Restes* and *Carusia*) and *Dorsetisaurus* are supported. Also corroborating previous studies (Gao and Norell 1998; Nydam 2000) is the recovery of two varanoid crown groups, the Monstersauria and Varanidae including the addition of *Telmasaurus* and *Paravaranus* to the Varanidae. The placement of *Ovoo*, also within the Varanidae, supports the previous studies in which it was included (Norell et al. 2008; Conrad et al. 2010). *Vulpesaurus* forms a sister-group relationship with a clade containing *Aigialosaurus* and *Pontosaurus* and this group in turn forms a polytomy with the Varanidae, Monstersauria and all remaining platynotans. Interestingly, *Bahndwivici*, described by its author as a shinisaurid (Conrad

2006), rests within the basal platynotan polytomy while *Shinisaurus* is recovered in a position corroborated by numerous studies (McDowell and Bogert 1954; Rieppel 1980; Gauthier 1982; Estes et al. 1988; Gao and Norell 1998; Nydam 2000) with Xenosaurus at the base of Anguimorpha. This is in direct contrast to Conrad (2006) and Conrad et al. (2010) in which *Shinisaurus and Bahndwivici* formed a sister-group relationship at the base of Platynota. Lastly, previous analyses of similar taxonomic scope have consistently recovered a monophyletic Anguidae with *Gerrhonotus* and *Diploglossus* either forming a polytomy at is base (Gao and Norell 1998; Nydam 2000) or as successive sister taxa to the remaining anguids (Balsai 2001). The placement of *Gerrhonotus* in this first analysis, within the basal anguimorphan polytomy outside the Anguidae, reflects a greater instability within the present analysis with respect to the relationships between basal xenosaurids, anguids and a taxon not included in the aforementioned studies, *Dorsetisaurus*.

Analysis B–Analysis A placed Gekkota as the proximal outgroup as opposed to Scincomorpha; a result shared by two previous analyses (Gao and Norell 1998; Nydam 2000) using Iguania, Gekkota and Scincomorpha as successive outgroups and in opposition to the proposed phylogeny presented by Estes et al. (1983). When the analysis was run with Gekkota excluded, the number of shortest trees (50 000) and the topology of the resultant consensus tree were unchanged while computation time dropped significantly and so it was removed from analysis B. Also removed from the analysis were *Dorsetisaurus* and *Parviraptor* based on the following reasons.

Known first from the late Jurassic of England (Hoffstter 1967), later from Portugal (Seiffert 1973) and Wyoming (Prothero and Estes 1980), and described by Estes (1983) as poorly understood, *Dorsetisaurus purbeckensis* was not included by previous authors of recent anguimorph analyses (Gao and Norell 1998; Nydam 2000; Balsai 2001) and their reasons for exclusion were not explained. Hoffstetter (1967) proposed an anguimorphan placement for *Dorsetisaurus* based on varanoid features of the dentition and anguid features of the braincase, while noting the pattern of scutellation on the frontals resembled scincomorphs. Although Estes (1983) provided the first diagnosis for Dorsetisauridae and provisionally placed it between Xenosauridae and Anguidae, he was careful to point out his own uncertainty with regard to its placement within the Anguimorpha more generally. The characters shared by *Dorsetisaurus* and anguimorphans appear very distinctive in the former taxon and while its placement in the base of Anguimorpha is corroborated in the present analysis the apparent paradox of an early (late Jurassic) primitive anguimorph in possession of a highly distinctive anguid braincase and a relatively derived varanoid dentition suggests further study of *Dorsetisaurus* at the alpha-taxonomic level is needed before it can be confidently placed within Anguimorpha. Given the polytomy recovered at the base of Anguimorpha in analysis A of this paper (a result not seen in similar analyses excluding *Dorsetisaurus*) and the above argument, *Dorsetisaurus* was removed from subsequent analyses.

Parviraptor estesi, named and proposed by Evans (1994) as a basal platynotan, presents difficulties similar to those presented above for *Dorsetisaurus*. Also from the late Jurassic of England and Portugal, *Parviraptor* displays a mixture of characters that are primitive for Anguimorpha (lack of cervical hypapophyses, paired parietal) and advanced within Platynota (absence of osteodermal ornamentation, subolfactory processes nearly meeting below olfactory tract), while still others are superficially platynotan, but so distinct and derived as to be unique within the group (dramatically recurved teeth lacking plicidentine, shape of maxilla with extreme suborbital elongation). As was the case with *Dorsetisaurus*, the diffuse suite of characters possessed by *Parviraptor* may serve in part to exacerbate the formation of a basal polytomy, this time within Platynota, and for this reason *Parviraptor* was removed from the remaining analyses.

Lastly, the initial inclusion of the basal mosasauroid *Aigialosaurus* and the dolichosaur *Pontosaurus* in analysis A, served to test the potential relationship between *Vulpesaurus magdalenae* and the mosasaur stem. This was done as a direct result of the observation of unique (for terrestrial platynotans) features of the latter taxon including an anteroposteriorly elongate articular surface of the basipterygoid processes of the basisphenoid, the lack of projection or constricted 'neck' on those processes and the general form of the pterygoid. These characters occur variably within mosasaurs, a group that has been traditionally placed within crown Varanoidea (Owen 1877; Marsh 1880; Baur 1890; Williston 1898; Nopsca 1903) with examples of modern cladistic analyses either constraining them to within Anguimorpha (Lee 1997; Rieppel et al. 2007) or recovering a varanoid placement for them within the broader analysis of squamate relationships (Conrad 2008, 2010). The recovery in analysis A of a clade containing *Vulpesaurus magdalenae* as sister taxon to an *Aigialosaurus/Pontosaurus* crown was supported by three unambiguous synapomorphies: 39(1) basipterygoid processes short, not projecting beyond the body of the basisphenoid; 40(1) articular facet for pterygoid at distal end of basipterygoid process large and anteroposteriorly elongate; and 50(1) palatine process of pterygoid equal to or greater in length than the quadrate process of the pterygoid. The first two of these are exclusive to the clade recovered and are from Lee (1997), a study explicitly attempting to resolve mosasaur relationships within Anguimorpha, while the third was created for the present study and is a character shared with *Shinisaurus*. The opinion that mosasaurs are varanoid anguimorphs is by no means universally shared and two recent objections in particular present cogent and compelling arguments against the a priori inclusion of mosasauroids in anguimorph phylogenies. The first, presented by Caldwell (2012), demonstrates the influence that historical notions of similarity in morphology between varanids and mosasaurs have had over the construction and coding of character data for mosasaurs and their kin. Caldwell's (2012) review is thorough and carefully lays out evidence against the hypotheses of the primary homology of several characters traditionally thought to be shared between mosasaurs and varanoids. The second, by Gauthier et al. (2012), consists of the most thorough phylogenetic analysis of Squamata yet undertaken and argues against an anguimorphan position for mosasaurs based both on the resultant topology as well as on the logical impossibility for mosasaurs of the late Jurassic to have inherited varanoid characters of which many do not appear in any terrestrial varanoids until the Paleogene or even Neogene, well after the extinction of the former group. In order to test the position of *Vulpesaurus magdalenae* in the absence of the mosasaurian taxa and their potentially confounding influence on topology, *Aigialosaurus* and *Pontosaurus* were removed from all subsequent analyses.

Analysis B recovered 50,000 (pre-set maximum) MPT's of 337 steps with a CI=0.558, and RI=0.714. The strict consensus tree of these, Tree B (Fig. 5-2), shows crown-ward movement of *Gerrhonotus* into a basal anguid polytomy with *Diploglossus*, and root-ward movement of *Gobiderma* and *Paleosaniwa* out of the Monstersauria and into the basal platynotan polytomy. The most significant change in Tree B is the formation of a novel clade containing '*Saniwa' feisti* in a sister group position with a clade containing a polytomy made up of the two *Necrosaurus* species and a dichotomy consisting of *Vulpesaurus* and *Bahndwivici*. *Paleosaniwa* was cited by previous authors (Gao and Norell 1998; Nydam 2000) as a source of instability, perhaps due in part to the number of characters for which it cannot be scored. Balsai (2001) added significant information on the taxon and in an analysis recovered it in a monstersaurian position similar to that seen in analysis A of this study. The movement in analysis B of *Gobiderma* and *Paleosaniwa* into the basal platynotan polytomy suggests that the latter taxon continues to generate instability in the base of Monstersauria and it was removed from subsequent analyses. *Colpodontosaurus*, coded for only 9% of characters, was also removed in an attempt to improve resolution at the base of Platynota.

Analysis C–The third analysis generated 38,136 MPT's of 335 steps (CI = 0.561, RI = 0.741). The strict consensus of these trees (Fig. 5-3) shows greater resolution within Platynota, recovering a trichotomy between *Eosaniwa*, a monophyletic Monstersauria, including *Gobiderma* and a clade containing all other remaining platynotans. The necrosaurid clade recovered in analysis B is maintained and placed as the sister group to a varanid stem including several fossil forms. *Bainguis* and *Carusia* were again recovered in anguid and xenosaurids polytomies, respectively, and were removed from the final analysis in the hopes of reducing the number of most parsimonious trees.

Analysis D–The fourth and final analysis generated 2061 MPT's of 334 steps (CI = 0.563, RI = 0.737), the strict consensus of which (Fig.5-4) retained the platynotan topology of analysis C and also recovered a resolved anguid crown, and Xenosauridae (sensu. Gao and Norell 1998) including *Xenosaurus* and *Shinisaurus*. This tree represents the preferred phylogenetic hypothesis of anguimorphan relationships and the character distributions supporting the constituent clades are discussed below.

CHARACTER DISTRIBUTIONS

Character distributions were examined for each of the major clades recovered and figured on Tree D (Fig. 5-4) using MacClade 4 (Maddison and

Maddison 2005) and are listed below. Unambiguous synapomorphies recovered under DELTRAN optimization are marked with an asterisk.

Anguimorpha Fürbringer 1900

(*Carusia,* Xenosauridae, (Anguidae, Platynota))–Supported by 10 synapomorphies: 2(1), incisive process of premaxilla bipartite; 11(1), subolfactory processes of frontals well developed as lateral wall of olfactory tract; 42(1), distinct medial projection anteroventral to mesopterygoid fossa present to enhance basipterygoid/pterygoid articulation; 54(1), retroarticular process directed medially; 55(1), strong mediolateral reduction of mandibular fossa present; 61(1), intramandibular septum within Meckelian canal present as oblique or vertical septum; 66(1), Meckelian canal open ventrally anterior to anterior inferior alveolar foramen; 78(1), dermal ornamentation on parietal present as distinct projections consistent with presence of osteoderms; 82(1), ossified palpebrals present; 87(1), number of presacral vertebrae 26 or more.

Xenosauridae Camp 1923

(*Xenosaurus, Shinisaurus*)–Supported by 6 unambiguous synapomorphies: *9(1), frontonasal suture a single anteromedial apex; *21(1), dilation of postorbital branch of jugal present; *23(1), canthal crest on temporal arch present; *51(1), ectopterygoid exposed on ventral edge of skull; *56(1), surangular extends slightly beyond coronoid eminence; *77(1), dermal ornamentation of postorbital branch of jugal present.

Anguiformes Conrad 2006

(Anguidae, Platynota)–Supported by 8 synapomorphies, 7 of which are unambiguous: *7(1), portion of narial border formed by maxilla posterodorsally sloped; *17(0), jugal/squmosal contact on supratemporal arch absent; 38(1), foramen ovale located anterior to the sphenoccipital tubercle; *44(1), aperture of jacobsen's organ separated from narial opening by vomer-maxillary contact; *56(2), surangular extends anteriorly well beyond coronoid eminence (reversed in necrosaurids); *63(2), subdental shelf strongly reduced as a slope; *67(1), premaxillary teeth abruptly smaller than maxillary teeth; *94(1), rib attachments on sternum three pairs.

Anguidae Gray 1825

(*Diploglossus*, *Gerrhonotus*, (*Ophisaurus*, (*Anguis*, *Aniella*)))–Supported by 8 synapomorphies: 53(1) retroarticular process widened; 78(0), dermal ornamentation on parietal; 79(1), fused cephalic osteoderms present as large, thin polygonal plates; 80(1), body osteoderms present as flat, imbricating plates; 89(2), caudal chevrons fused to centrum; 95(1), strong elongation of symphasial process of pubis present; 100(1), M. genioglossus lateralis subdivided into separate bundles and inserted into hyobranchials; 110(0), second epibranchial present.

Platynota Baur 1890

(*Eosaniwa*, Monstersauria, Varaniformes)–Supported by 21 synapomorphies: 6(1), nasal process of maxilla located at the middle part of maxilla; 43(1), vomer elongate, roughly twice the length of the palatine; 45(1), palatal shelves of vomer narrow; 46(1), palatine equally wide as long; 47(0), palatine teeth present; 52(1), ectopterygoid in palatal view contacts palatine anteriorly, excluding maxilla from suborbital fenestra; 57(1), anterior process of coronoid is elongate and extensively exposed dorsally; 58(1), anterior extension of splenial retracted to or posterior to midpoint of tooth row; 59(1), posterior extension of splenial terminates anterior to or below the eminence; 60(1), splenial dentary suture loose, with much connective tissue between the two bones; 64(1), posterodorsal extension of dentary not overlapping base of coronoid eminence; 68(1), marginal tooth bases bearing distinct ridges; 69(1), marginal teeth widely spaced; 70(1), tooth bases are expanded; 71(1), replacement teeth develop without presence of resorption pits; 72(1), replacement teeth develop posterolingually; 73(1), maxillary teeth number 10-13 positions; 84(1), cervical intercentrum sutured to posterior part of preceding centrum; 85(1), vertebral condyle/cotyle articulation slightly oblique with condylar surface broadly visible in ventral view; 88(1), autotomy on caudal vertebrae absent; 93(1), mesosternum absent.

Monstersauria Norell and Gao 1997

(*Gobiderma*, (*Paraderma*, *Primaderma*, (*Estesia*, *Eurheloderma*, *Heloderma*))) –Supported by 4 unambiguous synapomorphies: *32(1), pterygoid lappet of quadrate present; *49(1), anterolateral process of pterygoid extended dorsally on ectopterygoid to contact jugal; *75(1), dentary teeth number 12 to 9 positions; *79(3), fused cephalic osteoderms present as large, thick sub-conical mounds.

Varaniformes Conrad 2008

(Necrosauridae, (*Parasaniwa*, *Parviderma*, (*Proplatynotia*, *Saniwides*, (*Paravaranus*, (*Telmasaurus*, (*Cherminotus*, *Lanthanotus*, *Ovoo*, *Saniwa ensidens*, *Varanus*))))))–Supported by 6 unambiguous synapomorphies: *25(0), descensus parietalis present as an anteroposteriorly elongate, ventrolaterally projecting crest; *27(0), origin of temporal musculature on dorsolateral aspect of parietal table; *29(1), supratemporal process of parietal in dorsal aspect narrow with sharp crest; *31(1), tympanic crest of quadrate strongly reduced; *78(1), dermal ornamentation on parietal present as distinct projections consistent with presence of osteoderms; *79(2), fused cephalic osteoderms present as small, low lying bumps.

Necrosauridae Hoffstetter 1943

(‘*Saniwa’ feisti*, (*Necrosaurus cayluxi*, *N. eucarinatus*, (*Vulpesaurus magdalenae* gen. et sp. nov., *Bahndwivici*)))–Supported by 3 unambiguous synapomorphies: *56(1), surangular extends anteriorly slightly beyond coronoid eminence; *80(2), body osteoderms present as ovoid scutes with a sagittal keel; *81(1), osteodermal ornamentation forms a mid-sagittal keel on the frontal.

Varanidae Gray 1827

(*Paravaranus*, (*Telmasaurus*, (*Cherminotus*, *Lanthanotus*, *Ovoo*, *Saniwa ensidens*, *Varanus*)))–Supported by 11 synapomorphies, 10 of which are unambiguous: 3(1), nasal bones fused; *4(2), nasal and prefrontal bones separated by gap; *5(1), nasal and maxillary bones separated by gap; *6(2), nasal process of maxilla located at the posterior part of maxilla; *13(2), prefrontal contributing to the external narial border owing to a retraction of the external nares; *19(1), posteroventral process of jugal nearly or entirely lost; *22(1), postorbital/postfrontal present; *37(0), spheno-occipital tubercle short and ventrally directed; *38(0), foramen ovale located above or slightly posterior to the spheno-occipital tubercle; *78(0), dermal ornamentation on parietal absent; *79(0), fused cephalic osteoderms absent.

DISCUSSION

The phylogenetic hypothesis presented here as Tree D (Fig. 5-4) matches most closely that of Gao and Norell (1998), with notable differences including the recovery of a monophyletic Necrosauridae and a reduction in resolution within the Varanidae. The most notable similarities are the recovery of an anguid, platynotan dichotomy exclusive of the more basal Xenosauridae, a topology corroborated by Conrad (2006) and Gauthier et al. (2012), and the placement of most fossil platynotans not already included within Monstersauria on a stem leading to Varanidae. Four major clades presented in Tree D are discussed below in relation to their implications for platynotan evolution, classification and biogeography.

Anguiformes: Gao and Norell (1998) recovered, but did not name, a clade containing a monophyletic Anguidae in a sister-group relationship with Platynota (their Varanoidea), a topology shared with the present analysis. Conrad (2006) also recovered this clade along with a basal platynotan grouping consisting of *Shinisaurus* and *Bahndwivici* (his Shinisauria), and applied the name Anguiformes to it citing the support of 5 unambiguous synapomorphies. Five synapomorphies support Anguiformes in Gao and Norell (1998) all of which are included in the present analysis along with three additional synapomorphies; only one of these 8 characters (premaxillary teeth marked smaller than maxillary teeth) is also included in Conrad's (2006) list of anguiform synapomorphies. Gauthier et al. (2006) also recovered a similar clade including a "fossorial group", but left the grouping unnamed. While three separate, and very different, studies find support for an Anguidae/Platynota clade it should be noted that the constituent members and characters uniting them vary considerably and a consensus among topologies does not equate to a consensus among characters. However, when in the present study testing the potential influence on topology of the poorly known taxa *Eosaniwa* and *Paravaranus*, removal of those taxa resulted in the collapse of the Anguidae with all anguid genera forming successive sister-groups to the Platynota and several ingroup platynotans moving from the varanid stem to the monstersaur stem. Despite this, the anguid/platynotan clade was retained, suggesting strong support for Anguiformes in the present analysis, though with the exclusion of *Shinisaurus* contra the original author's definition (Conrad 2006).

Monstersauria: As introduced and defined by Norell and Gao (1997) Monstersauria has been corroborated in numerous studies (Gao and Norell 1998; Nydam 2000; Balsai 2001; Rieppel et al. 2007; Conrad 2008; Conrad et al. 2010; Conrad et al. 2011) and is well supported here. Gauthier et al. (2012) failed to recover a Monstersauria inclusive of *Gobiderma* and *Estesia*, though those were the only fossil members of that clade included in their analysis. The most significant aspect of the Monstersauria as recovered in the present analysis is the group's placement, being separated from the Varanidae by several platynotan taxa lying on the latter family's stem. This topology was also shared with Gao and Norell (1998), Nydam (2000) and Balsai (2001) though not with Rieppel et al. (2007), Conrad (2008) and Conrad et al. (2010), and it creates an unnamed clade with implications for the usage and meanings of the terms Platynota and Varanoidea.

Varaniformes: Gao and Norell (1998) placed their Monstersauria within Platynota and in apposition to a clade containing Varanidae and numerous fossil taxa to which they applied the term Varanoidea. Although this solved the problem of what to name the expanded varanid lineage, no other published study has applied the term Varanoidea in this way and it continues to be used to represent the common ancestor of *Heloderma* and *Varanus* and all of its descendents (Conrad 2006, 2008; Rieppel et al. 2007; Conrad et al. 2010; Conrad et al. 2011; Gauthier et al 2012) and thus to include Monstersauria. Gauthier et al. (2012) include none of the fossil forms found on the varanid stem included in the present study and others (Gao and Norell 1998; Nydam 2000; Balsai 2001), and thus avoid the problem of what to call the lineage including all varanoids more closely related to *Varanus* than to monstersaurs. In their analysis of crown group varanid relationships, Conrad et al. (2008) include numerous fossil forms lying basal to the Varanidae, acknowledging their close relationship to the family, but do not apply a name to the grouping. Conrad (2008) defined Varaniformes to include all those taxa sharing a more recent common ancestor with *Varanus* than with *Heloderma*. While the constituent members of the clade outlined in that study are different from those being discussed here, the need for a stem-based taxon incorporating fossil forms close to the Varanidae is clear and the term Varaniformes is here applied. The transposition of several, formerly basal platynotans, onto the stem leading to Varanidae has clear implications for the evolution of many of the characters traditionally used to unite *Heloderma* with *Lanthanotus* and *Varanus*, specifically those related to 'narial retraction'. Several basal Varaniformes ('*Saniwa*' *feisti*, *Necrosaurus*, *Bahndwivici*, *Parasaniwa*) as well as at least two basal monstersaurs (*Gobiderma*, *Primaderma*) display anteriorly restricted external narial openings demonstrating the convergent nature of the expansion of the external nares seen within crown-group varanids and crown-group monstersaurs (see also Nydam 2000). Development of an intramandibular hinge may begin at the base of Platynota and be shared by all crown-group varanoids but the assessment of this feature is difficult in light of specimens which are either disarticulated and fractured or articulated and obscured, making unclear the degree of overlap shared between the dentary and post-dentary elements. The suite of dental characters associated with predation in crown varanoids appears very early within Platynota with few examples of secondary loss (absence of plicidentine in *Proplatynotia*, *Vulpesaurus* and *Bahndwivici*) and additional specializations seen in some (venom grooves in *Estesia*, *Eurheloderma*, *Heloderma*; convergent reduction in tooth number in *Heloderma*, Varanidae).

Necrosauridae: Named by Hoffstetter (1943) and diagnosed by Estes (1983), Necrosauridae has been conventionally used and described as a ‘meta-taxon’ (Estes 1988), whose composition is likely paraphyletic (Estes 1983; Borsuk-Białynicka 1984; Gao and Fox 1996; Gao and Norell 1998). The loose diagnosis provided by Estes (1983) is at the root of the necrosaurid paraphyly problem and chapter 3 of this thesis provides a more precise diagnosis of *Necrosaurus* and the Necrosauridae with the aim of clarifying the potential monophyly and membership of the Necrosauridae. The present analysis recovers a novel and monophyletic Necrosauridae at the base of Varaniformes. Two of the characters used to diagnose Necrosauridae in chapter 3 of this thesis are recovered as unambiguous synapomorphies supporting its monophyly (the presence of keeled body osteoderms and the formation of a mid-sagittal keel on the frontal) while a third diagnoses all necrosaurs above the level of ‘*Saniwa’ feisti* (constriction of the posterior portion of the parietal table). It is worth noting that *Shinisaurus* also shares the presence of keeled osteoderms and a constriction of the posterior portion of the parietal table, but is recovered in its typical placement as a xenosaurid based on the 6 unambiguous synapomorphies supporting the Xenosauridae. The tree topology adjacent to the Necrosauridae seems little affected by its emergence as other stem-Varaniformes are placed similarly on topologies presented in Gao and Norell (1998), Nydam (2000) and Balsai (2001).

Biogeography of Platynota: Platynota, like its sister-group the Anguidae, was geographically widespread by the late Cretaceous with the greatest diversity occurring in central Asia. The oldest known platynotan, *Primaderma nessovi* (Cifelli and Nydam 1995; Nydam 2001) from the Albian –Cenomanian boundary of Utah, demonstrates the early divergence between Monstersauria and Varaniformes, and suggests a North American origin for the former clade. Extant monstersaurs are exclusively North American but the late Cretaceous occurrence of *Gobiderma* and *Estesia* in central Asia supports the likelihood of an early cretaceous land connection between Asia and North America (Currie 1992; Kirkland et al. 1997).

The oldest Varaniformes are those from the Gobi Desert, Mongolia (Gilmore 1943; Borsuk-Białynicka 1984; Gao and Norell 2000; Norell et al. 2008) dating from the late Santonian and early Campanian (Byan Dzak locality) and middle Campanian (Barun Goyot, and Khermeen Tsav Formations) (Gradziński et al. 1968; Gradziński and Jerzykiewicz 1972; Gradziński et al. 1977), but others are common if somewhat less diverse by the late Cretaceous in North America (Gilmore 1928). Given the earlier occurrence and the much more diverse fauna present in central Asia it seems prudent to propose an Asian origin for Varaniformes, and the fossil record of other lizard groups in the early (Aptian-Albian) and early late Cretaceous (Albian-Cenomanian) of North America supports the hypothesis of an early Cretaceous radiation coming from Asia (Nydam and Cifelli 2002; Nydam 2002).

As defined by the current analysis, the oldest necrosaurid is *Vulpesaurus magdalenae* from the Maastrichtian of southern Saskatchewan, followed by *Bahndwivici* (Conrad 2006) from the early Eocene of Wyoming. European necrosaurs '*Saniwa' feisti* and *Necrosaurus eucarinatus* are found in the middle Eocene of Germany (Kuhn 1940; Hoffstetter 1943; Estes 1983; Stritzke 1983), while specimens of both *Necrosaurus cayluxi* and *N. eucarinatus* are abundant in the late Eocene of western Europe (Filhol 1873; Lydekker 1888; Fejérváry 1935; Hoffstetter 1943; Rage 1978; Augé 2005). The older North American necrosaurs appear slightly more primitive in that they lack plicidentine. Placed as they are, in the necrosaurid crown, this feature may be interpreted as a reversal but there are few characters separating the necrosaurs and many characters remain uncoded in all but '*Saniwa*' *feisti*. The amount of character optimization required by the necrosaurid topology suggests that the relationships within Necrosauridae should be treated as tentative at best, and no clear conclusions about necrosaur origins can be made as yet.

The stem leading to Varanidae has been steadily increasing in length with more and more of the formerly 'necrosaurian' taxa being appended to that branch in recent analyses (Gao and Norell 1998; Nydam 2000; Balsai 2001; Conrad 2008; Norell et al 2008; Conrad et al. 2010). With the exception of *Parasaniwa* and *Saniwa ensidens*, the entire lineage leading to crown Varanidae from the basal varaniform split with Necrosauridae is Asian. *Parasaniwa* is frequently recovered in a position basal to the monstersaur/varaniform dichotomy (Norell and Gao 1997; Balsai 2001; Rieppel et al. 2007; Conrad

2008; Conrad et al. 2010) and its appearance here on the varanid stem is not well corroborated. *Saniwa ensidens* occurs in the early to middle Eocene of North America (Leidy 1970; Gilmore 1922, 1928; Estes 1983) with at least one European record from the early Eocene of Belgium (Dollo 1923) and may represent the sister taxon to the genus *Varanus* (Conrad et al. 2008) with the oldest member of *Varanus* appearing in the late Eocene-early Oligocene of Egypt (Smith et al. 2008; Holmes et al. 2010). The evidence presented here and corroborated by numerous studies (Gao and Norell 1998; Nydam 2000; Balsai 2001; Conrad 2008; Conrad et al. 2008; Norell et al. 2008; Conrad et al. 2010) strongly supports an Asian origin for the varanid stem with a possible Eurasian or African origin for the genus *Varanus* (Conrad et al. 2008; Smith et al. 2008; Holmes et al. 2010) and independent molecular analyses of extant *Varanus* also support an African origin for the genus (Fuller et al. 1998; Ast 2001).

CONCLUSIONS

Platynotan biogeography is problematic in part because the majority of platynotan diversity is extinct. Recent improvements in phylogenetic resolution of platynotan relationships are related to an increase in the numbers of relatively complete platynotan taxa (Borsuk-Białynicka 1984; Norell and Gao 1997; Conrad 2006; Norell et al. 2007; Rieppel and Grande 2007), but basal platynotan relationships rapidly lose resolution when certain fragmentary taxa, like *Colpodontosaurus* and *Paleosaniwa* are included. As presented here, the Platynota is supported by 21 synapomorphies none of which are unambiguous. This is not surprising given the wide variety of morphologies represented by the constituent members and may be due in part to the inability to score many taxa for particular characters. Many reversals and convergences within Platynota are apparent but a few consistent trends emerge. The dental adaptations attributed to the predatory life habits observed in extant varanoids (expanded tooth bases, basal fluting, interdental tooth replacement, trenchant recurved crowns) are consistently distributed throughout Platynota as are characters relating to an elongation of the rostrum and expansion of the external bony nares (posterior movement of nasal process of maxilla, elongation of vomers) and those associated with the development of an intramandibular hinge (reduction in dentary and postdentary overlap, loose splenial dentary suture).

The common thread uniting these features is the presence of presumed selection pressure for a predaceous habit that includes relatively large prey. As such the suite of characters that defines Platynota might be argued to be likely to have evolved several times in parallel as a result of similar selection pressures acting on a more generalized anguimorphan bauplan. While there is no positive evidence to support the supposition that the 'platynotan' form evolved more than once, the possibility exists and should not be discounted based on the repeated recovery of a monophyletic Platynota in phylogenetic analyses. The data sets supporting Platynotan monophyly (including the present one) rely heavily on the characters discussed above. Many of these characters co-vary to such a great extant that their use in tandem may have the effect of artificially weighting the data. Trenchant, recurved teeth don't appear to develop in the absence of expanded bases or interdental tooth replacement and the separation of the prefrontal from the nasal by a gap seems unlikely to ever coincide with an anteriorly placed nasal process of the maxilla.

With the bulk of platynotan diversity occurring in the fossil record, the emergence of more numerous and complete taxa presents an excellent opportunity to re-asses the construction of morphological data sets addressing platynotan diversity. The striking morphological disparity apparent in forms like *Eosaniwa*, *Paravaranus* and *Proplatynotia* strongly suggests the possibility of discovering novel characters for use in phylogenetic analyses. The construction of characters based on observed similarities, while entirely necessary, need not distract the researcher from attempting to discover what characters set various taxa apart. The morphology of extant platynotans is well understood as numerous complete specimens are widely available and character construction will continue to be based largely on that data. However, in light of the ever-growing morphological diversity represented by fossil platynotans, the frame of reference provided by building characters based only on the morphology represented in extant taxa may simply be too limited. As demonstrated with *Necrosaurus* in the current analysis, the clear diagnosis of a taxon followed by the identification of characters potentially useful for phylogenetic analysis, based on features of that diagnosis and coded for other possibly related taxa, may provide testable hypotheses of monophyletic relationships not yet proposed.

FIGURE 5-1. Tree A: Strict consensus of 50, 000 MPTs recovered in analysis A of complete data matrix. Tree length=392, CI=0.581, RI=0.714.

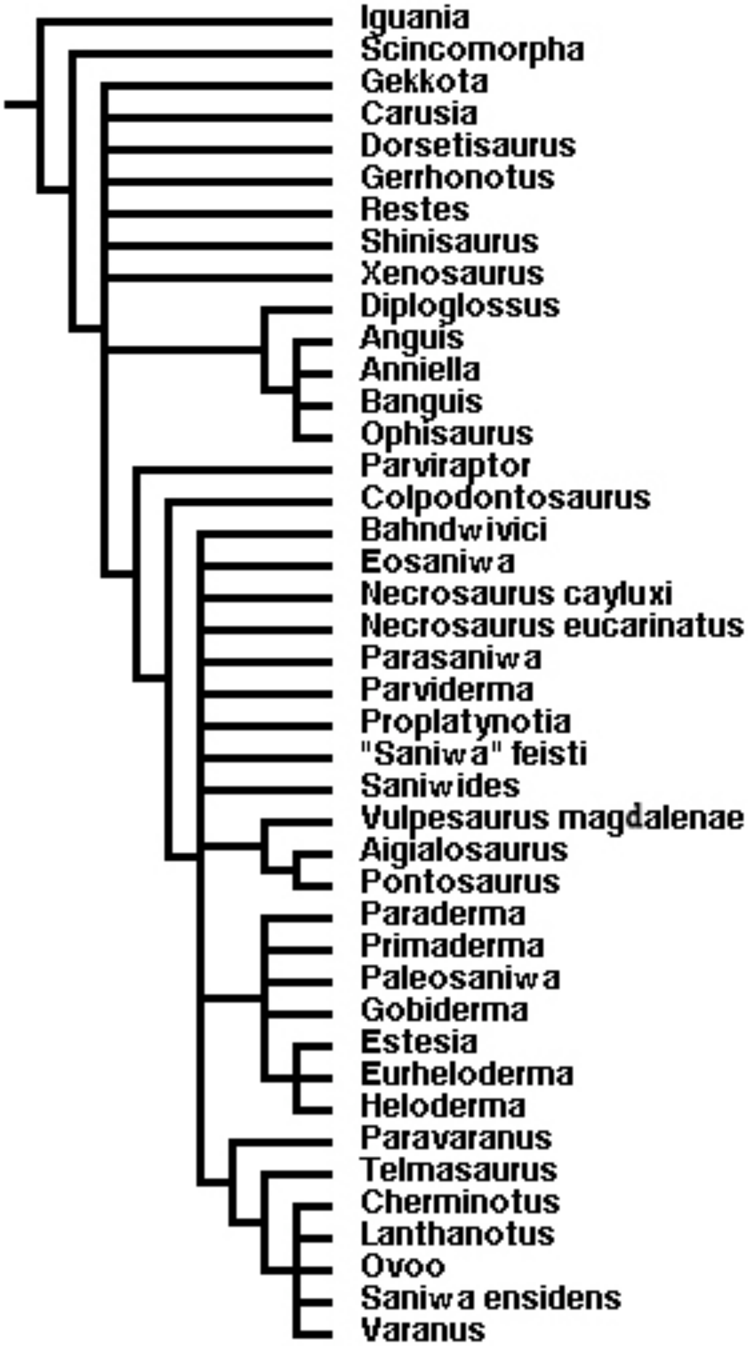

Iguania
Scincomorpha
Gekkota
Carusia
Dorsetisaurus
Gerrhonotus
Restes
Shinisaurus
Xenosaurus
Diploglossus
Anguis
Anniella
Banguis
Ophisaurus
Parviraptor
Colpodontosaurus
Bahndwivici
Eosaniwa
Necrosaurus cayluxi
Necrosaurus eucarinatus
Parasaniwa
Parviderma
Proplatynotia
"Saniwa" feisti
Saniwides
Vulpesaurus magdalenae
Aigialosaurus
Pontosaurus
Paraderma
Primaderma
Paleosaniwa
Gobiderma
Estesia
Eurheloderma
Heloderma
Paravaranus
Telmasaurus
Cherminotus
Lanthanotus
Ovoo
Saniwa ensidens
Varanus

FIGURE 5-2. Tree B: Strict consensus of 50, 000 MPTs recovered in analysis B of data matrix after the removal of Gekkota, *Dorsetisaurus*, *Parviraptor*, *Aigialosaurus* and *Pontosaurus*. Tree length=337, CI=0.558, RI=0.741.

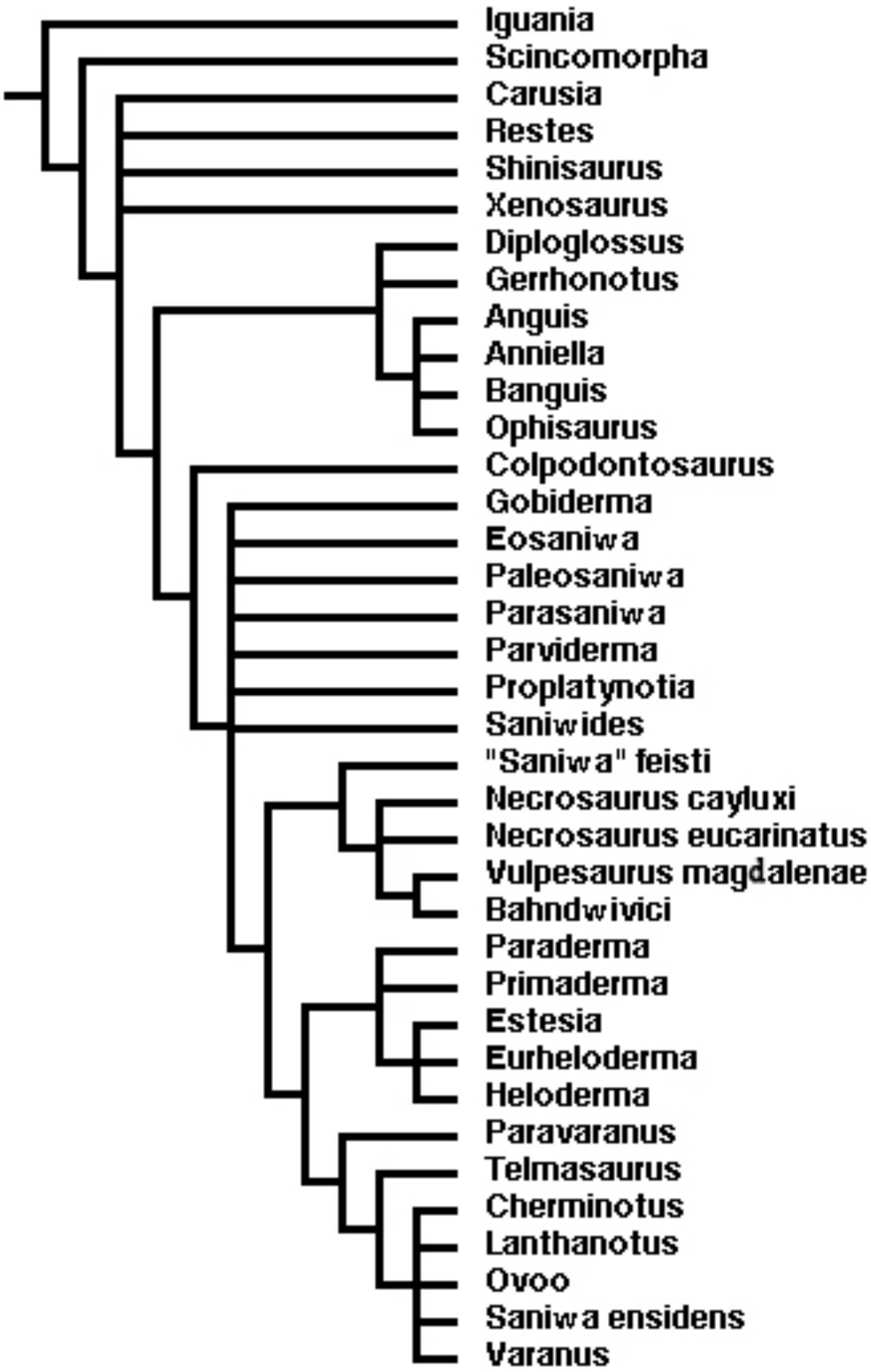

Iguania
Scincomorpha
Carusia
Restes
Shinisaurus
Xenosaurus
Diploglossus
Gerrhonotus
Anguis
Anniella
Banguis
Ophisaurus
Colpodontosaurus
Gobiderma
Eosaniwa
Paleosaniwa
Parasaniwa
Parviderma
Proplatynotia
Saniwides
"Saniwa" feisti
Necrosaurus cayluxi
Necrosaurus eucarinatus
Vulpesaurus magdalenae
Bahndwivici
Paraderma
Primaderma
Estesia
Eurheloderma
Heloderma
Paravaranus
Telmasaurus
Cherminotus
Lanthanotus
Ovoo
Saniwa ensidens
Varanus

FIGURE 5-3. Tree C: Strict consensus of 38,136 MPTs recovered in analysis C of data matrix after the removal of *Colpodontosaurus* and *Paleosaniwa*. Tree length=335, CI=0.561, RI=0.741.

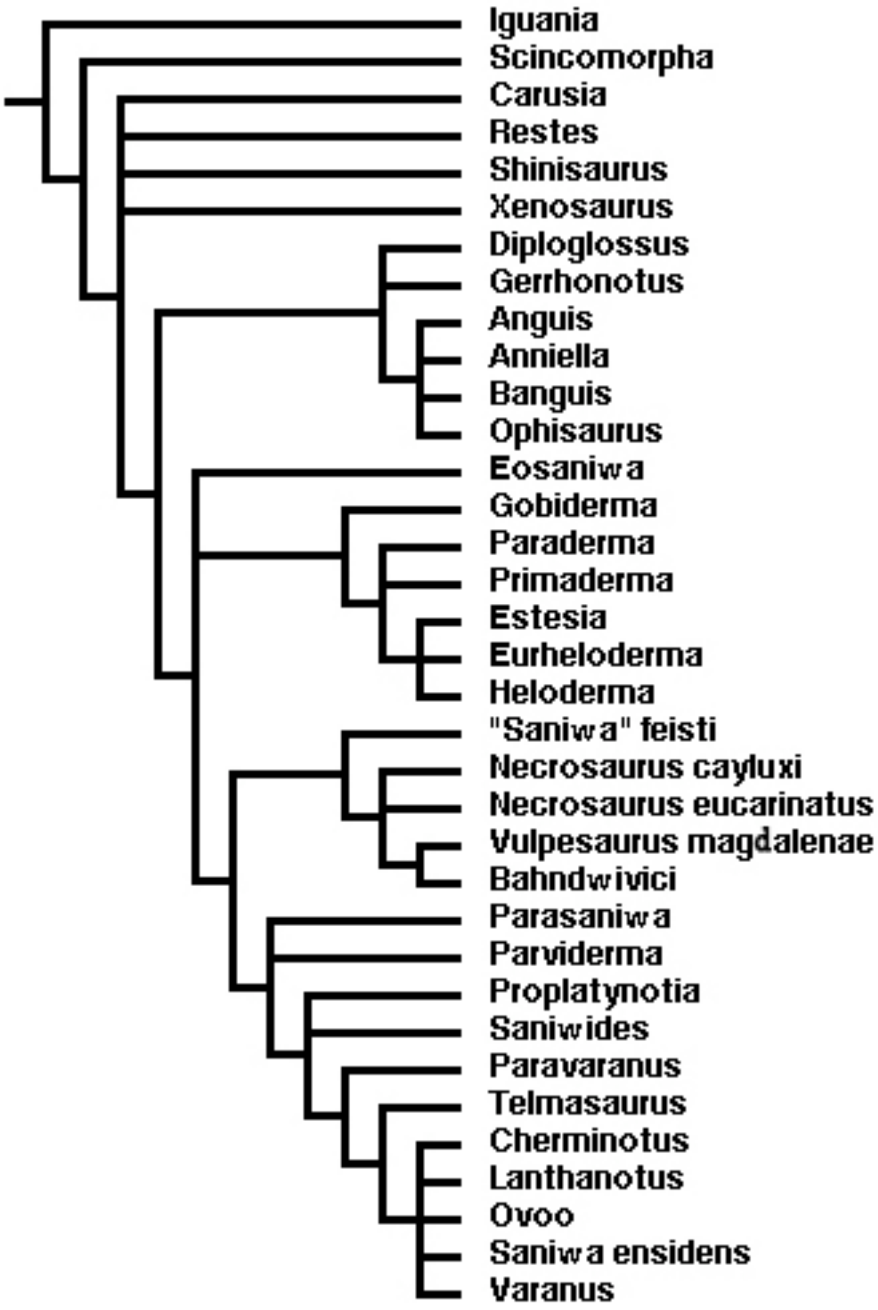
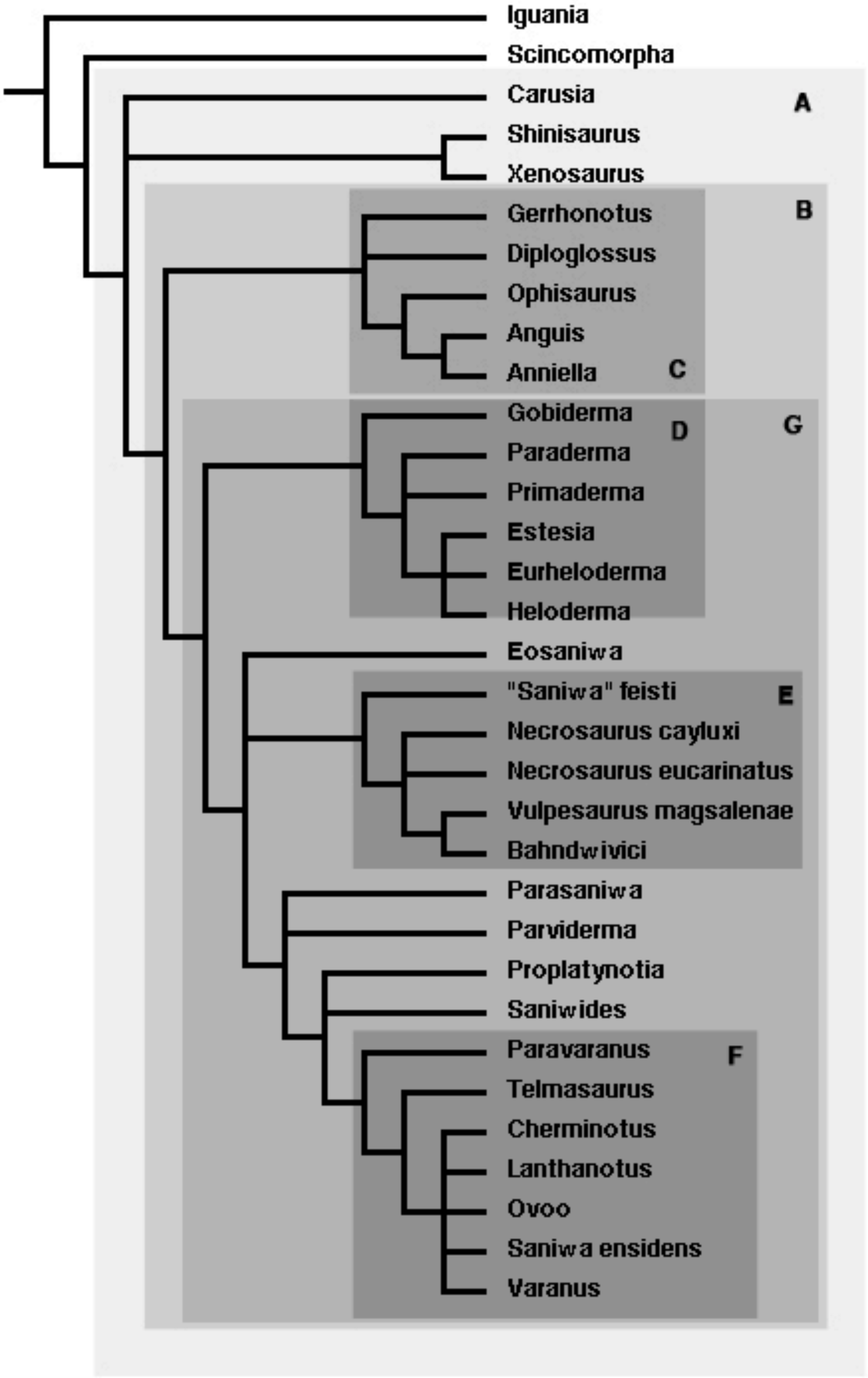

Iguania
Scincomorpha
Carusia
Restes
Shinisaurus
Xenosaurus
Diploglossus
Gerrhonotus
Anguis
Anniella
Banguis
Ophisaurus
Eosaniwa
Gobiderma
Paraderma
Primaderma
Estesia
Eurheloderma
Heloderma
"Saniwa" feisti
Necrosaurus cayluxi
Necrosaurus eucarinatus
Vulpesaurus magdalenae
Bahndwivici
Parasaniwa
Parviderma
Proplatynotia
Saniwides
Paravaranus
Telmasaurus
Cherminotus
Lanthanotus
Ovoo
Saniwa ensidens
Varanus

FIGURE 5-4. Tree D: Strict consensus of 2061 MPTs recovered in analysis D of data matrix after the removal of *Restes* and *Bainguis*. Tree length=334, CI=0.563, RI=0.737. Major clades outlined in shaded boxed and labeled A-Anguimorpha, B-Anguiformes, C-Anguidae, D-Monstersauria, E-Necrosauridae, F-Varanidae and G-Platynota.


Iguania
Scincomorpha
Carusia
A
Shinisaurus
Xenosaurus
Gerrhonotus
B
Diploglossus
Ophisaurus
Anguis
Anniella
C
Gobiderma
D
G
Paraderma
Primaderma
Estesia
Eurheloderma
Heloderma
Eosaniwa
"Saniwa" feisti
E
Necrosaurus cayluxi
Necrosaurus eucarinatus
Vulpesaurus magsalenae
Bahndwivici
Parasaniwa
Parviderma
Proplatynotia
Saniwides
Paravaranus
F
Telmasaurus
Cherminotus
Lanthanotus
Ovoo
Saniwa ensidens
Varanus

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APPENDIX 1

List of specimens used in the character scoring. Data matrix presented in Appendix 3.

Institutional abbreviations: BMNH, British Museum of Natural History; FMNH, Field Museum of Natural History; OMNH, RSM, Royal Saskatchewan Museum; UAMZ, University of Alberta Museum of Zoology; UALVP, University of Alberta Laboratory for Vertebrate Paleontology; USNM, United States National Museum of Natural History. ZPAL, Institute of Paleobiology, Polish Academy of Sciences.

Iguania–*Agama agama* FMNH 22189; *Anolis carolinensis* FMNH 229898; *Basilicus vittatus* FMNH 98361.

Gekkota–*Cyrtodactylus cavernicolis* FMNH 131508; *Cyrtopodion scabrum* FMNH 236232; *Gekko gecko* FMNH 14448, 31013.

Scincomorpha–*Cordylus giganteus* FMNH 211837, 257130; *Gerrhosaurus validus* FMNH 228400, 214858; *Tiliqua scincoides* FMNH 51702, 51710.

Vulpesaurus–*Vulpesaurus magdalena* gen. et sp. nov. RSM P2622.2

Anguis–*Anguis fragilis* UAMZ 370.

Anniella–*Anniella pulchra* FMNH 130477, 130479.

Bahndwivici–*Bahndwivici ammoskius* FMNH PR 2260.

Bainguis*–Bainguis parvus* ZPAL MgR-II/46, MgR-II/90, MgR-II/9, MgR-II/10, MgR-II/11.

Carusia*–Carusia intermedia* ZPAL MgR-III/34.

Cherminotus*–Cherminotus longifrons* ZPAL MgR-III/59, ZPAL MgR-III/67.

Colpodontosaurus*–Colpodontosaurus cracens* UALVP 33388, 29781, 29782.

Diploglossus*–Diploglossus millepunctatus* FMNH 19248.

Dorsetisaurus*–Dorsetisaurus purbeckensis* BMNH R 8129, R 8244.

Eosaniwa*–Eosaniwa koehni* GM XXXVIII/57.

Eurheloderma*–Eurheloderma gallicum* BMNH R3487.

Gerrhonotus*–Gerrhonotus liocephalus* 38525, 99594.

Gobiderma*–Gobiderme pulchra* ZPAL MgR-III/64.

Heloderma*–Heloderma horridum* FMNH 22038; *Heloderma suspectum* FMNH 218077, UAMZ 387.

Lanthanotus*–Lanthanotus borneensis* FMNH 130981, 134711.

Necrosaurus cayluxi*–* BMNH R 3486, R 6822.

Necrosaurus eucarinatus*–* GM CeIII-4139.

Ophisaurus*–Ophisaurus apodus* FMNH 22359.

Paleosaniwa*–Paleosaniwa Canadensis* UALVP 33337, 33339, 33310.

Paraderma–*Paraderma bogerti* UALVP 29845, 33385, 29902, 29903, 33387.

Parasaniwa–*Parasaniwa wyomingensis* UALVP 33347, 33348, 33349, 33350, 33354.

Paravaranus–*Paravaranus angustifrons* ZPAL MgR-I/67.

Parviderma–*Parviderma inexacta* ZPAL MgR-I/43.

Primaderma–*Primaderma nessovi* OMNH 26742, OMNH 27750, OMNH 27022, OMNH 28444, OMNH 34399, OMNH 22071, OMNH 22122, OMNH 34311.

Proplatynotia–*Proplatynotia longirostrata* ZPAL MgR-I/68.

Saniwa ensidens– USNM 2185, FMNH PR 2378, PR 2380.

Saniwides–*Saniwides mongoliensis* ZPAL MgR-I/72.

Shinisaurus–*Shinisaurus crocodilurus* 233130, 234242.

Telmasaurus–*Telmasaurus grangeri* ZPAL MgR-I/65.

Varanus–*Varanus acanthurus* FMNH 98935; *Varanus albigularis* FMNH 22354; *Varanus bengalensis* FMNH 22495; *Varanus komodensis* FMNH 22199, 22200; *Varanus niloticus* FMNH 12300, 17144; *Varanus rudicollis* FMNH 145710.

Xenosaurus–*Xenosaurus grandis* FMNH 211833.

APPENDIX 2

List of characters used in plylogenetic analysis of *Vulpesaurus magdalena* ge. et sp. novum. References for characters in parentheses following character description.

Cranial characters

1. Premalillary-maxillary aperture absent (0); or present (1). [Rieppel 1980, character 3; Lee 1997, character 66; Norell and Gao 1997, character 1; Gao and Norell 1998, character 1]

2. Incisive process of premaxilla a single spine (0); or bipartite (1). [Rieppel 1980, character 5; Gao and Norell 1998, character 46]

3. Nasal bones paired (0); or fused (1). [Modified from Gao and Norell 1998, character 2]

4. Nasal and prefrontal bones in broad contact (0); or separated by contact of frontal with maxilla (1); or separated by gap (2). [Rieppel 1980, character 18; Preghill et al. 1986, character 2; Estes et al. 1988, character 4; Norell et al. 1992, character 2; Norell and Gao 1997, character 3; Gao and Norell 1998, character 3]

5. Nasal and maxillary bones in broad contact (0); or entirely or largely separated by gap (1); or separated by prefrontal (2). [Pregill et al. 1986, character 4; Norell et al. 1992, character 4; Norell and Gao 1997, character 4; Gao and Norell 1998, character 4]

6. Nasal process of maxilla located at the anterior (0); or middle (1); or posterior part of maxilla (2). [Pregill et al. 1986, character 5; Norell et al. 1992, character 5; Lee 1997, character 8; Norell and Gao 1997, character 5; Gao and Norell 1998, character 5]

7. Portion of narial border formed by maxilla vertical (0); or posterodorsally sloped (1). [New]

8. Frontals are paired in adult stage (0); or fused (1). [Rieppel 1980, character 13; Estes et al. 1988, character 6; Lee 1997, character 14; Gao and Norell 1998, character 6]

9. Frontonasal suture W-shaped with distinct anterolateral and anteromedial points of the frontal (0); or with a single anteromedial apex (1). [New]

10. Lateral border of frontals more or less parallel-sided (0); or hourglass-shaped (1), or trapezoidal (2). [Rieppel 1980, character 15; Pregill et al. 1986, character 6; Estes et al. 1988, character 7; Norell et al. 1992, character 6; Norell and Gao 1997, character 6; Gao and Norell 1998, character 7]

11. Subolfactory processes of frontals poorly defined (0); or well developed as lateral wall of olfactory tract (1). [Gao and Norell 1998, character 8]

12. Subolfactory processes of frontals do not contact each other ventrally (0); enxtensive contact along midline (1); closely approach or contact anteromedially (2); or closely approach or contact posteromedially (3). [Rieppel 198, character 16; Pregill et al 1986, characters 7, 8 and 9; Estes et al. 1988, character 10;

Norell et al. 1992, character s 7, 8 and 9; Lee 1997, character 15; Norell and Gao 1997, characters 7, 8 and 9; Gao and Norell 1998, character 9]

13. Prefrontal not contributing to the external narial opening (0); or contributing to the external narial opening due to strong anterior extension of the prefrontal (1); or contributing to the external narial border owing to a retraction of the external nares (2). [Gao and Norell 1998, character 10]

14. Prefrontal does not (0); or does contact postfrontal above orbit (1). [Pregill et al. 1986, character 10; Estes et al. 1988, character 5; Norell et al. 1992, character 10; Lee 1997, character 13; Norell and Gao 1997, character 10; gao and Norell 1998, character 11]

15. Posterior lacrimal foramen single (0); or double with both upper and lower foramina bordered medially by prefrontal (1); double with upper bordered medially by prefrontal and lower housed completely within lacrimal (2); double with both upper and lower housed entirely within lacrimal (3). [New/heavily modified]

16. Maxillae form lateral margins of muzzle only (0); or contribute to the anterolateral margins as well (1). [New - related to muzzle shape]

17. Jugal/squmosal contact on supratemporal arch absent (0); or present (1). [Estes et al. 1988, character 18; Gao and Norell 1998, character 12]

18. Jugal well developed and angulated (0); or strongly reduced with little or no angulation (1). [Gao and Norell 1998, character 13]

19. Posteroventral process of jugal well developed (0); nearly or entirely lost (1). [Gao and Norell 1998, character 14]

20. Jugal contacts postorbitofrontal, completing postorbital bar (0); or does not (1). [Rieppel 1980, character 26; Estes 1988, character 32; Gao and Norell 1998, character 15]

21. Dilation of postorbital branch of jugal absent (0); or present (1). [Gao and Norell 1998, character 16]

22. Postorbital/postfrontal fusion absent (0); or present (1). [Rieppel 1980, character 20; Estes et al. 1988, character 14; Lee 1997, character 11; Gao and Norell 1998, character 20]

23. Canthal crest on temporal arch absent (0); or present (1). [Gao and Norell 1998, character 21]

24. Parietal foramen present (0); or absent (1). [Rieppel 1980, character 30; Pregill et al. 1986, character 11; Estes et al. 1988, character 26; Norell et al. 1992, character 11; Lee 1997, character 21; Norell and Gao 1997, character 12; Gao and Norell 1998, character 22]

25. Descensus parietalis present as an anteroposteriorly elongate, ventrolaterally projecting crest (0); or as an anterposteriorly narrow ventral projection (1). [Modified Conrad 2008, character 76]

26. Supratemporal arch present (0); or absent (1). [Rieppel 1980, character 35; Pregill et al. 1986, characters 12 and 13; Estes et al. 1988, characters 16 and 33;

Norell et al. 1992, characters 12 and 13; Lee 1997, character 22; Norell and Gao 1997, character 13; Gao and Norell 1998, character 24]

27. Origin of temporal musculature on dorsolateral aspect (0); or on ventral aspect of parietal table (1). [Pregill et al. 1986, character 14; Estes et al 1988, character 54; Norell et al. 1992, character 14; Norell and Gao 1997, character 14; Gao and Norell 1998, character 26]

28. Posterior parietal table broad (0); or constricted (equal to or less than minimum frontal width) (1). [New]

29. Supratemporal process of parietal in dorsal aspect flat (0); or narrow with sharp crest (1). [Pregill et al. 1986, character 18; Norell et al. 1992, character 18; Norell and Gao 1997, character 29; gao and Norell 1998, character 33]

30. Anterior extension of supratemporal does not reach (0); reaches (1); or exceeds the level of the apex of the parietal notch (2). [New/Modified]

31. Tympanic crest of quadrate large (0), or crest strongly reduced (1) [Gao and Norell 1998, character 35]

32. Pterygoid lappet of quadrate absent (0); or present (1). [Estes et al. 1988, character 37; Norell and Gao 1997, character 32; Gao and Norell 1998, character 36]

Braincase characters

33. Hypoglossal foramen not enlarged (0); or enlarged and confluent with vagal foramen (1). [Pregill et al. 1986, character 16; Norell et al. 1992, character 16; Norell and Gao 1997, character 16; Gao and Norell 1998, character 27]

34. Posterior opening of vidian canal located at prootic/basisphenoid suture (0); or penetrates basisphenoid only (1). [Estes et al. 1988, character 53; Lee 1997, character 19; Gao and Norell 1998, character 28]

35. Facial foramen in recessus vena jugularis single (0); or double (1). [Rieppel 1980, character 59; Lee 1997, character 42; Norell and Gao 1997, character 1998, character 29]

36. Basioccipital/basisphenoid suture obtusely angulate and laterally diagonal (0); or roughly a straight line suture in keeping with anterior shifting of spheno-occipital tubercle (1). [Norell and Gao, 1997, character 26; Gao and Norell 1998, character 31]

37. Spheno-occipital tubercle short and ventrally directed (0); or elongate and posterolaterally directed (1). [Norell and Gao 1997, character 23]

38. Foramen ovale located above or slightly posterior to the spheno-occipital tubercle (0); or anterior to the tubercle (1). [Norell and Gao 1997, character 25]

39. Basipterygoid processes long, projecting aterolaterally from the body of the basisphenoid (0); or short, not projecting beyond the body of the basisphenoid (1). [Lee 1997, character 33]

40. Articular facet for pterygoid at distal end of basipterygoid process limited to a small sub-circular area (0); or large and anteroposteriorly elongate (1). [Lee 1997, character 34]

41. Crista tuberalis weakly developed, proximal portion of stapes visible in ventral view (0); or strongly developed, proximal portion of stapes not visible in ventral view (1). [Modified Lee 1997, character 47]

Palate characters

42. Distinct medial projection anteroventral to mesopterygoid fossa absent (0); or present to enhance basipterygoid/pterygoid articulation (1). [Rieppel 1980, character 53; Gao and Norell 1998, character 32]

43. Vomer not elongate roughly equal to palatine length (0); or elongate roughly twice the length of the palatine (1). [Modified Gao and Norell 1998, character 47]

44. Aperture of jacobsen's organ confluent with internal narial opening (0); or separated from narial opening by vomer-maxillary contact (1). [Rieppel 1980, character 42; Estes et al. 1988, character 42; Gao and Norell 1998, character 48]

45. Palatal shelves of vomer wide (0); or narrow (1). [Pregill et al. 1986, character 32; Norell et al. 1992, character 32; Lee 1997, character 51; Norell and Gao 1997, character 44; Gao and Norell 1998, character 50]

46. Palatine longer than wide (0); or equally wide as long (1). [Pregill et al. 1986, character 33; Norell et al. 1992, character 33; Norell and Gao 1997, character 45; Gao and Norell 1998, character 51]

47. Palatine teeth present (0); or absent (1). [Gao and Norell 1998, character 52]

48. Pterygoid teeth present as a patch (0); or as a single row (1); or absent (2). [New]

49. Anterolateral process of pterygoid short and fits into a notch of ectopterygoid (0); or extended dorsally on ectopterygoid to contact jugal (1). [Gao and Norell 1998, character 54]

50. Palatine process of pterygoid roughly half as long as the quadrate process of the pterygoid (0); or equal to or greater in length than the quadrate process of the pterygoid (1). [New]

51. Ectopterygoid laterally concealed by maxilla and jugal (0); or exposed on ventral edge of skull (1). [Rieppel 1980, character 49; Gao and Norell 1998, character 18]

52. Ectopterygoid in palatal view does not contact palatine anteriorly (0); or does, excluding maxilla from suborbital fenestra (1). [Rieppel 1980, character 9; Pregill et al. 1986. Character 36; Estes et al. 1988, character 45; Norell et al

1992, character 36; Norell and Gao 1997, character 48; Gao and Norell 1998, character 55]

Mandibular characters

53. Retroarticular process not widened (0); or widened (1). [Estes et al. 1988, character 78; Gao and Norell 1998, character 69]

54. Retroarticular process posteriorly directed (0); or directed medially (1). [Estes et al. 1988, character 75; Gao and Norell 1998, character 71]

55. Strong mediolateral reduction of mandibular fossa absent (0); or present (1). [Modified Gao and Norell 1998, character 67]

56. Surangular does not extend anteriorly beyond (0); or slightly beyond (1); or well beyond coronoid eminence (2). [Rieppel 1980, character 65; Pregill et al. 1986, character 40; Norell et al 1992, character 40, Gao and Norell 1998, character 58]

57. Anterior process of coronoid is not (0); or is elongate and extensively exposed dorsally (1). [Gao and Norell 1998, character 63]

58. Anterior extension of splenial far beyond midpoint of tooth row (0); or retracted to or posterior to midpoint of tooth row (1). [Estes et al 1988, character 65; Norell and Gao 1997, character 52; Gao and Norell 1998, character 59]

59. Posterior extension of splenial beyond coronoid eminence (0); or terminates anterior to or below the eminence (1). [Rieppel 1980, character 62; Pregill et al. 1986, character 42; Estes et al. 1988, character 66; Lee 1997, character 72;

Norell et al. 1992, character 42; Norell and Gao 1997, character 53; Gao and Norell 1998, character 60]

60. Splenial dentary suture firm (0); or loose, with much connective tissue between the two bones (1). [Pregill et al. 1986, character 43; Estes et al. 1988, character 67; Norell et al. 1992, character 43; Norell and Gao 1997, character 54; Gao and Norell 1998, character 61]

61. Intramandibular septum within Meckelian canal absent (0); or present as oblique or vertical septum (1). [Estes et al. 1988, character 56; Gao and Norell 1998, character 62]

62. Surangular and angular processes of dentary, large and pointed (0); or small and rounded (1). [New]

63. Subdental shelf present (0); or lost in keeping with the fusion of the dentary tube (1); or strongly reduced as a slope (2). [Estes et al. 1988, characters 58 and 59; Lee 1997, character 67; Gao and Norell 1998, character 64]

64. Posterodorsal extension of dentary overlapping base of coronoid eminence present (0); or absent (1). [New]

65. Dentary curved in lateral view, with concave dorsal edge (0); or completely straight in lateral view (1). [Lee 1997, character 71]

66. Meckelian canal open medially for the entire length (0); or open ventrally anterior to anterior inferior alveolar foramen (1); or completely closed as a

dentary tube (2). [Estes et al. 1988, character 57; Lee 1997, character 69; Gao and Norell 1998, character 66]

Dental characters

67. Premaxillary teeth large (0); or abruptly smaller than maxillary teeth (1). [Pregill et al. 1986, character 23; Norell et al. 1992, character 23; Npreall and Gao 1997, character 35; Gao and Norell 1998, character 39

68. Marginal tooth bases smooth (0); or bearing distinct ridges (1). [Modified from on Estes et al. 1988, character 86]

69. Marginal teeth are not (0); or are widely spaced (1). [Based on Pregill et al. 1986, character 25; Gao and Norell 1998, character 41]

70. Tooth bases are not (0); or are expanded (1). [Based on Pregill et al. 1986, character 25; Gao and Norell 1998, character 41]

71. Replacement teeth developed entirely or partially in resorption pits (0); or develop without presence of resorption pits (1). [Pregill et al. 1986, character 26; Estes et al. 1988, character 85; Norell et al. 1992, character 26; Lee 1997, character 89; Norell and Gao 1997, character 38; Gao and Norell 1998, character 42]

72. Replacement teeth develop ventrolingually to previous tooth (0); or posterolingually (1). [Modified from Gao and Norell 1998, character 42]

73. Maxillary tooth row extends extensively suborbital (0); or slight suborbital with no more than three tooth positions (1); or entirely antorbital (2). [Gao and Norell 1998, character 43]

74. Maxillary teeth number more than 13 positions (0); 10-13 positions (1); or nine or fewer positions (2). [Pregill et al. 1986, characters 28 and 29; Norell et al. 1992, characters 28 and 29; Lee 1997, character 92; Norell and Gao 1997, characters 40 and 4; Gao and Norell 1998, character 44]

75. Dentary teeth number 13 or more positions (0); or 12 to 9 positions (1); or 8 or fewer positions (2). [Lee and Caldwell 2000, character 174]

76. Venom groove on marginal teeth absent (0); or present (1). [Pregill et al. 1986, character 30; Norell et al. 1992, character 30; Lee 1997, character 92; Norell and Gao 1997, character 42; Gao and Norell 1998, character 45]

Osteodermal characters

77. Dermal ornamentation of postorbital branch of jugal absent (0); or present (1). [Gao and Norell 1998, character 17]

78. Dermal ornamentation on parietal absent (0); or present as distinct projections consistent with fusion of osteoderms (1). [New/extensively reformatted]

79. Fused cephalic osteoderms absent (0); present as large, thin polygonal plates (1); or present as small, low lying bumps (2); or present as large, thick sub-conical mounds (3). [New/extensively reformatted]

80. Body osteoderms absent (0); present as flat, imbricating plates (1); present as ovoid scutes with a sagittal keel (2); or present as round, sub-conical mounds (3). [New]

81. Osteodermal ornamentation does not (0); or does form a mid-sagittal keel on the frontal (1). [New]

82. Ossified palpebrals absent (0); or present (1). [Pregill et al. 1986, character 78; Estes et al. 1988, character 36; Norell et al. 1992, character 78; Norell and gao 1997, character 87; Gao and Norell 1998, character 74]

Vertebral characters

83. Number of cervical vertebrae eight or less (0); nine (1) ten or more (2). [Pregill et al. 1986, character 49; Estes et al. 1988, character 108; Norell et al. 1992, character 49; Lee 1997, character 108; Norell and Gao 1997, character 60; Gao and Norell 1998, character 76]

84. Cervical intercentrum intervertebral or fixed under anterior part of following centrum (0); sutured to posterior part of preceding centrum (1); or fused to posterior part of preceding centrum (2). [Rieppel 1980, character 72; Estyes et al. 1988, character 97; Gao and Norell 1998, character 77]

85. Vertebral condyle/cotyle articulation vertical (0); slightly oblique with condylar surface broadly visible in ventral view (1); or very oblique with condylar surface only slightly or not visible in ventral view (2). [Extensively modified from Lee 1997, character 88]

86. Vertebral precondylar constriction absent (0); present, weakly constricted (1); or strongly constricted to less than 80% of the maximum condylar diameter (2). [Lee 1997, character 96; Conrad 2008, character 233]

87. Number of presacral vertebrae fewer than 26 (0); or 26 or more (1). [Pregill et al. 1986, character 51; Estes et al. 1988, character 106; Norell et al. 1992, character 51; Norell and Gao 1997, character 62; Gao and Norell 1998, character 80]

88. Autotomy on caudal vertebrae present (0); or absent (1). [Pregill et al. 1986, character 52; Estes et al. 1988, character 103; Norell et al, 1992, character 52; Norell and Gao 1997, character 63; Gao and Norell 1998, character 81]

89. Caudal chevrons contact centrum condyle (0); suture to centrum only (1); or fuse to centrum (2). [Pregill et al. 1986, character 54; Norell et al. 1992, character 54; Norell and Gao 1997, character 65; Gao and Norell 1998, character 83]

Appendicular characters

90. Epicoracoid contacts suprascapula and mesoscapula (0); or not (1). [Pregill et al. 1986, character 55; Estes et al. 1988, character 114; Norell et al. 1992, character 55, Norell and Gao, 1997, character 66; Gao and Norell 1998, character 84]

91. Posterior coracoid emargination absent (0); or present (1). [Pregill et al. 1986, character 57; Estes et al. 1988, character 113; Norell et al. 1992, character 57; Lee 1997, character 126; Norell and Gao 1997, character 67; Gao and Norell 1998, character 85]

92. Interclavicle T or anchor shaped without anterior process (0); cruciform with prominent anterior process (1); or vestigial or entirely lost in adults (2). [Pregill et al. 1986, character 59; Estes et al. 1988, characters 118 and 120; Norell et al. 1992, character 59; Lee 1997, character 119; Norell and Gao 1997, character 69; Gao and Norell 1998, character 86]

93. Mesosternum present (0); or absent (1). [Pregill et al. 1986, character 60; Norell et al. 1992, character 60; Norell and Gao 1997, character 70; Gao and Norell 1998, character 87]

94. Rib attachments on sternum more than three pairs (0); or three pairs (1); or two or fewer pairs (2). [Pregill et al. 1986, character 61; Estes et al. 1988, character 109; Norell et al. 1992, character 61; Lee 1997, characters 122 and 123; Norell and gao 1997, character 71; Gao and Norell 1998, character 88]

95. Strong elongation of symphasial process of pubis absent (0); or present (1). [Estes et al. 1988, character 124; Gao and Norell 1998, character 89]

Soft tissue characters

96. M. episterno-cleido-mastoideus inserts mainly on paroccipital process (0); or has extensive insertion on the parietal (1). [pregill et al. 1986, character 62; Norell and Gao 1997, character 72; Gao and Norell 1998, character 91]

97. M. constrictor colli does not (0); or does extensively cover first ceratobranchials (1). [Pregill et al. 1986, character 63; Norell and Gao 1997, character 73; Gao and Norell 1998, character 92]

98. Origin of 3b-layer of MAME profundus from supratemporal and parietal (0); or supratemporal only (1). [Pregill et al. 1986, character 64; Norell and Gao, 1997, character 74; Gao and Norell 1998, character 93]

99. M. geniomyohyoideus absent (0); present but completely superficial to m. genioglossus (1); or insertion at least partly invades deep to m. genioglossus medialis (2). [Pregill et al. 1986, character 65; Norell and Gao 1997, character 75; Gao and Norell 1998, character 94]

100. M. genioglossus lateralis single bundle and not inserted into hyobranchial skeleton (0); or subdivided into separate bundles and inserted into hyobranchials (1). [Pregill et al. 1986, character 66; Norell and gao 1997, character 76; Gao and Norell 1998, character 95]

101. Insertion of m. levator pterygoidii extends posteriorly beyond columellar fossa of pterygoid (0); or restricted anteriorly (1). [Pregill et al. 1986, character 67; Norell and Gao 1997, character 77; gao and Norell 1998, character 96]

102. Anterior head of m. pseudotemporalis profundus absent (0); or present but not expanded (1); or present and expanded (2); or lost by fusion (3). [Pregill et al. 1986, character 68; Estes et al. 1988, character 133; Norell and gao 1997, character 78; Gao and Norell 1998, character 97]

103. Bodenaponeurosis with broad base extending onto lateral edge of mandibular fossa (0); or narrow base attached only to caudomesial edge of coronoid (1). [Pregill et al. 1986, character 69; Norell and Gao 1997, character 79; Gao and Norell 1998, character 98]

104. Hemibacula (mineralized horns of hemipenis) absent (0); or present (1). [Gao and Norell 1998, character 99]

105. Foretongue not notched or cleft for less than 10% of length (0); cleft for 10-20% of length (1); or deeply cleft from 20% up to 50% of length (2). [Pregill et al. 1986, characters 71 – 72; Estes et al. 1988, character 137; Norell and Gao 1997, character 81; Gao and Norell 1998, character 100]

106. Carotid duct present (0); or absent (1). [Gao and Norell 1998, character 101]

107. Gland of Gabe absent (0); or present (1). [Gao and Norell 1998, character 102]

108. Cochlear duct not robust (0); or robust and broad, limbus elongate and heavy (1). [Pregill et al. 1986, character 75; Norell and Gao 1997, character 84; Gao and Norell 1998, character 103]

109. Ulnar nerve superficial (0); or deep in the forearm (1). [Pregill et al. 1986, character 76; Estes et al. 1988, character 142; Norell and Gao 1997, character 85; Gao and Norell 1998, character 104]

110. Second epibranchial present (0); or absent (1). [Pregill et al. 1986, character 77; Norell and Gao 1997, character 86; Lee 1997, character 143; gao and Norell 1998, character 105]

APPENDIX 3

Data matrix (42 Taxa, 110 characters) used in phylogenetic analysis of *Vulpesaurus magdalena* gen. et sp. novum. See Appendix I for character descriptions and text (Chapter 6) for discussion of character construction and modifications.

Iguania:

0&1	0	0	0	0	0	0	1	0	1
0	0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0&1	0&1	0&1
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1&2	0	0
0	0	0	0	0	0	0	0	0&1	0
0	1	0	0	0	0&2	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0

Gekkota:

0	0	0	0&1	0	1	0&1	0&1	0	0
1	1	0	0	0	0&1	0	1	1	1
0	0	-	1	0	1	1	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0&1	0	0	0	1	2	0	0

0	0&1	1	1	0	0	1	1	0	0
0	0	1	0&1	0	2	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0&1	0	0&1
0&1	0	0	0&1	0	?	0&1	0	0	0
0	0&1	0	0	0	0	0	0	0	0

Scincomorpha:

0&1	0	0	1	0	1	0&1	0&1	0	0
0	0	0	0	0	0	0&1	0	0	0
0	0&1	0	0	1	0	0&1	0&1	0	0
0	0&1	0	0&1	0	0&1	0	0	0	0
0	0	0	0	0	0	1	1&2	0	0
0	0	0	0	0	0&1	0&1	0	0	0
0	1	0	0&1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0&1	0
0	0&1	0	0	0	0	0	0	0	0&1
0&1	1	0	0	1	?	0	0	0	0
0	1	0	0	0&1	0	0	0	0&1	0

Vulpesaurus:

?	?	?	?	?	?	?	?	?	?
?	?	?	0	?	?	0	?	?	0
?	0	?	0	0	0	0	1	1	2

?	?	0	?	0	0	1	1	1	1
0	1	1	?	1	?	?	1	0	1
0	1	?	?	1	1	?	0	?	1
?	0	?	?	?	?	?	0	1	1
1	?	1	?	?	?	?	0	0	?
?	?	?	1	1	0	0	0	0	0
0	0&1	?	?	?	?	?	?	?	?
0	?	?	?	?	?	?	?	?	?

Aigialosaurus:

?	?	?	?	?	0	1	1	?	0
?	?	?	0	?	?	0	0	0	0
0	1	0	0	0	0	0	1	1	0
0	?	?	?	?	?	0	?	1	1
?	1	1	?	?	?	?	1	?	1
?	?	?	?	?	0	?	0	?	?
?	1	?	1	1	?	?	1	1	0
1	?	1	0	0	0	0	0	0	0
-	?	0	?	2	0	1	0	?	?
?	2	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Anguis:

1	1	0	0	0	1	1	0	0	0
1	0	0	0	0	0	0	1	1	0
0	0&1	0	0&1	0	0	1	0	0	0
1	0	0	0	0	0	0	0	0	0
0	1	0	1	0	0	1	1&2	1	0
0	0	1	1	1	2	0	1	0	0
1	0	2	0	0	1	1	0	0	0
0	0	1	2	0	0	0	0	1	1
0	1	0	2	0	0	1	0	2	0
0	2	0	1	1	0	0	0	1	0
0	2	0	0	1	0	0	0	0	1

Anniella:

0	0	0	0	0	1	1	0	0	0
1	1	0	1	0	0	0	1	1	1
0	0	-	0	1	1	0	0	0	1
1	0	0	0	0	0	0	0	0	0
0	1	1	1	0	0	1	2	1	0
1	1	1	1	1	2	0	1	0	0
1	0	2	0	0	1	1	0	0	0
0	0	2	2	0	0	0	0	0	0
0	1	2	2	0	0	1	0	2	-

1	2	1	-	1	0	0	0	1	0
0	3	1	0	1	?	0	?	0	1

Bahndwivici:

0	?	0	?	?	1	1	1	0	0
?	?	?	0	?	0	?	0	0	0
0	0	0	0	0	0	0	1	1	0
1	0	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	0	?	1	1	1	?	?	?
?	?	2	1	0	?	?	0	1	1
?	?	1	0	0	0	0	1	2	2
1	?	?	?	1	0	1	0	0	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Banguis:

?	?	?	?	?	?	?	0	?	0
1	0	0	?	?	?	?	1	1	?
?	?	?	?	?	?	?	0	?	?
1	?	?	?	?	0	0	0	0	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	2	?	0	?	?	?	?	?

?	?	?	?	?	?	?	?	?	1
0	?	?	?	0	0	?	0	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Carusia:

0	1	0	1	0	0	0	1	0	1
1	0	0	0	0	0	1	0	0	0
0	1	0	0	1	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	1	0	0
0	0	0	0	1	1	0	0	0	0
1	1	0	0	0	1	0	0	0	0
0	0	0	0	0	0	1	1	2	?
0	1	?	?	0	0	?	?	?	?
0	1	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Cherminotus:

0	1	0	2	1	2	?	0	0	0
1	3	2	?	0	1	0	1	1	0
0	?	-	0	0	?	0	0	1	?
1	0	1	?	?	0	0	0	0	0
1	1	1	?	1	1	?	1	?	0

0	1	0	?	1	2	1	1	1	1
?	1	2	?	0	1	?	1	1	1
1	?	2	2	?	0	0	0	0	?
-	?	?	?	2	0	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Colpodontosaurus:

?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	1
1	?	2	?	0	1	?	0	0	1
1	?	?	?	?	0	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Diploglossus:

1	1	0	1	0	1	1	0	0	0
1	0	0	0	0	0	0	0	0	0
0	0&1	0	0	1	0	1	0	0	0

0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	1	2	0	0
0	0	1	1	1	2	0	0&1	0	0
1	0	2	0	0	1	1	0	0	0
0	0	0	0	0	0	0	0	1	1
0	1	0	2	0	0	1	0	2	0
0	1	0	1	1	0	0	0	1	0
1	1	0	0	1	0	0	0	0	1

Dorsetisaurus:

?	?	?	?	?	1	1	1	0	1
1	0	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	0	?	0	0	0	0	0	0
0	?	?	?	?	?	?	?	0	?
?	?	?	?	0	?	?	?	?	?
?	?	2	?	?	?	?	?	1	0
?	?	?	2	0	0	?	0	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Eosaniwa:

?	?	0	?	0	0	?	0	?	0
1	0	0	0	?	?	?	0	?	0
0	?	?	?	?	?	?	?	?	?
0	?	?	?	?	?	?	?	?	?
?	1	1	?	1	0	0	1	0	0
?	?	1	1	1	2	1	1	?	1
?	?	2	?	1	1	?	1	1	1
1	?	0	0	0	0	0	?	2	2
0	1	?	1	?	0	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Estesia:

0	1	0	2	1	2	1	0	0	0
1	0	2	1	0	1	0	0	1	0
0	1	0	1	0	0	1	?	0	1
0	1	0	0	0	0	1	1	0	0
0	1	1	1	1	1	?	?	1	0
0	1	0	?	1	2	1	?	?	?
?	1	2	1	0	1	1	1	1	1
1	?	2	1	1	1	0	?	?	?
-	?	?	?	?	?	?	?	?	?

?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Eurheloderma:

?	?	?	?	?	1	1	?	?	?
?	?	?	?	?	1	?	?	?	?
?	?	?	1	1	?	1	0	0	0
?	?	?	?	?	?	?	?	?	?
?	1	?	?	?	?	?	1	?	?
?	?	?	?	?	2	?	1	?	?
1	?	2	?	0	1	?	1	1	1
1	?	2	1	1	1	?	1	3	?
?	?	?	?	1	0	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Gerrhonotus:

0	1	0	0&1	0	1	1	1	0	1
1	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	1	1&2	0	0
0	0	1	1	1	2	0	0	0	0
1	0	2	0	0	1	1	0	0	0

0	0	0	0	0	0	0	0	1	1
0	1	?	2	0	0	1	0	2	0
0	1	0	1	1	0	0	0	1	0
0	0	0	0	1	0	0	0	0	0

Gobiderma:

0	1	0	0	0	1	1	0	0	0
1	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	1	0	0	2
0	1	0	0	?	0	1	1	0	0
0	1	1	1	1	1	0	0	1	0
0	1	0	1	1	2	1	1	1	1
?	?	2	1	0	1	1	1	1	1
1	?	1	1	1	?	0	?	3	?
0	?	?	?	?	0	?	?	0	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Heloderma:

0	1	0	2	1	1	1	0	0	2
1	2	2	1	0	1	0	0	0	0
0	1	-	1	1	1	1	0	0	2
0	1	0	0	0	0	0	0	0	1
0	1	1	0	1	1	0	1&2	1	0

0	1	0	1	1	2	1	1	1	1
1	0	2	1	0	1	1	1	1	1
1	1	2	2	1&2	1	0	0	3	3
0	0	0	1	2	0	1	1	0	1
0	-	1	1	0	1	0	1	2	1
0&1	1	1	0	2	1	1	1	1	0

Lanthanotus:

0	1	1	2	1	2	1	0	0	2
1	3	2	1	1	1	0	1	1	0
0	1	-	1	0	1	0	0	1	1
1	0	1	1	1	1	0	0	0	0
1	1	1	1	0	1	0&1	1	0	0
1	1	0	1	1	2	1	1	1	1
1	1	2	1	0	1	1	1	1	1
1	1	2	1	1	0	0	0	0	3
-	0	1	1	2	1	1	1	1	1
1	0	1	2	0	1	1	1	1	1
1	2	0	1	2	1	1	1	1	1

N. cayluxi:

?	1	?	?	?	1	1	1	0	0
1	0	?	0	?	0	?	?	?	?
?	?	?	0	0	?	0	1	1	0

?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	0	?
?	?	?	?	?	1	?	1	?	1
1	?	2	?	0	1	?	1	1	1
1	1	?	0	0	0	?	1	2	2
1	?	?	1	1	0	?	1	0	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

N. eucarinatus:

?	1	?	?	?	1	1	1	0	0
1	0	?	0	?	0	?	0	0	?
0	?	?	0	0	?	0	1	1	0
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	1	1	?	1	?	1
1	?	2	?	0	1	?	1	1	1
1	1	1	0	0	0	?	1	2	2
1	?	?	1	1	0	?	1	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Ophisaurus:

1	1	0	0	1	1	0	0	0	2
1	0	0	0&1	0	0	0	1	1	0
0	0	0	0	1	0	1	0	0	0
1	0	0	0	0	0	0	0	0	0
0	1	0	1	0	0	0	0	1	0
1	0	1	1	1	2	0	0	0	0
1	0	2	0	0	1	1	0	0	0
0	0	0	0&1	0	0	0	0	1	1
0	1	0	2	0	0	1	0	2	0
0	0&2	0	1	1	0	0	0	1	0
0	2	0	0	1	0	0	0	0	1

Ovoo:

1	1	0	0	1	2	1	0	0	0
1	3	2	1	?	0	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	1	1	0	1	1	0	1	0	0
1	1	?	?	?	?	?	?	?	?
?	?	?	?	?	?	1	1	1	1
1	1	1	1	?	0	?	?	0	?
0	?	?	?	?	?	?	?	?	?

?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Paleosaniwa:

?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	1	0	?	?
?	?	?	?	?	?	1	?	?	?
?	?	?	?	?	?	?	0	?	?
?	?	?	?	?	?	?	1	?	?
1	?	2	?	0	1	?	1	1	1
1	?	?	1	?	0	?	?	?	?
0	?	?	?	2	1	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Paraderma:

?	1	?	?	?	1	1	?	?	?
?	?	?	?	?	1	?	?	?	?
?	?	?	0	1	?	1	0	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	1	?	?
1	?	2	?	0	1	?	1	1	1

1	?	?	1	?	?	?	?	3	?
0	?	?	?	1	0	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Parasaniwa:

?	?	?	?	?	1	0	1	?	0
1	0	?	?	?	?	?	?	?	?
?	?	?	0	0	?	0	0	?	?
?	?	?	?	?	?	?	1	?	?
?	?	?	?	?	?	?	0	?	?
?	?	?	?	?	2	?	1	?	?
1	?	2	?	0	1	?	1	1	1
1	?	?	1	?	0	?	?	3	?
0	?	?	?	1	0	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Paravaranus:

?	?	1	2	1	2	1	1	0	0
0	0	2	0	0	?	?	0	1	0
0	?	0	0	0	0	0	0	1	0
?	?	0	?	?	0	0	0	0	0
?	1	1	?	1	1	1	0	?	?

0	?	?	?	1	?	?	?	?	?
?	?	2	?	?	?	?	?	?	?
1	?	?	?	?	?	0	0	0	?
-	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Parviderma:

?	?	0	1	0	?	?	1	0	1
1	0	?	0	?	?	?	?	?	?
?	?	?	0	0	?	0	0	?	?
?	?	?	?	?	0	?	?	0	0
0	1	?	?	?	?	0	0	?	?
?	?	?	?	1	2	1	?	1	1
?	?	2	?	?	1	0	1	1	1
1	?	?	?	?	?	?	1	2	?
0	1	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Pontosaurus:

?	?	0	2	1	2	1	1	0	1
?	?	2	0	?	0	0	0	0	0
0	1	0	0	0	0	0	1	1	0

0	?	?	?	?	?	0	?	?	?
0	1	1	?	?	?	1	?	?	?
?	?	1	0	?	0	1	1	?	?
?	1	?	1	1	1	0	0	1	0
?	?	1	0	0	0	0	0	0	0
-	?	1	1	?	?	1	0	0	?
0	2	?	?	0	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Parviraptor:

?	?	?	?	0	0	1	0	?	0
1	2	?	?	?	0	?	?	?	?
?	?	?	0	-	?	?	?	1	0
?	?	?	?	?	?	?	?	?	?
?	1	0	0	?	1	1	?	0	0
?	1	?	?	?	?	?	?	?	?
1	?	2	?	?	1	?	0	0	0
0	?	0	0	0	0	?	?	?	?
-	?	?	?	?	0	?	0	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Primaderma:

?	?	?	?	0	1	1	?	?	?
?	?	?	?	?	1	?	?	?	?
?	?	?	?	1	?	1	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	1	?	?	?	?	?	?
?	?	?	?	?	?	?	1	?	?
1	?	2	?	?	1	?	1	1	1
1	?	?	?	?	0	?	?	3	?
?	?	?	1	1	0	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Proplatynotia:

1	1	0	1	0	2	1	0	0	0
1	0	0	0	0	0	?	0	1	0
0	0	?	0	0	0	0	0	?	?
?	?	?	?	?	0	?	?	?	?
?	?	1	1	1	1	0	0	0	?
0	?	0	?	1	2	1	1	1	1
?	?	2	1	0	1	1	0	1	1
1	?	1	1	0	0	0	1	2	?
0	?	?	?	?	?	?	?	?	?

?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Restes:

?	?	?	?	?	0	0	1	?	0
1	0	?	0	?	?	?	0	0	0
1	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	0	0	0
0	?	0	0	?	0	1	0	2	?
0	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Saniwa:

1	?	1	2	1	1	1	0	0	0
1	3	2	0	3	1	?	0	1	0
0	1	0	0	0	0	0	1	1	0
1	0	1	1	1	0	0	0	0	0
?	1	1	1	1	1	0	1	?	0
0	1	?	?	1	2	1	1	?	?
?	?	2	1	0	1	1	1	1	1

1	?	1	0	0	0	0	0	0	0
-	1	1	1	2	2	1	1	0	?
0	1	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

"Saniwa" feisti:

?	?	0	0	0	1	1	1	0	0
?	?	0	0	?	0	?	0	0	0
0	0	0	0	0	0	0	0	1	0
1	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
0	?	0	?	?	1	1	?	?	?
?	?	?	?	1	?	?	1	1	1
?	?	1	0	0	0	0	1	2	2
1	?	?	?	?	?	1	1	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Saniwides:

0	1	0	1	?	2	?	0	0	0
1	0	?	0	0&1	0	0	?	1	0
0	1	0	0	?	0	0	?	1	?
1	0	0	?	?	0	0	0	0	0
1	1	1	?	1	1	0	0	?	0

0	1	0	1	1	2	1	1	1	1
?	?	2	?	?	1	1	1	1	1
1	?	1	1	0	0	0	1	2	?
-	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?

Shinisaurus:

0	1	0	0	2	0	0	1	1	0
1	0	1	0	0	0	1	0	0	0
1	1	1	0	0	0	0	1	0	0
0	0	0	0	0	0	0	1	0	0
0	1	0	0	0	0	1	1	0	1
1	0	0	1	1	1	0	0	1	0
1	0	2	0	0	1	0	0	0	0
0	1	0	0	0	0	0&1	1	2	3
0	1	0	2	1	0	1	0	0	0
0	1	?	0	0	0	?	0	1	?
0	1	0	0	1	0	0	0	0	1

Telmasaurus:

?	?	?	?	?	2	?	0	?	0
1	3	?	0	?	?	0	1	1	0
0	0&1	0	0	0	0	0	0	1	0

1	0	0	?	?	0	0	0	0	0
0	1	?	?	?	1	0	0	?	0
0	1	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	1	1	1
1	?	?	?	?	?	0	0	0	?
-	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	0	?	?	?
?	?	?	?	?	?	?	?	?	?

Varanus:

1	1	1	2	1	2	1	0	0	0
1	3	2	0	2	0&1	0	1	1	1
0	1	0	0	0	0	0	0	1	1
1	0	1	1	1	1	0	0	0	0
1	1	1	1	1	1	1	2	0&1	0
1	1	0	1	1	2	1	1	1	1
1	1	2	1	0	1	1	1	1	1
1	1	2	1	1	0	0	0	0	3
-	1	1	1	2	2	1	1	1	1
1	0&1	1	2	0	1	1	1	2	1
1	2	0&1	1	2	1	1	1	1	1

Xenosaurus:

0	1	0	0	0	0	0	1	1	1
1	0	0	0	0	0	1	0	0	0
1	1	1	0	1	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	1	2	0	0
1	0	0	1	1	1	0	0	0	0
1	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	1	1	2	3
0	1	0	2	0	0	1	1	0	0
0	0	0	0	0	0	0	0	1	1
0	1	1	0	1	0	0	0	0	1

CHAPTER SIX

GENERAL CONCLUSIONS

The three living genera of varanoid lizards represent a small subset of a formerly much larger and more morphologically diverse clade, the Platynota. The fossil record yields evidence of 100 million years of platynotan evolution (Nydam 2000) and provides a glimpse of a period in Earth's history when predatory lizards from very small to very large, expanded and radiated over a geographic range far greater than that seen today. Close study of extant platynotans has provided some insight on their evolution (Mertens 1942; McDowell and Bogert 1954; Rieppel 1980; Pianka and King 2004; Beck 2005) but with the discovery of more and more extinct forms our understanding of the precise relationships within Platynota has lessened instead of deepened.

The history of investigation into platynotan relationships, and indeed the relationships of most fossil groups, is marked by the habit of attempting to understand fragmentary fossil forms in terms of how they correspond to modern, well-understood groups (Owen 1860; Leidy 1870; Marsh 1872; Filhol 1873; Gilmore 1922, 1928; Camp 1923). These methods lie at the foundation of paleontological work and have almost unilaterally kept alive the comparative anatomist's art; the simple act of looking for commonality among forms and recognizing patterns suggestive of relationship may be the single most valuable skill a paleontologist can possess. The problem lies not in the method of anatomical comparison but with the anatomical context within which fossil taxa are examined. The fragmentary nature of lizard fossils has often restricted research to narrow morphological concepts (tooth types, scale types) that necessarily limit the number of comparisons available. It is highly unlikely that this problem will ever go away and it is not the intent of the author to admonish anyone who undertakes the difficult task cataloguing and categorizing the vast quantities of fossil fragments housed in the worlds collecting institutions. On the contrary, this work remains vital to our understanding of broad shifts in regional and global diversity (Cifelli et al. 1999; Nydam and Cifelli 2002; Nydam 2002; Smith 2006, 2009; Rage and Augé 2010; Klembara and Green 2010) and improves our understanding of the world inhabited by these forms.

The primacy of the type of work described above aside, it does not encompass all that paleontologists do. The discovery of articulated and complete or nearly complete (or for squamates, even remotely complete) specimens provides a rare opportunity to record an animal not just in time and space, but within the context of phylogeny as well. That context, the phylogeny of known organisms, is and will continue to be vastly weighted in favour of neontology but the fossil record plays a key role in building our understanding of the evolution of life on Earth (Patterson 1981; Donoghue et al. 1989). Indeed for some clades, like Platynota, fossil evidence suggests that extant diversity pales in comparison that which has expired. The role of paleontologists may have begun with the task of placing fossils into the framework as evidenced by living forms, but a modern understanding of evolution and deep time have made abundantly clear the need to place modern organisms within the context of fossil diversity.

With this in mind, the taxonomic diversity and morphological disparity displayed by fossil platynotans must be examined and defined in its own terms.

It is not enough that we ask if a fossil platynotan is ‘like’ *Varanus*, or ‘like’ *Heloderma*; it is becoming increasingly clear that many platynotans were neither and the growing number of potentially well-defined platynotan taxa allow us to build a new vocabulary for describing Platynota as a whole. The thesis presented here contributes to this goal in three ways: through the clarification of the generic diagnoses of taxa near the crown and base of platynota; by examining and identifying patterns of similarity among fossil taxa not observed in extant material; and through the introduction of a new platynotan genus and species, displaying novel morphology and thus adding to the concept of what platynotans are or can be.

The discovery of a beautifully preserved specimen of *Saniwa* (FMNH PR2378) from the early Eocene of Wyoming (Rieppel and Grande 2007) is a boon not fully utilized yet. While the specimen undoubtedly adds a great deal to our knowledge of the evolution of varanid morphology, it may yet provide information key to understanding patterns of diversity and dispersal in Paleogene platynotans between North America and Laurasia. Numerous species of *Saniwa* have been proposed on the basis of isolated vertebrae (Marsh 1872; Dollo 1923; Brattstrom 1955) and dismissed on the basis lack of information regarding intervertebral variation (Estes 1983; Rieppel and Grande 2007). A species level placement of FMNH PR2378 supported by robust evidence is as yet uncertain and direct comparison with the holotype of *Saniwa ensidens* (USNM 2185) reveals clear differences. Specific determination and an analysis of the intervertebral variation present in FMNH PR2378 may provide a benchmark against which other putative *Saniwa* species may be assessed.

Long recognized as one of the most well known and abundant of fossil platynotan genera (Hoffstetter 1943; Estes 1983; Rage 1988; Augé 1990, 2005; Rage and Augé 2010) *Necrosaurus* has rarely been adequately figured or described (Filhol 1877; Fejérváry 1935; Estes 1983; Augé 2005). Worse, the only formal diagnoses published for *Necrosaurus* and Necrosauridae (Estes 1983) are too reliant on pleisiomorphies and are unnecessarily broad in concept, rendering them all but useless as taxonomic tools. An examination of the known anatomy of *Necrosaurus* and other platynotans thought to be closely related revealed apomorphic traits at the level of species, genus and family. Phylogenetic analysis incorporating the newly described features recovered a monophyletic Necrosauridae including five distinct genera. The discoveries of necrosaurids in North America and Europe corroborate the biogeographic patterns observed in other crown platynotan clades, and their monophyly demonstrates the occurrence of at least one diverse platynotan lineage of which there appear to be no survivors.

The introduction of a new platynotan genus and species, *Vulpesaurus magdalenae*, adds to the known diversity of Platynota and introduces novel morphologies to the clade. As a member of Necrosauridae, *Vulpesaurus* expands the history of that group by over 10 million years to the late Cretaceous. Utilization of High Resolution X-Ray Computed Tomograpy, permits the presentation of detailed anatomical information on *Vulpesaurus* and greatly increases the amount of character data for which it would otherwise have been coded.

The preceding work is an attempt to bring some small amount of resolution to a part of the platynotan clade that has been long neglected. Examination of several morphologically disparate and geographically widespread taxa reveals that the growing diversity of platynotan lizards may require a fundamental re-thinking of what constitutes a platynotan, and that the characters traditionally used to parse one platynotan group from another are insufficient in the face of such burgeoning diversity. The arrival of new specimens representing long established taxa (Rieppel and Grande 2007; Conrad et al. 2011) allow for re-examination old ideas, while the discovery of unique new taxa (Gao and Norell 2000; Conrad 2006; Norell et al. 2008; Chapter 4 of this thesis) provide the opportunity to develop new hypotheses. The knuckles of opportunity are as red (and raw) as nature is in tooth and claw.

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