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University of Alberta

Systematics of Albanerpetontids and Other Lissamphibians from the Late Cretaceous of Western North America

by

James Douglas Gardner ©

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

Department of Biological Sciences

Edmonton, Alberta
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Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Systematics of Albanerpetontids and Other Lissamphibians from the Late Cretaceous of Western North America submitted by James Douglas Gardner in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

The Cretaceous Period was an important interval in the evolution of lissamphibians, or so-called "modern amphibians," and one of the best fossil records from this time occurs in the Western Interior of North America. The taxonomic diversity and systematics of Cretaceous lissamphibians from the Western Interior is investigated, with emphasis on occurrences from the Campanian and Maastrichtian stages that span about the last 18 million years of the Cretaceous Period. Lissamphibians from these horizons are more diverse taxonomically than was previously known. Frogs, salamanders, and albanerpetontids are represented and some 20 species, seven of which are new, are recognized among 17 genera and six families. Albanerpetonid and salamander species are assignable to families, but just one frog species can be confidently assigned to a known family. Albanerpetontids were most diverse during the middle Campanian, while salamanders and frogs achieved their maximum diversity later during the late Maastrichtian. New and previously reported material from the Western Interior and elsewhere permit a detailed examination of the Albanerpetontidae, an extinct and enigmatic group of salamander-like amphibians. Seven species, three of which are new, are recognized for the Euramerican type genus Albanerpeton. The first phylogenetic analysis for the genus implies that its early evolution was centered in the Western Interior and that the three North American Campanian and Maastrichtian congeners are members of two sister-clades, the origins of which can be traced back to the Early/Late Cretaceous boundary in the Western Interior. A larger scale analysis for the Albanerpetontidae corroborates monophyly of the clade and nests the family within the Lissamphibia as the sister-taxon of frogs plus salamanders. None of the character states previously advanced as salamander–albanerpetontid synapomorphies convincingly ally the two groups.

Albanerpetontids are better regarded not as aberrant salamanders as some workers have argued, but as a distinct clade of lissamphibians in which numerous cranial and vertebral novelties related to feeding and burrowing are superimposed on an otherwise relatively basic lissamphibian body plan.

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G. Braybrook took the scanning electron micrographs in chapters 3–6; Dr. R. C.

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LIST OF ABBREVIATIONS

Institutional Abbreviations

AMNH	American Museum of Natural History, New York, New York.
BMNH	Natural History Museum, London, England.
CCMGE	Chernyshev Central Museum of Geological Exploration, Saint Petersburg, Russia.
DORCM	Dorset County Museum, Dorchester, England.
FMNH	Field Museum of Natural History, Chicago, Illinois, USA.
IPB	Instituto de Paleontologia de Sabadell, Barcelona, Spain.
KU	University of Kansas Museum of Natural History, Lawrence, Kansas, USA.
KUA	Kansas University Archives, University of Kansas, Lawrence, Kansas, USA.
KUVP	University of Kansas Vertebrate Paleontology collection, Lawrence, Kansas, USA.
LH	Museo de Cuenca, Cuenca, Spain.
LSUMG	Louisiana State University Museum of Geology, Baton Rouge, Louisiana.
MCZ	Museum of Comparative Zoology, Harvard, USA.
MNHN.LGA	Muséum National d'Histoire Naturelle (collection from La Grive-St. Alban, France), Paris, France.
MNHN.MNM	Muséum National d'Histoire Naturelle (collection from Anoual, Morocco), Paris, France.
MNP	Museo di Paleontologia dell'Università di Napoli, Naples, Italy.
MPT	Museo Provincial de Teruel, Spain.
OMNH	Oklahoma Museum of Natural History, Norman, Oklahoma, USA.
RSMNH	Royal Saskatchewan Museum of Natural History, Regina, Saskatchewan.
SMM	Science Museum of Minnesota, Milwaukee, USA.
SMU	Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas, USA.
TMM	Texas Memorial Museum, Austin, Texas.
TMP	Royal Tyrrell Museum of Palaeontology, Drumheller, Canada.

UALP	University of Arizona Laboratory of Paleontology, Tucson, Arizona.
UALVP	University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada.
UCBL	Université Claude Bernard, Lyon, France.
UCK	University College London, London, England.
UCM	University of Colorado Museum, Boulder, Colorado, USA.
UCMP	University of California Museum of Paleontology, Berkeley, USA.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.
USNM	Museum of Natural History, Smithsonian Institution, Washington, D.C, USA.
UW	University of Wyoming, Laramie, Wyoming, USA.
ZIN	Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Anatomical Abbreviations

aco	anterior cotyle
alp	anterolateral process
ang	angular
ang + art	fused angular and articular
apb	area of attachment for post-dentary bones
art	articular
as	anterior slot in albanerpetontid frontal for receipt of nasal
as fro	articular surface on albanerpetontid prefrontal for contact with frontal
as pmx	articular surface on albanerpetontid lacrimal for contact with premaxilla
at	atlas
ax	axis
b	dorsal boss
bp	raised bony patch on albanerpetontid maxilla for contact with lacrimal
bo	basioccipital
bsp	basapophysis
cor	coronoid

den	dentary
dp	dental parapet
ect	ectopterygoid
enfo	external nutritive foramen
enm	external narial margin
eno	external narial opening
exo	exoccipital
fa	facet
fap	facet on undersurface of albanerpetontid frontals for contact with anteriorly projecting flange on parietal
fj	facet on albanerpetontid maxilla for contact with jugal
fm	facet on albanerpetontid premaxilla for contact with premaxillary process on maxilla
fn	facet on underside of albanerpetontid frontal for contact with neurocranium
fr	frontal (fused in albanerpetontids)
frpa	frontoparietal
gn	groove along lateral face of internasal process on Albanerpeton frontals for tongue-in-groove contact with medial edge of nasal
ip	internasal process on albanerpetontid frontal
is	internal strut
it	intertemporal
ju	jugal
la	lacrimal
lan	lacrimal notch
lafo	lacrimal foramen
mf	medial flange
mx	maxilla
mxp	maxillary process
mxpal	maxillopalatine
na	nasal
nap	nasal process
nar	neural arch

neu	neurocranium
np	nasal process
ob	os basale
om	orbital margin
omc	posterior opening for Meckelian canal
op	odontoid process
ouc	lingual opening in albanerpetontid dentaries for unnamed canal
or	orbit
pa	parietal
pal	palatine
pas	parasphenoid
pco	posterior cotyle
pde	pars dentalis
pdo	pars dorsalis
pdp	premaxillary dorsal process
pf	pars facialis
pfo	palatine foramen
pfr	prefrontal
plp	premaxillary lateral process
pml	pterygomaxillary ligament
pmx	premaxilla
po	postorbital
pofr	postfrontal
pop	polygonal pits on dorsal surface of albanerpetontid frontals
pozy	postzygapophysis
pp	pars palatinum
ppa	postparietal
pra	prearticular
pro	prootic
przy	prezygapophysis
ps	posterior slot in albanerpetontid frontal for receipt of prefrontal
psa	pseudoangular
psd	pseudodentary

pt	pterygoid
qj	quadratojugal
qu	quadrate
r	rib
s	stapes
seam	scar for attachment of external adductor muscles
sds	subdental shelf
sfo	spinal foramen
sim	scar for attachment of intermandibularis muscles
sla	surface on albanerpetontid maxilla for contact with lacrimal
sm	septomaxilla
sp	splenial
spp	suprapalatal pit
sptr	splenial tooth row
sph	sphenethmoid
sq	squamosal
st	supratemporal
syf	symphyseal fang
sypr	symphyseal process
sytr	symphyseal tooth row
sur	surangular
ta	tabular
tp	transverse process
tr	trough on albanerpetontid maxilla for contact with palatal bone(s)
t1	first trunk vertebra
t2	second trunk vertebra
ufo	unnamed foramen
up	unnamed process
vlc	ventrolateral crest
vo	vomer
vp	vomerine process

CHAPTER 1 — INTRODUCTION

INTRODUCTORY COMMENTS AND OBJECTIVES

The Lissamphibia Haeckel or so-called "modern amphibians" are a diverse group of non-amniotic tetrapods, whose extant members number over 4500 recognized species and occur on every continent except Antarctica (Duellman and Trueb, 1986; Duellman, 1993). The Lissamphibia are widely regarded as a monophyletic clade nested within the more inclusive Temnospondyli Zittel (e.g., Bolt, 1977, 1979, 1991; Rage and Janvier, 1982; Milner, 1988, 1990, 1993a, b; Trueb and Cloutier, 1991); this is the view accepted here. Others regard the Lissamphibia as a monophyletic clade within the Lepospondyli Zittel (Laurin and Reisz, 1997; Laurin, 1998a, b) or as a paraphyletic assemblage whose major groups are descended independently from various Late Paleozoic lepospondyl and temnospondyl ancestors (e.g., Carroll and Currie, 1975; Carroll and Holmes, 1980; Carroll, 1988, 1998). Four groups of lissamphibians are generally recognized, three of which have extant representatives: Salientia Laurenti (frogs), Early Triassic (Scythian) to Recent; Gymnophiona Rafinesque (caecilians), Early Jurassic (Sinemurian) to Recent; Caudata Scopoli (salamanders), Middle Jurassic (Bathonian) to Recent; and Allocaudata Fox and Naylor (albanerpetontids), Middle Jurassic (Bathonian) to middle Miocene (Milner, 1993a). The fossil record of lissamphibians is stratigraphically and geographically patchy and is biased towards aquatic taxa and disarticulated elements. Nevertheless, these records remain the only direct evidence for elucidating the evolutionary history of the group.

Evidence to date points to the Late Cretaceous (ca. 99-65 million years ago; Gradstein et al., 1995) as having been an important episode in the history of lissamphibians. This interval saw the rise of a number of groups (e.g., albanerpetontids, scapherpetontid and batrachosauroidid salamanders, and palaeobatrachid frogs) that were to become important components in lissamphibian assemblages during the last part of the Mesozoic and into the Tertiary and saw the first appearances of several groups (e.g., amphiumid and sirenid salamanders) with living representatives. One of the best records of Late Cretaceous lissamphibians, in terms of the number and quality of specimens and taxonomic representation, occurs in deposits of Campanian and Maastrichtian age (ca. 83.5–65 million years ago; Gradstein et al., 1995) in the Western Interior of North America, from Texas north into southern Alberta and Saskatchewan. Of the four major lissamphibian clades, only caecilians are unrecorded.

The first report of latest Cretaceous lissamphibians from these deposits was by Cope (1876), who named two genera and five species of salamanders based on isolated vertebrae from type area of the Judith River Formation (middle Campanian in age), Montana. The name of one of these species, *Scapherpeton tectum* Cope, is still considered valid; names of the other four species are junior synonyms of the name *S. tectum* (Auffenberg and Goin, 1959; Estes, 1964). Over a half century later, Gilmore (1928) described the supposed lizard *Habrosaurus dilatus* for four dentaries from the type area of the Lance Formation (late Maastrichtian in age), Wyoming; these specimens have since been identified as belonging to sirenid salamanders (Estes, 1964). Other early reports from the type area of the Lance Formation were trunk vertebrae that Goin and Auffenberg (1958) described for the new sirenid salamander *Adelphesiren olivae* and isolated jaws and vertebrae that Auffenberg (1961) described for the new salamander *Opisthotriton kayi*. During this time, Auffenberg and Goin (1959) reviewed the taxonomic status of the salamanders described by Cope (1876) and erected the fossil family Scapherpetontidae for receipt of *Scapherpeton tectum*. A landmark contribution to the study of latest Cretaceous lissamphibians came with the publication of Estes' (1964) monograph on lower vertebrates from the Lance Formation. Estes (1964) synonymized the name *Adelphesiren* Goin and Auffenberg with that of *Habrosaurus* Gilmore, described abundant and better preserved skull and postcranial elements for the previously named salamanders *Habrosaurus*, *Opisthotriton* Auffenberg, and *Scapherpeton* Cope, described the new salamander genus and species *Prodesmodon copei* for characteristic vertebrae and jaws, the latter of which were later recognized as belonging to albanerpetontids (Naylor, 1979; Fox and Naylor, 1982), and described the supposed squamate *Cuttysarkus mcnallyi* for distinctive dentaries that subsequently were transferred to *Prodesmodon* (Naylor, 1979). Estes (1964) also reported on a series of isolated frog elements, some of which were later interpreted as belonging to a pelobatid *sensu lato* and to a new species of palaeobatrachid (Estes, 1970; Estes and Sanchíz, 1982a). A series of papers during the next three decades reported on new lissamphibian taxa and fossils from the late

Maastrichtian Lance Formation (Fox, 1976; Naylor, 1979; Estes, 1981; Estes and Sanchíz, 1982a; Breithaupt, 1982) and Hell Creek Formation, Montana (Estes, 1965, 1969a, b; Estes et al., 1969; Naylor, 1979, 1983; Estes and Sanchíz, 1982a), the late Campanian–early Maastrichtian Fruitland Formation, New Mexico (Armstrong-Ziegler, 1980), the middle Campanian Judith River Formation, Montana (Sahni, 1972), and Aguja Formation, Texas (Rowe et al., 1992), and the early Campanian Milk River Formation (Fox and Naylor, 1982; Naylor, 1983).

By the mid-1980s some 15 species distributed among 13 genera and eight families were recognized from the Campanian and Maastrichtian of the Western Interior (Table 1-1). Although the phylogeny of these taxa has not been investigated in depth, many of these taxa are potentially important for assessing character state polarities and relationships within and among clades: some, such as the amphiumid salamander Proamphiuma Estes, are the geologically oldest members of more inclusive clades, whereas others, such as the scapherpetontid salamanders Scapherpeton and Lisserpeton Estes, are among the anatomically best known members of more inclusive clades. Still others, such as the frog Theatonius Fox, are enigmatic taxa that cannot readily be assigned to or associated with any larger clade. The North American record of Campanian and Maastrichtian lissamphibians is also biogeographically interesting, in part, because many taxa have been assigned to families (e.g., discoglossid and palaeobatrachid frogs) that have been reported from other continents and, in part, because for much of the Late Cretaceous the Western Interior was separated from the eastern part of the continent by an extensive seaway and was, instead, connected to the northwest via a land bridge with the Eurasian continent.

Our understanding of Campanian and Maastrichtian lissamphibians in the Western Interior is founded largely on original descriptions and descriptive accounts for species published in the late 1950s to mid-1980s (Goin and Auffenberg, 1958; Auffenberg and Goin, 1959; Auffenberg, 1961; Estes, 1964, 1965, 1969a–c, 1975, 1976, 1981; Estes et al., 1969; Fox, 1976; Naylor, 1979, 1983; Naylor and Krause, 1981; Fox and Naylor, 1982; Estes and Sanchíz, 1982a). Most of this work relied on specimens from latest Maastrichtian horizons. Of the 12 named species considered valid when I began my study, ten were named on specimens from latest Maastrichtian horizons and only two were named from older horizons: the salamander Scapherpeton tectum from the middle

Campanian and the albanerpetontid Albanerpeton galaktion Fox and Naylor from the early Campanian. New discoveries from the Albian and Cenomanian in the Western Interior (Cifelli et al., 1997; Cifelli et al., 1999) and from the Cretaceous of the eastern USA (Denton and O'Neill, 1998), Europe (e.g., McGowan and Evans, 1995; Duffaud, 1995; Duffaud and Rage, 1999; Le Loeuff and Buffetaut, 1995; Buffetaut et al., 1996) and Asia (e.g., Nessov, 1981, 1988, 1997; Roček and Nessov, 1993) have added to our knowledge of Cretaceous lissamphibians. The latest Cretaceous record of lissamphibians from the Western Interior deserves to be re-assessed in light of these recent advances. An extensive assemblage of largely undescribed specimens (isolated and rare articulated skull and postcranial elements) in the collection of the University of Alberta Laboratory for Vertebrate Paleontology, supplemented with specimens from other collections, provides the opportunity to conduct such a study.

My study focuses on isolated and rare associated skull and postcranial elements from sites in the Western Interior (see Fig. 6-1) in the Hell Creek Formation, Montana, the Lance Formation, Wyoming, and the Dinosaur Park Formation, Oldman Formation (sensu Eberth and Hamblin, 1993), and Deadhorse Coulee Member of the Milk River Formation, all in Alberta. These formations are terrigenous units comprised largely of fluviodeltaic sediments deposited during the Campanian and Maastrichtian across a broad coastal plain in the North American Western Interior (e.g., Clemens, 1963; Estes, 1964; Estes et al., 1969; Meijer Drees and Mhyr, 1981; Eberth and Hamblin, 1993; Lofgren, 1995). The relative ages of uppermost Cretaceous terrigenous deposits in the Western Interior are commonly expressed using North American Land Mammal ages (NALMAs), which are provincial time units or biochrons based on successions of mammalian assemblages (see L. Russell, 1964, 1975; Fox, 1978; Lillegraven and McKenna, 1986). In ascending stratigraphical order, the four Late Cretaceous NALMAs are the Aquilan (= early Campanian), Judithian (= middle Campanian), Edmontonian (= late Campanian to early Maastrichtian), and Lancian (= late Maastrichtian). The Hell Creek and Lance formations are conventionally regarded as lateral equivalents and dated as late Maastrichtian or Lancian in age (Dorf, 1942; L. Russell, 1964; Lillegraven and McKenna, 1986), the Oldman and Dinosaur Park formations (sensu Eberth and Hamblin, 1993) are dated as middle Campanian or Judithian in age (L. Russell, 1964; Lillegraven and McKenna, 1986; Eberth and Hamblin, 1993), with the latter overlying the former

(Eberth and Hamblin, 1993) and thus slightly younger, and the Deadhorse Coulee Member of the Milk River Formation is conventionally dated as early Campanian or Aquilan in age (L. Russell, 1964; Lillegraven and McKenna, 1986). Recent work by Leahy and Lerbekmo (1995) suggests that the Deadhorse Coulee Member of the Milk River Formation may be late Santonian in age or span the Santonian-Campanian boundary. Lofgren (1995) also proposed that the Bug Creek Anthills locality, which lies in a paleochannel and is the source for all specimens reported herein from the Hell Creek Formation, contains a mixture of youngest Paleocene and reworked latest Maastrichtian fossils. Pending more detailed assessments of both proposals, here I accept the conventional age interpretations for both the Deadhorse Coulee Member and the Bug Creek Anthills.

My study is not restricted to material from the five units listed above. Where available and informative, specimens from stratigraphically equivalent units elsewhere in Saskatchewan, Colorado, Utah, and Texas are included. Many of the species identified from the Campanian and Maastrichtian of the Western Interior range into the Paleocene or have geologically older and younger relatives of interest; examples of these specimens are included in my study where they further our understanding of the latest Cretaceous representatives or taxa of interest.

The objectives of my study are threefold:

(1) Identify, diagnose, and describe lissamphibian taxa from the Campanian and Maastrichtian of the Western Interior. My study confirms that the 12 previously accepted species are valid (i.e., diagnosable; see Table 1-1), although some specimens and elements have been incorrectly associated. I provisionally continue to recognize an Eopelobates-like frog, first reported by Estes (1964), for distinctive skull bones and ilia from the Lance Formation. In addition, I name another six species (two of these were informally recognized by Naylor [1983]) distributed among three new and three established genera from Campanian and Maastrichtian horizons in the Western Interior and informally recognize another two genera and species from the middle Campanian of Alberta. A new species of albanerpetontid, with relatives of Campanian and Maastrichtian age, is also described from the Turonian of Utah. Because I regard this taxonomic and descriptive component as forming the core of my study and the foundation for all subsequent interpretations, I have made a concerted effort to examine most of the important,

previously described specimens, to provide detailed descriptions and comments as warranted, and to extensively figure relevant specimens. In general, I have employed differential diagnoses because I find these to be the most useful for identifying taxa and, where possible, I have explicitly identified inferred polarities for character states used in diagnoses.

(2) Examine the taxonomic diversity of lissamphibians during the Campanian and Maastrichtian in the Western Interior. In particular, can distinctive lissamphibian assemblages be identified based on taxonomic composition and geological age? Similar assemblages have been documented for mammals (e.g., L. Russell, 1964, 1975; Fox, 1978; Lillegraven and McKenna, 1986) and lizards (Gao and Fox, 1996) that reveal interesting patterns of evolutionary change and diversity through time in these groups.

(3) Interpret taxa in a phylogenetic and paleobiogeographic context. This has met with varying levels of success: new information on the phylogenetic and paleobiogeographic histories of all groups has been forthcoming and, just as importantly, limitations in our understanding of these topics have been highlighted.

An unexpected development of my research has been the wealth of new insights into albanerpetontids. When I began my studies, the Albanerpetontidae were a poorly known group of superficially salamander-like animals. Limited numbers of specimens had been reported, few taxa were recognized, none of these were well known and, as a consequence, relationships within the Albanerpetontidae had not been considered and the higher level relationships of the family were contentious (e.g., Estes, 1981; Fox and Naylor, 1982; Estes and Sanchíz, 1982b; Milner, 1988). Two stratigraphically separate species had been recognized from the latest Cretaceous of the Western Interior: A. galaktion Fox and Naylor from the early Campanian and A. nexuosus Estes from the middle Campanian and Maastrichtian (Estes, 1981; Fox and Naylor, 1982). My initial expectation was that albanerpetontids would form an interesting, but relatively minor component of my study. It soon became apparent that the latest Cretaceous record was more complex and, in order to properly approach the problem, I needed to broaden the scope of my research to include albanerpetontid fossils and taxa from elsewhere. Ultimately, I was able to document a previously unrecognized diversity of albanerpetontid taxa in the Western Interior and, more significantly, identify phylogenetically informative characters that enabled me to examine relationships within the Euramerican genus

Albanerpeton and to examine monophyly and the position of the Albanerpetontidae relative to other lissamphibians.

The main body of my dissertation consists of 11 chapters arranged taxonomically into three parts. Chapters 2–8 deal with albanerpetontids, as follows: Chapter 2, survey of taxonomically informative characters for albanerpetontids, revised diagnoses for the family and its two genera, and comments on other named and unnamed Old World taxa; chapters 3–6, species accounts for the French Miocene type species of Albanerpeton and the five congeners, two of which are new, from the Cretaceous of the Western Interior; Chapter 7, assessment of monophyly and intra-generic relationships of Albanerpeton; and Chapter 8, assessment of monophyly and relationships of the Albanerpetontidae. The next three chapters are descriptive and systematic accounts devoted to salamanders, as follows: Chapter 9, the amphiumid Proamphiuma; Chapter 10, the sirenid Habrosaurus; and Chapter 11, latest Cretaceous species of batrachosauroidids and scapherpetontids. The final descriptive and systematic chapter (Chapter 12) is devoted to Campanian and Maastrichtian frogs. I conclude (Chapter 13) with an overview of the taxonomic diversity and evolutionary history of lissamphibians in the Western Interior.

ANATOMICAL TERMS, MEASUREMENTS, AND CONVENTIONS

Osteological terms used herein for albanerpetontids are shown in Figure 1-1. Originally I (Gardner, 1999) coined the term "prefrontal notch" for the laterodorsal indentation on the pars dorsalis, based on my belief that this notch articulated with the prefrontal in life. This interpretation is incorrect. Re-examination of MNHN.LGA 1226, a referred maxilla, lacrimal, and prefrontal of Albanerpeton inexpectatum Estes and Hoffstetter, shows that the large lacrimal would have excluded the relatively smaller prefrontal from contact with the nasal. Hence, I propose the replacement term "lacrimal notch." Osteological terms for salamanders follow Estes (1964, 1981; see also Figs. 8-4 to 8-7), with two minor differences. First, I use the term "post-cervical anterior trunk vertebra(e)" to denote anterior trunk vertebrae behind the first trunk vertebra. This distinction is warranted because the structure of the first trunk vertebra in many salamanders is markedly different from that of all subsequent vertebrae in the trunk series. Second, I use the terms anterior, dorsal, and posterior alar processes for the three flanges that extend along the transverse process on the trunk and anterior caudal vertebrae. Osteological terms for frogs follow Trueb (1973), Roček (1980), and Sanchíz (1998); see also Figure 8-3.

All measurements are straightline distances. Premaxillary and frontal measurements for albanerpetontids are depicted in Figure 1-2. Maxillary and dentary lengths are taken in occlusal view between the anterior and posterior ends of the bone. Centrum length is the distance midventrally along the centrum, between the anterior and posterior cotyles in postatlantal vertebrae and between the posterior cotyle and anterior end of the odontoid process in the atlas.

Head-body length in herpetological studies is typically described as the snout-vent length (SVL), a straight line measurement between the tip of the snout and the anterior or, more rarely, posterior edge of the cloaca (Peters, 1964:324). Because the cloaca is rarely preserved in fossils, palaeontologists typically use a skeletal marker, such as the pelvic girdle or sacrum, as a proxy for the position of the cloaca. A more appropriate term for a measurement made in this way is snout-pelvis length (SPL) which, for my purposes here, I define as the straight line distance between the tip of the snout and the midpoint of the pelvis. The distinction between the two head-body values is important, as evidenced by Blob's (1998) survey of extant lizards in which he showed that SPL routinely underestimates SVL. Blob (1998) also discusses some implications of underestimating actual SVL and difficulties associated with using pelvic markers.

Positions along the tooth row are counted from the medial end on the premaxilla and from the anterior end on the maxilla and dentary.

For definitions and ages of the European Neogene Mammal Faunal zones (MN zones), I follow Bruijn et al. (1992) and Steininger et al. (1996).

TABLE 1-1. Lissamphibians from the Campanian and Maastrichtian of the Western Interior identified in the mid-1980s versus this study. Information for left column is from Fox and Naylor (1982), Estes (1981), Estes and Sanchíz (1982a), and Naylor (1983).

Circa mid-1980s	Current Study
Allocaudata	Allocaudata
Albanerpetontidae	Albanerpetontidae
Albanerpeton nexuosus	*Albanerpeton nexuosus*
Albanerpeton galaktion	*Albanerpeton galaktion*
	Albanerpeton gracilis, sp.nov.
Urodela	Urodela
Amphiumidae	Amphiumidae
Proamphiuma cretacea	*Proamphiuma cretacea*
Sirenidae	Sirenidae
Habrosaurus dilatus	*Habrosaurus dilatus*
	Habrosaurus prodilatus, sp. nov.
Batrachosauroididae	Batrachosauroididae
Opisthotriton kayi	*Opisthotriton kayi*
	"morph I atlantes"
	"morph II atlantes"
Prodesmodon copei	*Prodesmodon copei*
	Esteserpeton robustus, gen. et sp. nov.
Genus & Species Unnamed	*Verdigriserpeton bifurcatus*, gen. et sp. nov.
Scapherpetontidae	Scapherpetontidae
Scapherpeton tectum	*Scapherpeton tectum*
Lisserpeton bairdi	*Lisserpeton bairdi*
Piceoerpeton sp.	*Piceoerpeton naylori*, sp. nov.
	Irvinetriton elongatus, gen. et sp. nov.
Anura	Anura
Palaeobatrachidae	Palaeobatrachidae
Palaeobatrachus occidentalis	*Palaeobatrachus*? *occidentalis*
Discoglossidae *sensu lato*	Family Indeterminate
Scotiophryne pustulosa	*Scotiophryne pustulosa*
Paradiscoglossus americanus	*Paradiscoglossus americanus*
Pelobatidae *sensu lato*	?"*Eopelobates*" sp.
Eopelobates sp.	*Theatonius lancensis*
Incertae Sedis	Genus & Species Unnamed A
Theatonius lancensis	Genus & Species Unnamed B

FIGURE 1-1. Osteological terms for albanerpetontid jaws, frontals, and atlas. Premaxilla (**A**–**D**): idealized right premaxilla, in (**A**) labial, (**B**) lingual, (**C**) lateral, and (**D**) occlusal views. Maxilla (**E**–**G**): idealized left maxilla, in (**E**) labial, (**F**) lingual, and (**G**) dorsal views. Dentary (**H**–**J**): idealized left dentary, in (**H**) labial, (**I**) lingual, and (**J**) occlusal views. Fused frontals (**K**, **L**): idealized frontals, in (**K**) dorsal and (**L**) ventral views. Atlas (**M**): idealized atlas, in anterior view. Figures approximately to scale.

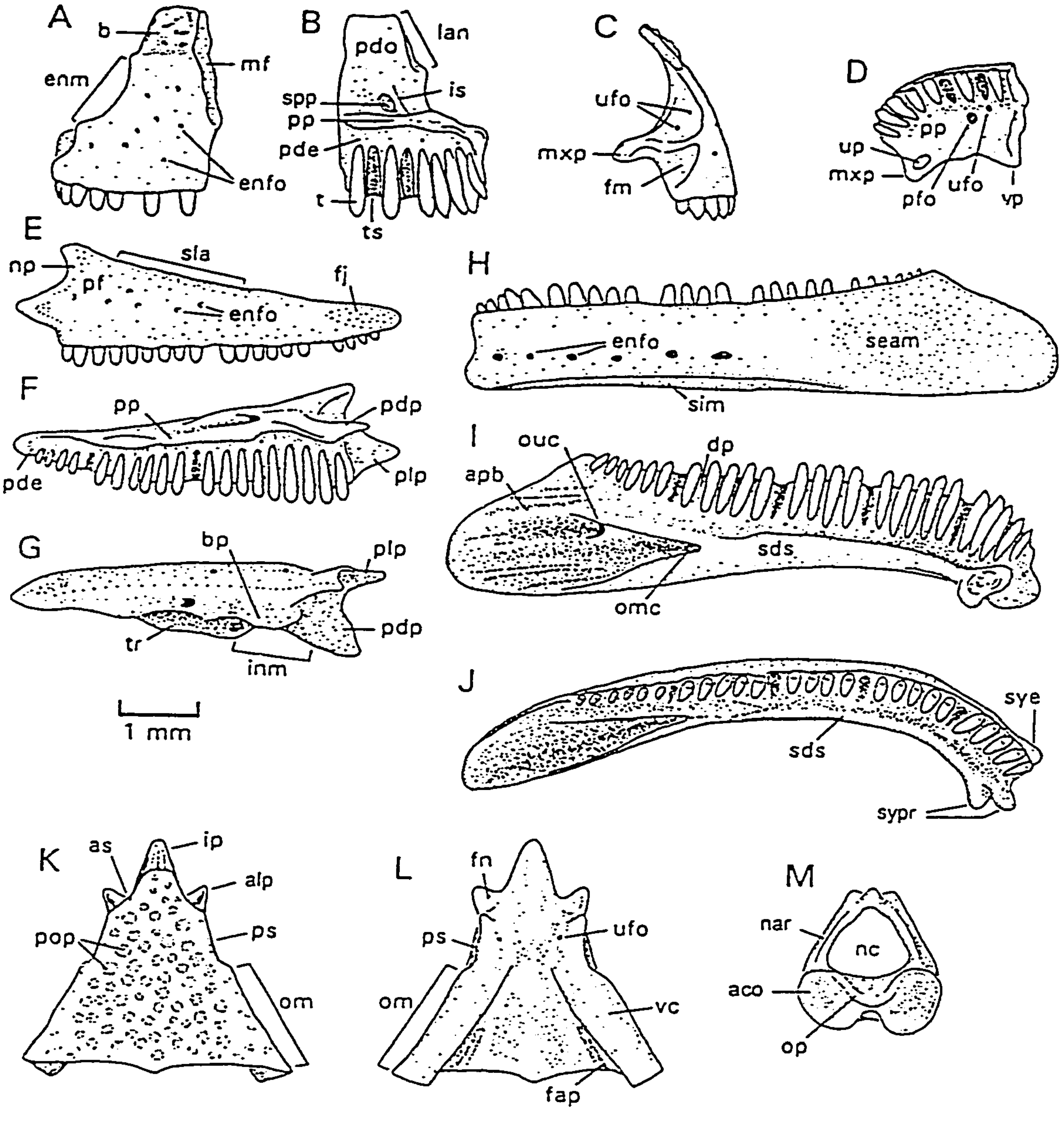
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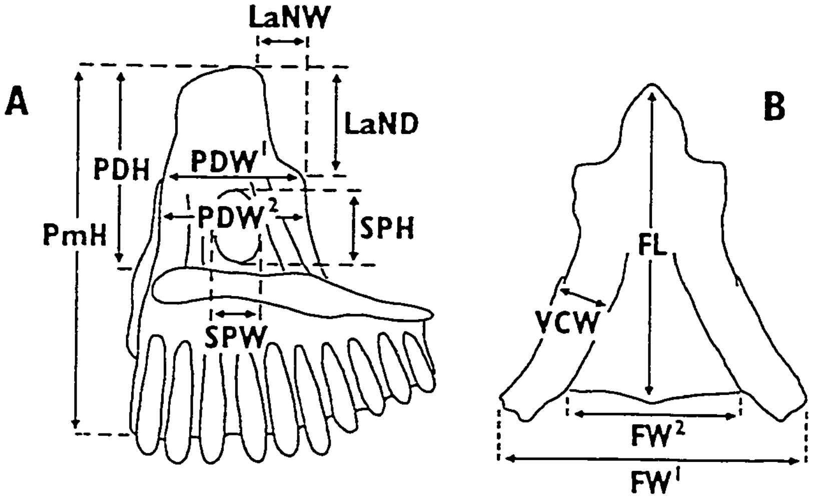
FIGURE 1-2. Measurements for albanerpetontid premaxillae and frontals. **A**, right premaxilla, in lingual view; **B**, fused frontals, in ventral view. Measurements: FL, midline length of frontal; FW^1, maximum width across posterior margin of frontals; FW^2, width between ventrolateral crests, across posterior edge of frontal roof; LaND, depth of lacrimal notch; LaNW, maximum horizontal width of lacrimal notch; PDH, maximum height of pars dorsalis; PDW^1, horizontal width of pars dorsalis across base of lacrimal notch; PDW^2, horizontal width of pars dorsalis across approximate midpoint of suprapalatal pit; PmH, total height of premaxilla, excluding teeth; SPH, maximum height of suprapalatal pit; SPW, maximum horizontal width of suprapalatal pit; and VCW, width of ventrolateral crest, behind slot for receipt of prefrontal, and perpendicular to margins of crest. Figures not to scale.


A
LaNW
LaND
PDH
PDW¹
PDW²
SPH
PmH
SPW
B
FL
VCW
FW²
FW¹

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CHAPTER 2 — SURVEY OF TAXONOMIC CHARACTERS FOR ALBANERPETONTID AMPHIBIANS, WITH REVISED DIAGNOSES AND NOTES FOR THE FAMILY, GENERA, AND SPECIES[1]

INTRODUCTION

Albanerpetontids are readily identified by such distinctive features as their non-pedicellate and chisel-like marginal teeth, interlocking intermandibular joint, fused frontals with polygonal dorsal ornament, and highly modified cervical vertebrae that convergently resemble the mammalian axis-atlas complex. Jaws and frontals are the most commonly recovered albanerpetontid elements at most sites, and characters of these elements have been widely used to diagnose genera and species (Estes, 1981; Nessov, 1981, 1997; Fox and Naylor, 1982; McGowan and Evans, 1995; McGowan, 1998a; Gardner, 1999a, b, c, 2000a, in press a; Rage and Hossini, 2000). In many cases, however, the reliability of such characters has not been adequately established. This is the result of a combination of factors: scarcity of well-preserved specimens; a reluctance on the part of some workers to examine appropriate comparative collections; and misinterpretations of structure. To cite a recent example, McGowan (1998a) used frontal characters alone to diagnose the two currently recognized genera—Albanerpeton Estes and Hoffstetter and Celtedens McGowan and Evans—and their respective species. McGowan's (1998a) claims about the diagnostic utility of frontals for Albanerpeton and its species are suspect because he considered just two of the four named species then included in the genus (I recognize seven species), examined only material of the type species A. inexpectatum Estes and Hoffstetter, and misinterpreted the structure of the frontal in A. galaktion Fox and Naylor based on photographs (Fox and Naylor, 1982:fig. 1d, e) of a referred, incomplete specimen. McGowan's (1998a) reliance on frontal characters to diagnose species of Albanerpeton is further at odds with observations by myself (Gardner, 1999a, b, c, 2000a, in press a, this study) and others (Estes, 1981; Fox and Naylor, 1982; Rage and Hossini, 2000) that

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[1] A version of this chapter has been published. Gardner 2000. Acta Palaeontologica Polonica. 45: 55–70.

characters of the jaws are also useful for this purpose.

My objectives here are twofold. In the first part of this chapter I assess the taxonomic value of characters for albanerpetontids, with emphasis on frontals and jaws. Isolated examples of these bones are available for all species of Albanerpeton, except for a newly described Turonian species known only by the holotype premaxilla (Gardner, 1999c; here:Chapter 5). Frontals are also reasonably well known for Celtedens, both as disassociated elements from indeterminate species and articulated in the holotype skeletons of the two named species C. megacephalus (Costa) and C. ibericus McGowan and Evans (McGowan and Evans, 1995; McGowan, 1996, 1998a; McGowan and Ensom, 1997). Jaws in these skeletons are difficult to study because they are preserved in articulation and, in the case of the holotype of C. megacephalus, also poorly preserved (pers. obs., 1997). The only isolated, reasonably well-preserved jaws available to me for Celtedens are incomplete premaxillae and dentaries of an indeterminate species from the Early Cretaceous of Purbeck, England (McGowan and Ensom, 1997). In the second part of this chapter I present revised diagnoses and select comments for the Albanerpetontidae, Albanerpeton, and Celtedens, then report briefly on two previously unrecognized albanerpetontid taxa that are distinct at the generic level from Albanerpeton and Celtedens.

TAXONOMIC CHARACTERS FOR ALBANERPETONTIDS

Characters of The Frontals (Figs. 2-1 to 2-3; Table 2-1)

Albanerpetontid frontals are solidly fused medially and have a prominent internasal process, two pairs of slots anterior to the orbital margin for mortise and tenon style articulation with the posterior ends of the paired nasals and prefrontals, prominent ventrolateral crests adjacent to the orbital margin, and dorsal ornament comprised of polygonal pits enclosed by ridges. Outgroup comparisons indicate that the first three of these character states are synapomorphic for the family (Chapter 8).

McGowan and Evans (1995) used frontal characters to partition Albanerpeton and to diagnose their new genus Celtedens and its two species. Figure 2-1 depicts cranial reconstructions for the two genera. Subsequent studies have continued to regard variation in the structure and contacts of the frontals as diagnostic for the two genera (McGowan, 1996; McGowan and Ensom, 1997; Gardner, 1999a, b, c, 2000a, in press a; Rage and Hossini, 2000) and at least some species (McGowan, 1998a; Gardner, 1999a, Rage and Hossini, 2000).

Table 2-1 lists the 13 frontal characters that have been used to differentiate Albanerpeton, Celtedens, and their respective species. Seven characters (1–3, 6, 7, 10, and 11) differ between Albanerpeton and Celtedens, as follows (Figs. 2-1 to 2-3): 1, outline of frontals triangular in Albanerpeton, versus more nearly hourglass- or bell-shaped in Celtedens; 2, midline length of frontals relative to width across posterior edge between lateral edges of ventrolateral crests less than about 1.2 in Albanerpeton, versus more than about 1.2 in Celtedens; 3, outline of internasal process triangular in Albanerpeton, versus bulbous in Celtedens; 6, anterolateral process distinct from main body of frontal, extending anterolaterally, and pointed distally in Albanerpeton, versus a slightly differentiated, broadly rounded shoulder in Celtedens; 7, dorsal and ventral edges of slot for receipt of prefrontal excavated medially in Albanerpeton, versus unexcavated in Celtedens; 10, anterior end of orbital margin, as marked by posterior edge of slot for receipt of prefrontal, lies approximately in line with, or posterior to, anteroposterior midpoint of frontals in Albanerpeton, versus anterior end of orbital margin lies anterior to midpoint of frontals in Celtedens; and 11, outline of orbital margin uniformly shallowly curved to nearly straight in Albanerpeton, versus margin more concave medially and, occasionally, deflected posterolaterally near posterior end in Celtedens. Where known, the pattern of frontal–nasal contact (character 5) also differs between the two genera. Ventral facets on the internasal process of an incomplete frontal (Fig. 2-3A) of Celtedens sp. from Purbeck indicate that the lateral edges of the process dorsally overlapped the medial edges of the paired nasals. This differs from the condition in Albanerpeton, where a groove extending along the lateral face of the internasal process (Fig. 2-2G) held the medial edge of the nasal in a tongue-in-groove joint. Outgroup comparisons with other temnospondyls argue that the triangular-shaped and relatively short frontals (characters 1 and 2, respectively) of Albanerpeton and the bulbous-shaped internasal process (character 3) on frontals in Celtedens are derived within the family. Polarities for states of other frontal characters are uncertain at present.

Outlines of the frontals (character 1) also differ within genera. Among species of

Albanerpeton for which frontals are known the outline approximates that of an equilateral triangle in A. inexpectatum and an anteroposteriorly elongate, isosceles triangle in other congeners (cf., Fig. 2-2A versus B–F). This variation is associated with differences both in the relative length of the frontals (character 2: ratio of midline length to width across posterior edge of bone about 0.9–1.0 in A. inexpectatum, versus closer to about 1.2 in other congeners) and in the angle at which the lateral wall of the frontals diverges posterolaterally from the midline (character 9: about 30° in A. inexpectatum, versus about 15–25° in other congeners). As these characters vary consistently among species of Albanerpeton, I see no point in using all three to differentiate congeners. I favor using proportions of the frontals (character 1), because these values can be measured or estimated from specimens and reported in a relatively unambiguous manner. Judging by McGowan's figures (1998a:fig. 1C–F, H), frontal outlines in Celtedens range from hourglass-shaped, as in C. ibericus and specimens from Purbeck, to more nearly bell-shaped, as in C. megacephalus and specimens from Uña (cf., here:Fig. 2-3A, B versus C, D). Frontals from an indeterminate congener at Guimarota (Fig. 2-3E) are intermediate between these two extremes. Differences in frontal outlines within Celtedens are associated with variation in characters 8 and 11. In hourglass-shaped frontals, the width between the slots for receipt of the prefrontals is approximately two-thirds the width across the posterior edge of the frontals (McGowan, 1998a:table 1). The orbital margin is uniformly concave medially in C. ibericus; this is also the general pattern in the taxon from Purbeck, except that the posteriormost part of the margin is essentially straight and deflected lateroposteriorly. In bell-shaped frontals, the bone is markedly narrower anteriorly, with the width between the slots for receipt of the prefrontals about one-half the width across the posterior edge of the frontals (McGowan, 1998a:table 1), and the orbital margins are more or less parallel to a point about one-half to two-thirds of the distance from the anterior end of the bone, before curving more lateroposteriorly. No other frontal characters appear diagnostic for species of Celtedens.

A final three frontal characters (3, 4, and 12) differ significantly within Albanerpeton. Characters 3 and 4 describe, respectively, the outline and proportions of the internasal process. Among species of Albanerpeton these two characters are essentially identical: the process is either acuminate and relatively narrow or acute and relatively broad (cf., Fig. 2-2A–C versus D–F). As an aside, I should point out that

McGowan and Evans' (1995:fig. 3b) and McGowan's (1998a:fig. 1b) figures of fused frontals of A. galaktion incorrectly depict the internasal process as broad, short, and wedge-shaped. These authors' drawings were based on published photographs (Fox and Naylor, 1982:fig. 1d, e) of a referred frontal (UALVP 16216) that is broken anteriorly and lacks the internasal process entirely (Chapter 6). The surface that McGowan and Evans (1995) and McGowan (1998a) interpreted as the outline of the internasal process is actually the broken anterior end of the specimen. Other referred frontals in the collection of the UALVP show the proper form of the process for A. galaktion; this information is incorporated into my reconstruction in Figure 2-2E. Character 12 describes the transverse profile and relative width of the ventrolateral crest. In transverse profile, the crest is either convex ventrally or resembles a right-angled triangle, with the medial edge deep and the lateral edge shallow. The width of the crest immediately behind the slot for receipt of the prefrontal, in large specimens, is either less than about 0.40 or greater than about 0.45 the width across the posterior edge of the frontals between the medial edges of the crest. Frontals from large individuals of A. inexpectatum and A. arthridion Fox and Naylor exhibit the most extreme differences in the form of the ventrolateral crest (cf., Fig. 2-2A versus D).

Emargination of the slot for receipt of the prefrontal, relative length of the orbital margin, and pattern of dorsal ornament (characters 7, 10, and 13, respectively) are less variable among species of Albanerpeton than McGowan (1998a) suspected. McGowan's (1998a) belief that relative orbital lengths are diagnostic for species is, again, based on his misinterpretation of a figured frontal (UALVP 16216) of A. galaktion. The specimen is broken anteriorly, creating the impression that the anterior limit of the orbit lies more anterior. Emargination of the slot for receipt of the prefrontal and dorsal ornament both become more pronounced with growth in species of Albanerpeton; this is especially evident in A. inexpectatum (Chapter 3). Albanerpetontid frontals are typically ornamented dorsally with a system of polygonal pits enclosed by ridges. Occasional frontals are encountered in which the pits are so shallow and the ridges so low that the dorsal surface is virtually smooth. As this condition occurs in different-sized and, sometimes, well-preserved frontals of species in both genera, it appears to be neither ontogenetic or diagenetic in origin nor taxonomically significant.

Of the 13 frontal characters considered, characters 1-3, 6, 7, 10, 11, and, probably, 5 are taxonomically important at the generic level for albanerpetontids, whereas at the specific level characters 1–4, 9, and 12 are informative for Albanerpeton and characters 1, 8, and 11 are informative for Celtedens.

Characters of The Jaws (Figs. 2-4 and 2-5)

Albanerpetontid jaws are distinctive, but superficially resemble and have been confused with jaws of other lissamphibians and lizards. For this reason and because albanerpetontid jaws are not uncommon in nonmarine Jurassic and Cretaceous microvertebrate assemblages, a brief review of their characteristic features is appropriate. The premaxilla and maxilla each have a deep pars dentalis and the dentary has a tall dental parapet for attachment of the highly pleurodont teeth. Upper jaws are additionally characterized by having tiny, scattered external nutritive foramina labially, the tooth row extending along virtually the entire ventral margin of the pars dentalis, and a prominent, shelf-like pars palatinum lingually. The pars palatinum on the premaxilla is pierced by a palatal foramen and on the maxilla bears a trough dorsolingually for contact with one or more palatal bones. The premaxilla is further distinctive in having a facet on the labial face for contact with a complementary process from the maxilla. The pars dorsalis on the premaxilla is prominent, often with a dorsal boss labially and a lacrimal notch laterodorsally. The lingual face of the premaxillary pars dorsalis is excavated by the suprapalatal pit, a cavity that typically is bounded on either or both sides by a vertical strut. The maxilla is further characterized by having a low, posteriorly tapered pars facialis that dorsally bears a triangular-shaped internasal process. Anteriorly the maxilla bears an elongate premaxillary lateral process and a lingually broad, shelf-like premaxillary dorsal process, both of which articulate with the premaxilla. Additional diagnostic features of the dentary include a row of external nutritive foramina labially along about the anterior one-half to two-thirds of the bone, an elongate scar ventrally for attachment of the intermandibularis muscle, and a foramen in the base of a pit on the underside of the symphysis. Lingually, the Meckelian canal is closed anteriorly, the subdental shelf is low, narrow, and gutter-like anteriorly, becoming deeper and narrower posteriorly, and there is a broad area of attachment posteriorly for postdentary bones. One or two prominent symphyseal prongs project medially from the more posterior part of the symphysis. These articulate in a mortise and tenon fashion with complementary prongs from the opposite dentary to form a unique interlocking intermandibular joint. Symphyseal prongs are unique among gnathostomes to albanerpetontids and are unquestionably autapomorphic for the family (Milner, 1988; here:Chapter 8). The arrangement, attachment, and structure of the marginal teeth are also characteristic. Teeth are highly pleurodont in attachment—i.e., they are attached along most of the height of the pedicel to the inner wall of the jaw. Each tooth is relatively elongate, straight, and non-pedicellate. The base of each tooth is rarely perforated by a foramen and the pedicel is slightly compressed mesiodistally. The crown is chisel-like, labiolingually compressed, and bears three faint, mesiodistally aligned cuspules. Such crowns are autapomorphic for the family, at least among other temnospondyls, whereas non-pedicely is convergent with various other lissamphibian taxa (Chapter 8).

Jaws are too inadequately known for Celtedens to determine if these elements differ at the generic level for albanerpetontids or among species of Celtedens. I suspect that better jaw material would demonstrate at least species level differences, comparable to those documented below for Albanerpeton. Where known, jaws of Celtedens have a generalized albanerpetontid construction. Premaxillae of the indeterminate species from Purbeck primitively resemble those of A. arthridion in having a tiny suprapalatal pit located high on the lingual face of the pars dorsalis, well above the pars palatinum (cf., Fig. 2-4A versus B).

Characters of the upper and lower jaws differ within Albanerpeton and have been used to diagnose species (Estes, 1981; Fox and Naylor, 1982; Gardner, 1999a, b, c, 2000a, in press a; Rage and Hossini, 2000). Variation is particularly extensive in the structure and contacts of the premaxilla (Fig. 2-4B–F), making this the most informative element. I consider the following premaxillary characters useful for diagnosing species: build of bone (e.g., gracile versus robust); premaxillae paired or fused; proportions of pars dorsalis; pattern of contact dorsally with nasal; presence and relative size of dorsal boss; extent and pattern of labial ornament; position, shape, and relative size of suprapalatal pit; number and form of internal struts; form of vomerine process and of dorsal rim on lingual edge of maxillary process; and relative size of palatal foramen. Premaxillary characters that are not useful for differentiating species of Albanerpeton (contra Estes, 1981; Fox and Naylor, 1982; Rage and Hossini, 2000) include the proportions of the lacrimal notch, length of the medial flange, and relative development of the pars palatinum (chapters 4 and 6). Although I have not recognized any diagnostic premaxillary characters for Albanerpeton, subgeneric clades are identified by suites of premaxillary synapomorphies (chapters 3–7). For example in all congeners except A. arthridion, the suprapalatal pit is relatively larger and lies lower on the pars dorsalis (cf., Figs. 2-4B versus C, D, 4.5).

I attach considerable importance to the suprapalatal pit (Fig. 2-4A–D:arrow 1). Fox and Naylor's (1982) suggestion that the suprapalatal pit held a gland is reasonable, considering the position of the pit in the lingual face of the premaxillary pars dorsalis and its associated foramina. Although the identity of such a gland is unknown, it presumably functioned in olfaction, feeding, or both. The suprapalatal pit is intimately associated with the palatal foramen (Fig. 2-4E, F:arrow 2), a typically small foramen that extends dorsally through the pars palatinum to open beneath, or in the floor of, the suprapalatal pit, regardless of the position of the pit mediolaterally across the pars dorsalis. Assuming that the suprapalatal pit held a gland, the palatal foramen likely carried a duct between the gland and the roof of the mouth. Differences in the size, shape, and position of the suprapalatal pit are pronounced among species of Albanerpeton, and it is tempting to speculate that these modifications were reflected in life by variation in the form and function of the presumed gland.

Neither the maxilla nor dentary, where adequately known, are diagnostic for Albanerpeton or Celtedens. None of the dentary characters that Nessov (1981) believed were taxonomically useful at the generic level for albanerpetontids seem appropriate for this purpose (Gardner and Averianov, 1998). Taxonomically useful variation is, however, evident at the specific level in Albanerpeton in the following attributes (Fig. 2-4G–P): proportions and outline of the premaxillary lateral process on the maxilla; presence of a dorsal process immediately behind the tooth row on the dentary; presence of labial ornament on both jaws in large individuals; and labial outline of the ventral edge of the pars dentalis on the maxilla and of the dorsal edge of the dental parapet on the dentary. The last character is linked with size heterodonty of the teeth (see below).

Two tooth characters differ among species of Albanerpeton. Teeth located about a third of the distance posteriorly along the tooth row on the maxilla and dentary are usually only slightly longer than the more anterior and posterior teeth, but in A. nexuosus

Estes (Fig. 2-4J, P) teeth about a third of the distance along the row are relatively longer and, occasionally, more robust than adjacent teeth. Although not evident in Figure 2-3, the position of the anterior end of maxillary tooth row also varies: the anterior end of the tooth row is approximately in line with the leading edge of the nasal process in A. inexpectatum and two new North American species (middle Campanian and Paleocene), but extends several loci more anteriorward in other congeners.

Other Characters and Elements

The only other character that I have identified as being taxonomically important within the Albanerpetontidae is maximum head-body length (i.e., snout-pelvic length or distance from tip of snout to midpoint of pelvic girdle). This straightline value can be measured or estimated directly from skeletons or calculated from the midline length of frontals (Gardner, 1999b). Examination of the holotype skeleton of Celtedens megacephalus and measurements taken from McGowan and Evans' photograph (1995:fig. 1a) of the holotype skeleton of C. ibericus indicate that the fused frontals in both specimens are about one-tenth the snout-pelvic length. Head-body length is informative at the species level in Albanerpeton, where estimated maximum values range from about 30 to over 60 mm, depending on the species. This measurement does not appear to vary significantly among species of Celtedens.

The anteriormost three vertebrae in albanerpetontids are modified in a unique manner (see familial diagnosis, below and Chapter 8) and, in some respects, convergently resemble the mammalian atlas-axis complex (Fox and Naylor, 1982; Milner, 1988; McGowan, 1998b). Too few examples of these and more posterior vertebrae are available to determine if vertebral structure varies significantly among genera and species. Albanerpetontid atlantes described to date (e.g., Estes and Hoffstetter, 1976; Fox and Naylor, 1982; McGowan, 1998b; here:chapters 3-6) are remarkably similar, and there is no evidence for the extensive, diagnostically useful variation seen in, for example, salamanders (Naylor, 1978; Estes, 1981; here:chapters 9-11). The evidently conservative structure of the albanerpetontid atlas may be due to the specialized atlanto-axial joint (McGowan, 1998b; here:Chapter 8) having imposed severe structural constraints on the atlas.

SYSTEMATIC PALEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order ALLOCAUDATA Fox and Naylor, 1982
Family ALBANERPETONTIDAE Fox and Naylor, 1982

Type Genus—Albanerpeton Estes and Hoffstetter.

Included Genera—Two named genera: Albanerpeton, latest Aptian/earliest Albian-late Paleocene, North American Western Interior, and middle and ?early Miocene, France; and Celtedens McGowan and Evans, Kimmeridgian-early Albian, western Europe.

Distribution—Middle Jurassic-Miocene: early Bathonian-middle Miocene, Europe; Aptian/Albian-late Paleocene, North American Western Interior; Berriasian, northern Africa; and Cenomanian and Coniacian, Middle Asia. An older Asian record from the Middle Jurassic (Callovian) of Kirghizia is unproven, because the frontal reported by Nessov (1988) was neither figured nor described and it has not subsequently been located (Gardner and Averianov, 1998).

Revised Diagnosis—Clade of lissamphibians differing from all other vertebrates in the following two autapomorphies: mortise and tenon style intermandibular joint and first three vertebrae comprised of an atlas lacking postzygapophyses and having posterior cotyle with articular face indented by tripartite facets and with dorsal and ventrolateral margins deeply emarginate, a neomorphic "axis" lacking neural arch and transverse processes, and first trunk vertebra lacking prezygapophyses, but having anterior end of neural arch extending craniad above axis to fit into complementary notch in posterior edge of atlantal neural arch. Differs from other temnospondyls in five synapomorphies: crowns on marginal teeth labiolingually compressed and distally bear three faint cuspules arranged mesiodistally; joint between skull and mandible nearly vertical; and frontals fused, with prominent internasal process and two pairs of slots for mortise and tenon contact with paired nasals anteriorly and paired prefrontals anterolaterally. Differs further from some amphibamids and most lissamphibians in one homoplasy: marginal teeth non-pedicellate in adults. Among lissamphibians, lacks respective autapomorphies of gymnophionans, caudates, and salientians; more derived than gymnophionans and resembles caudates and batrachians in lacking surangular, splenials, and coronoids, but differs from last two groups in primitively retaining a posteriorly closed maxillary arcade, concave articular receiving convex quadrate, more than 20 presacral vertebrae, ossified pubis, and dermal scales. Primitively differs further from apodans, anurans, and many urodeles in retaining lacrimal and from apodans, salientians, and some urodeles in retaining odontoid process on atlas.

Remarks—In accordance with the International Code of Zoological Nomenclature (1985), I use both the ordinal name Allocaudata and the familial name Albanerpetontidae in formal classification. The revised diagnosis presented above for the Albanerpetontidae is based on my analysis in Chapter 8 (also Gardner, in press b) of the higher level relationships of the clade. This is the first diagnosis for the Albanerpetontidae that is differential and explicitly identifies the inferred polarities of character states (cf., Fox and Naylor, 1982; McGowan, 1998a).

Besides Celtedens and the type genus Albanerpeton, two other albanerpetontid genera have been formally named: Nukusurus Nessov (two species; Cenomanian and Coniacian, Uzbekistan) and Bishara Nessov (monotypic; Santonian or Campanian, Kazakhstan). The two species of Nukusurus are each named on a dentary, both of which are indeterminate below the familial level; hence, the generic name Nukusurus and the specific names N. insuetus Nessov (type species) and N. sodalis Nessov are nomina dubia within the Albanerpetontidae (Gardner and Averianov, 1998). The name Bishara denotes an indeterminate caudate taxon, not an albanerpetontid, because the holotype of the type and only species, B. backa Nessov, is an atlantal centrum from an indeterminate salamander (Gardner and Averianov, 1998). Two previously unrecognized albanerpetontid taxa (Middle Jurassic, England; basal Cretaceous, Morocco) are distinctive at the generic level from both Albanerpeton and Celtedens, but it is not yet clear whether these taxa constitute a third genus. For this reason and because the two new taxa are currently being studied in collaboration with Drs. S. E. Evans and D. Sigogneau-Russell, I do not include them in my differential diagnoses below for Albanerpeton and Celtedens.

ALBANERPETON Estes and Hoffstetter, 1976

(Figs. 2-1A, 2-2, 2-4B–P, 2-5)

Prodesmodon Estes, 1964 [jaws referred to type species by Estes, 1964:p. 88, figs. 43, 44a–c].

Prosiren Goin and Auffenberg, 1958 [jaws and humerus referred to type species by Estes, 1969d:p. 87, fig. 2a–j and 1981:p. 18, fig. 3B–E].

Type Species—Albanerpeton inexpectatum Estes and Hoffstetter.

Included Species—Seven species: Albanerpeton inexpectatum, middle and ?early Miocene, France; A. arthridion Fox and Naylor, latest Aptian–middle Albian, Texas and Oklahoma; A. nexuosus Estes and A. galaktion Fox and Naylor, both Campanian and Maastrichtian (Aquilan–Lancian), North American Western Interior; A. cifellii Gardner, late Turonian, Utah; a new species, middle Campanian (Judithian), North American Western Interior; and an unnamed species, late Paleocene, Alberta.

Distribution—Early Cretaceous–Miocene: latest Aptian/earliest Albian–late Paleocene, North American Western Interior, and middle and ?early Miocene, France.

Diagnosis (modified from Gardner, 2000a)—Genus of albanerpetontid differing from Celtedens in having fused frontals more derived in being triangular in outline and relatively shorter, with ratio of midline length to width across posterior edge between lateral edges of ventrolateral crests about 1.2 or less, and more primitive in retaining anteriorly pointed internasal process. Differs further from Celtedens in another five frontal character states of uncertain polarities: lateral face of internasal process indented by anteroposteriorly elongate groove for tongue-in-groove contact with medial edge of nasal; anterolateral process prominent and pointed distally; dorsal and ventral edges of slot for receipt of prefrontal excavated medially; anterior end of orbital margin located approximately in line with, or posterior to, anteroposterior midpoint of frontals; and orbital margin uniformly shallowly concave to nearly straight along entire length in dorsal or ventral outline.

Remarks—Species of Albanerpeton are known by isolated and occasional articulated bones. Albanerpeton is pivotal for interpreting the history of North American Cretaceous albanerpetontids because it is the only albanerpetontid genus identified from the continent. I consider the European Miocene type species and the five North American Cretaceous species in the next four chapters, as follows: Chapter 3, A. inexpectatum; Chapter 4, A. arthridion; Chapter 5, A. cifellii; and Chapter 6, A. nexuosus, A. galaktion, and the new Judithian species. The unnamed Paleocene species, hereafter called the "Paskapoo species," is represented by undescribed frontals (Fig. 2-2C), a parietal, and jaws from the upper Paleocene (Tiffanian in age; Fox, 1990) Paskapoo and Porcupine Hills formations of southern Alberta. As this species is not vital for my study, I will formally name and describe it at a later date. In Chapter 6 I argue that some elements originally referred to A. nexuosus and A. galaktion are incorrectly associated; hence, for chapters 3-5 note that I regard the second of the two premaxillary morphs that Fox and Naylor (1982:124) identified for A. galaktion as belonging instead to A. nexuosus. Figure 2-5 depicts a simplified version of my hypothesis of relationships within Albanerpeton (see Chapter 7), in which A. arthridion is the sister-taxon to the "post-middle Albian clade" comprised of two sister-clades: the "gracile-snouted clade" of A. galaktion, A. cifellii, and the new Judithian species and the "robust-snouted clade" of A. nexuosus, A. inexpectatum, and the Paskapoo species.

CELTEDENS McGowan and Evans, 1995
(Figs. 2-1B, 2-3, 2-4a)

Albanerpeton Estes and Hoffstetter, 1976 [in part: holotype skeleton and, perhaps, referred elements of "A. megacephalus" listed by Estes, 1981:p. 22].

Type Species—Celtedens megacephalus (Costa).

Included Species—Two species: Celtedens megacephalus, early Albian, Italy; and C. ibericus McGowan and Evans, late Barremian, Spain.

Distribution—Late Jurassic (Kimmeridgian)-Early Cretaceous (early Albian), Europe.

Diagnosis (modified from Gardner, 2000a)—Genus of albanerpetontid differing from Albanerpeton in having fused frontals more derived in bearing bulbous-shaped internasal process and in being relatively longer, with ratio of midline length to width across posterior edge between lateral edges of ventrolateral crests greater than about 1.2, and more primitive in having frontals hourglass- or bell-shaped in outline. Differs further from Albanerpeton in another five frontal character states of uncertain polarities: internasal process ventrolaterally has facet for dorsally overlapping medial edge of nasal; anterolateral process a poorly differentiated, broadly rounded shoulder; dorsal and ventral edges of slot for receipt of prefrontal not excavated medially; anterior end of orbital margin located anterior to anteroposterior midpoint of frontals; and orbital margin deeply concave in dorsal or ventral outline, occasionally deflected posterolaterally near posterior end.

Remarks—Celtedens is an exclusively European genus that consists of two named species, both represented by articulated skeletons from lacustrine deposits. The holotype skeleton and only specimen of C. megacephalus is poorly preserved and difficult to interpret (Costa, 1864; D'Erasmo, 1914; Estes, 1981; Barbera and Macuglia, 1991; pers. obs., 1997). McGowan and Evans (1995) briefly reported on two articulated skeletons of C. ibericus, one of which preserves details of the soft tissue. McGowan's (1994) more detailed interpretations of all three skeletons remain unpublished, although he (McGowan, 1998a, b) has since presented a controversial cranial reconstruction for C. ibericus (Gardner, 2000b). Celtedens is also reliably known by diagnostic frontals from another three localities: Uña (Barremian, Spain), Purbeck (Berriasian, England), and Guimarota (Kimmeridgian, Portugal) (McGowan and Ensom, 1997; McGowan, 1998a). McGowan (1998a) implied that frontals from Uña and Guimarota may pertain to previously unrecognized species. McGowan (1998a:192) also reported Celtedens from Galve (Barremian), Spain, but did not figure any diagnostic frontals. Reports of Celtedens from the Middle Jurassic (Bathonian) of England (McGowan, 1996, 1998a) are incorrect (see account below), meaning that the earliest unequivocal occurrence of the genus is raised to the Kimmeridgian (Late Jurassic).

Unnamed Genus and Species A

(Fig. 2-6)

Celtedens megacephalus (Costa); McGowan, 1996:233, figs. 1–9, 11–13.

"Celtedens cf. megacephalus" (Costa); McGowan and Ensom, 1997:p. 117; McGowan, 1998a:fig. 1G.

Celtedens ibericus McGowan and Evans; McGowan, 1998a:fig. 4.

Voucher Specimens—BMNH R.14157, UCK 14, 15, premaxillae; UCK 10, maxilla; UCK 01, 03, dentaries; BMNH R.14158–14160, UCK 26, 27, frontals.

Horizon and Locality—Forest Marble Formation; Middle Jurassic (late Bathonian); Kirtlington Cement Quarry, Oxfordshire, southcentral England.

Remarks—The Kirtlington Cement Quarry is one of four localities in the Forest Marble Formation to have produced albanerpetontid elements (Evans, 1992; Evans and Milner, 1994). These fossils are the second oldest occurrences (late Bathonian) for the family, after an atlantal centrum reported by Seiffert (1969) from Gardies (early Bathonian; Kriwet et al., 1997), southcentral France. McGowan (1996) described a modest collection of albanerpetontid skull and postcranial elements from Kirtlington and referred these to Celtedens on the strength of an incomplete frontal (UCK 26; Fig. 2-6A). While this specimen more closely resembled frontals of Celtedens than Albanerpeton in the apparent hourglass shape of the bone and the outline of the orbital margin, none of the frontals from Kirtlington available to McGowan at the time of his study preserved the diagnostic internasal process. Such a specimen is now available: BMNH R.14158 (Fig. 2-6B, C) consists of about the anterior one-third of a pair of fused frontals, broken posteriorly between the slots for receipt of the prefrontals. As there is no evidence from other specimens that more than one albanerpetontid taxon is represented at Kirtlington, BMNH R.14158 and UCK 26 evidently pertain to the same species. Whereas the poorly differentiated anterolateral processes on BMNH R.14158 recall the condition in Celtedens, the internasal process instead resembles that of Albanerpeton in being triangular in outline and in having an elongate groove along the lateral face for articulation with the nasal. Premaxillae from Kirtlington (Fig. 2-6D) are also distinctive in having the suprapalatal pit located more laterally within the external narial margin and facing laterolingually. In Celtedens and Albanerpeton the suprapalatal pit lies more medially in the lingual face of the pars dorsalis and opens lingually. This mixture of frontal and premaxillary character states excludes the taxon from Kirtlington—hereafter called the "Kirtlington species"—from membership in either of the two currently recognized albanerpetontid genera.

Unnamed Genus and Species B
(Unfigured)

Remarks—The first Gondwanan albanerpetontids were recently reported by Sigogneau-Russell et al. (1998) from a basal Cretaceous (Berriasian) limestone lens in the "Couches-Rouges" sandstone near Anoual, Morocco. The specimens in question are undescribed jaws and frontals in the collection of the MNHN.MCM. Premaxillae and frontals from Anoual exhibit the same suite of character states seen in the Kirtlington species and, thus, cannot be assigned to either Albanerpeton or Celtedens. Detailed differences between premaxillae and frontals from the two sites, however, indicate that specimens from Anoual and Kirtlington pertain to different taxa. Here I informally call the Moroccan albanerpetontid the "Anoual species."

CONCLUSIONS

Above I have presented an review of the Albanerpetontidae and its genera and species. The major points of this chapter are summarized below:

(1) Frontals are diagnostic for Albanerpeton, Celtedens, and species in both genera, whereas characters of the jaws and head-body size are also diagnostic for species of Albanerpeton. The relative diagnostic value of frontals for species of Celtedens may be inflated, because no other elements are as well known for members of the genus.

(2) I provide a revised, differential diagnosis for the Albanerpetontidae based on cranial and vertebral characters and for Albanerpeton and Celtedens based on frontal characters. These are the first diagnoses for these three taxa in which inferred polarities of character states are explicitly stated. Albanerpeton includes seven diagnosable species from the Aptian/Albian to Paleocene of North America and Miocene of Europe. Celtedens ranges from the Kimmeridgian to Albian of Europe and includes two named species.

(3) Two unnamed albanerpetontid taxa (Bathonian, England; Berriasian, Morocco) exhibit a suite of premaxillary and frontal character states that precludes their membership in either Albanerpeton or Celtedens. It is unclear at present whether these unnamed taxa constitute a third albanerpetontid genus.

TABLE 2-1. Putative frontal characters for albanerpetontid genera and species. References are: [1]McGowan and Evans, 1995; [2]McGowan, 1998a; [3]Gardner, 1999a; [4]Rage and Hossini, 2000; [5]S. E. Evans, pers. comm., 1999.

1. Dorsal or ventral outline of frontals[1,2,3].
2. Midline length of frontals relative to width across posterior edge between lateral edges of ventrolateral crests[2,3,4].
3. Dorsal or ventral outline of internasal process[1,2,3].
4. Length of internasal process relative to width across base[2].
5. Pattern of contact between internasal process and paired nasals[3].
6. Form of anterolateral process[5].
7. Medial emargination of slot for receipt of prefrontal[2].
8. Width of frontals between slots for receipt of prefrontal relative to width across posterior edge of bone[2].
9. Angle at which lateral wall of frontal diverges posterolaterally from midline[2].
10. Position of anterior limit of orbital margin relative to midline length of frontals[2].
11. Dorsal or ventral outline of orbital margin [1,2].
12. Form of ventrolateral crest[3].
13. Pattern of dorsal ornament[2].

FIGURE 2-1. Cranial reconstructions for albanerpetontids. **A**, Albanerpeton inexpectatum Estes and Hoffstetter; middle and ?early Miocene, France; reconstruction modified from Estes and Hoffstetter (1976:fig. 4B), with jugal added from McGowan (1998a:fig. 2). **B**, Celtedens ibericus McGowan and Evans; late Barremian, Spain; reconstruction modified from McGowan (1998a:fig. 2), with configuration of jugal based on left side of McGowan's original figure. Skulls approximately to scale; scale bar = 1 mm.

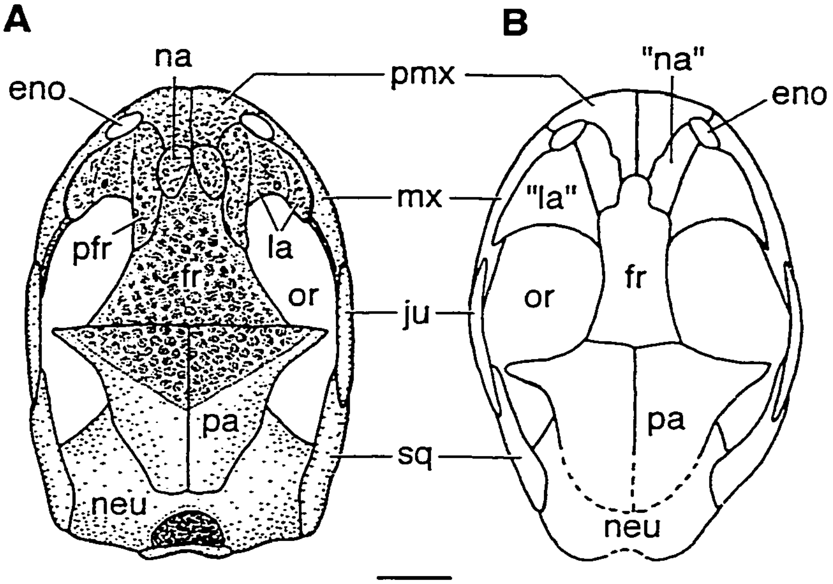
A
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FIGURE 2-2. Azygous frontals of *Albanerpeton* Estes and Hoffstetter. **A**, *A. inexpectatum* Estes and Hoffstetter, MNHN.LGA 1222, complete frontals, in ventral view; middle or ?early Miocene fissure fill, La Grive-St. Alban, France. **B**, *A. nexuosus* Estes, reconstructed frontals based on UALVP 39983, 39986, 39989, and 39996, in ventral view; Milk River Formation, early Campanian, Alberta. **C**. Paskapoo species (unnamed *Albanerpeton* sp.), UALVP unnumbered, incomplete frontals with internasal process warped to the right (left side in figure) and missing much of anterolateral process on right side, all of anterolateral process on left side, and posterior end of bone, in ventral view; Paskapoo Formation, late Paleocene, Alberta. **D**, *A. arthridion* Fox and Naylor, FMNH PR2026, nearly complete frontals missing distal end of both anterolateral processes, in ventral view; upper Antlers Formation, early-middle Albian, Texas. **E**, *A. galaktion* Fox and Naylor, reconstructed frontals based on UALVP 16216, 39946, 39949, and 39951, in ventral view; Milk River Formation, early Campanian, Alberta. **F**, new Judithian species, reconstructed frontals based on TMP 86.194.8, 86.242.74, 95.181.67, and 96.1.57, in ventral view; Dinosaur Park and Oldman formations, middle Campanian, Alberta. **G**. *A. inexpectatum*, MNHN.LGA 1220, complete frontals, in right lateral view. Figures at different scales: scale bars = 1 mm.

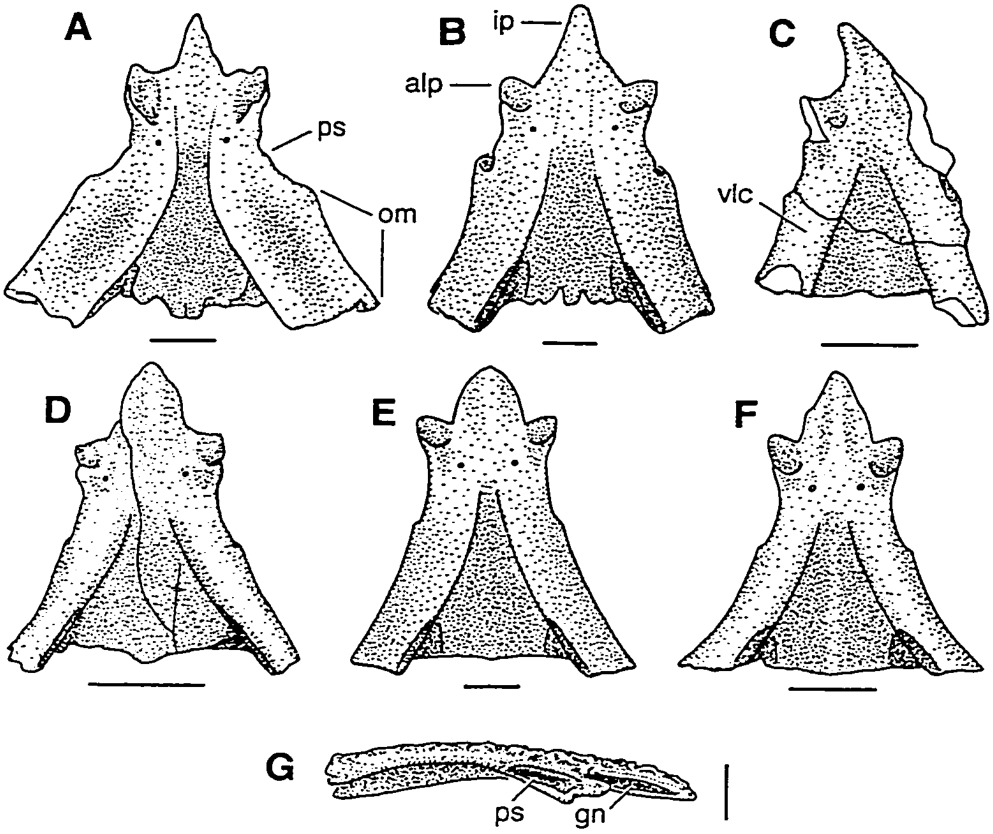
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FIGURE 2-3. Azygous frontals of Celtedens McGowan and Evans, all in ventral view. **A**, Celtedens sp. indet., DORCM GS35, incomplete frontals, in ventral view with arrow indicating anterior end of orbital margin, cross-hatching showing area once present but now missing (cf., McGowan and Ensom, 1997:fig. 2a), and hash marks indicating matrix; Purbeck, Berriasian, England. **B**, C. ibericus McGowan and Evans, outline drawing of frontals articulated in holotype skull LH 6020; Las Hoyas, late Barremian, Spain. **C**, C. megacephalus (Costa), outline drawing of frontals articulated in holotype skull MNP 542; Pietraroia, early Albian, Italy. **D**, Celtedens sp. indet., catalogue number unreported, outline drawing of frontals; Uña, Barremian Spain. **E**, Celtedens sp. indet., catalogue number unreported, outline drawing of frontals; Guimarota Kimmeridgian, Portugal. Frontals in figures **B–E** redrawn from McGowan (1998a:fig. 1). Figures at different scales: left (**A**) and right (**B**, **C**) scale bars = 1 mm; scales for figures **D** and **E** are unreported.

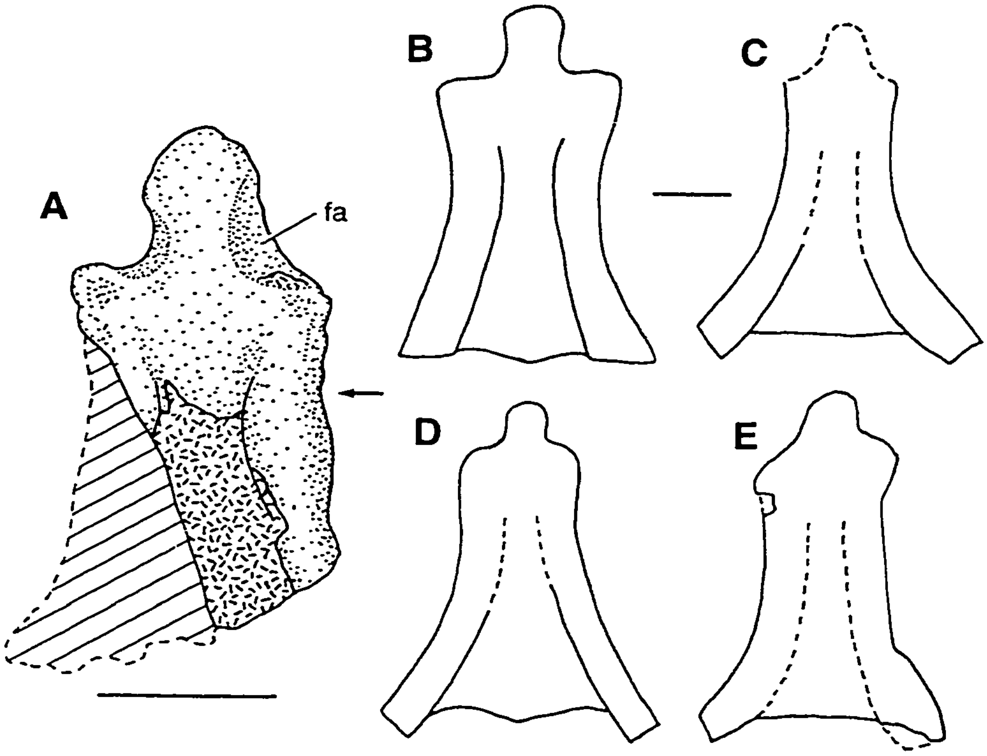
A
fa
B
C
D
E

FIGURE 2-4. Jaws of albanerpetontids. **A**, Celtedens sp. indet., DORCM GS34, incomplete left premaxilla lacking most of pars palatinum and dorsal part of pars dorsalis, in lingual view. **B**, Albanerpeton arthridion Fox and Naylor, reconstructed right premaxilla based on FMNH PR805 (holotype) and FMNH PR2023, in lingual view. **C**, A. galaktion Fox and Naylor, reconstructed left premaxilla based on UALVP 16203 (holotype), 16204, and 16212, in lingual view. **D**, **E**, A. nexuosus Estes, premaxillae: **D**, reconstructed fused premaxillae based on UALVP 16206 and 39955, in lingual view; **E**, UALVP 39960, left premaxilla, in occlusal view. **F**, A. galaktion, UALVP 16212, left premaxilla, in occlusal view. **G–I**, A. inexpectatum Estes and Hoffstetter, MNHN.LGA 1232, left maxilla, in (**G**) labial, (**H**) lingual, and (**I**) dorsal views. **J**, A. nexuosus, UALVP 16242, incomplete left maxilla missing about posterior one-third of bone and crowns of anteriormost teeth, with outline of anterolateral premaxillary process (dotted line) from UALVP 16239, in labial view. **K**, A. galaktion, UALVP 16240, incomplete left maxilla missing about posterior one-third of bone and crowns of anteriormost teeth, in labial view. **L–O**, A. inexpectatum, MNHN.LGA 1249, nearly complete right dentary missing posteriormost end, in (**L**) labial, (**M**) lingual, (**N**) occlusal, and (**O**) ventral views. **P**, A. nexuosus, UCMP 49547 (holotype), nearly complete left dentary missing posterior end, in lingual view. Provenances for listed specimens: Celtedens sp. indet. (**A**), Purbeck, Berriasian, England; A. arthridion (**B**), Antlers Formation, early–middle Albian, Texas; A. galaktion (**C**, **F**, and **K**) and UALVP specimens (**D**, **E**, and **J**) of A. nexuosus, Milk River Formation, early Campanian, Alberta; holotype (**P**) of A. nexuosus, Lance Formation, late Maastrichtian, Wyoming; and A. inexpectatum (**G–I** and **L–O**), middle and ?early Miocene fissure fills, La Grive-St. Alban, France. Arrow 1 (**A–D**) points to suprapalatal pit and arrow 2 (**E**, **F**) points to palatal foramen. Specimens in figures **L–O** redrawn from Gardner and Averianov (1998:fig. 2) and in figure **P** redrawn from Estes (1964:fig. 44c). Figures at different scales: uppermost left (**A**), upper left (**B**), and bottom (**C–P**) scale bars = 1 mm.

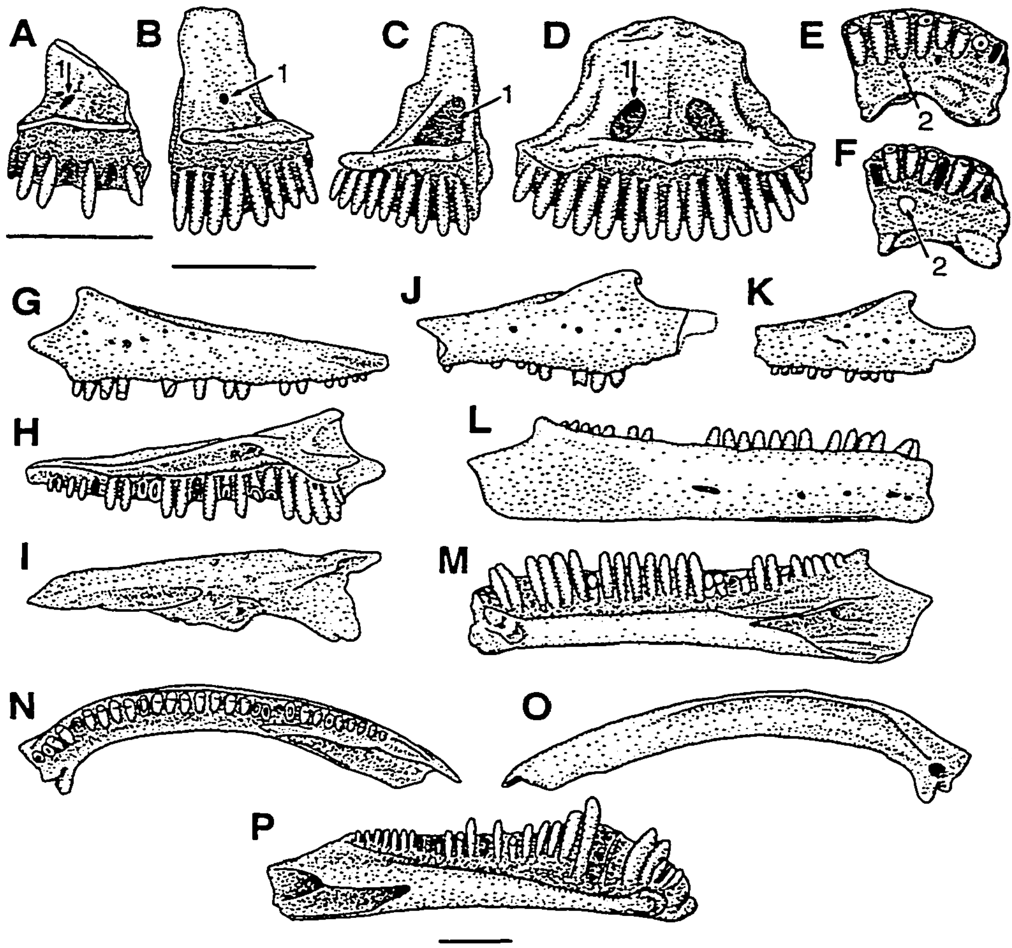
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FIGURE 2-5. Simplified phylogeny of inferred relationships within Albanerpeton with reconstructed premaxillae, in lingual view, to illustrate major patterns of premaxillary evolution in the genus. **A**, right premaxilla of A. arthridion Fox and Naylor, representative of the primitive albanerpetontid level of organization; based on FMNH PR805 (holotype) and FMNH PR2023 from the upper Antlers Formation, early-middle Albian, Texas. **B**, left premaxilla of A. galaktion Fox and Naylor, representative of the gracile-snouted clade; based on UALVP 16203 (holotype), 16204, and 16212 from the Milk River Formation, early Campanian, Alberta. **C**, fused premaxillae of A. nexuosus Estes, representative of the robust-snouted clade; based on UALVP 16206 and 39955 from the Milk River Formation, early Campanian, Alberta. Arrows point to suprapalatal pit. Specimens not to scale. See Chapter 7 for details of this phylogeny.

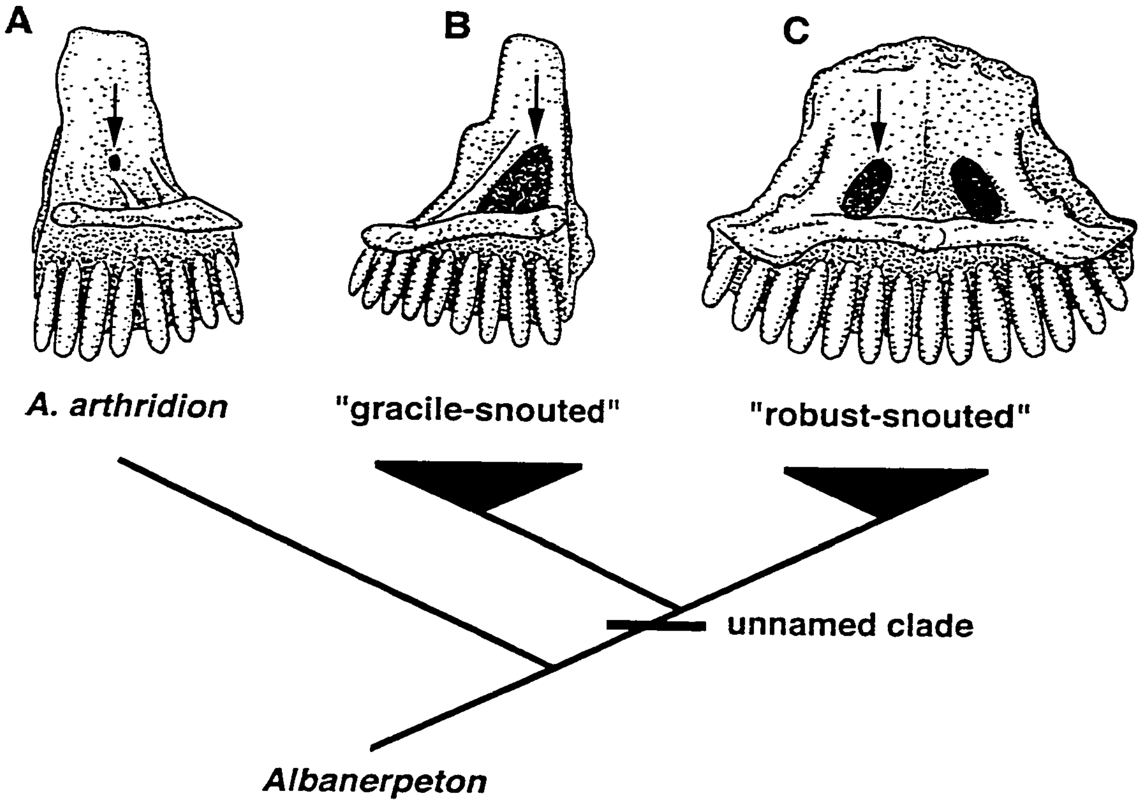
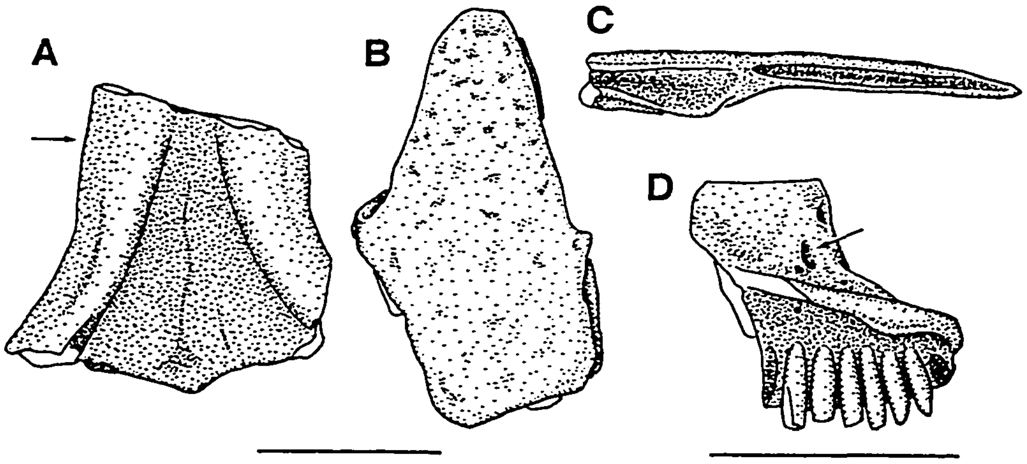

A
B
C
A. arthridion
"gracile-snouted"
"robust-snouted"
unnamed clade
Albanerpeton

FIGURE 2-6. Frontals and jaws of albanerpetontid Unnamed Genus and Species A (i.e., Kirtlington species); Forest Marble Formation, late Bathonian, Kirtlington Cement Quarry, England. **A**, UCK 26, posterior two-thirds of fused frontals missing posterior end of both ventrolateral crests, with arrow indicating anterior limit of orbital margin, in ventral view. **B, C**, BMNH R.14158, anterior one-third of fused frontals, in (**B**) dorsal and (**C**) right lateral views. **D**, UCK 15, incomplete right premaxilla, lacking dorsal end of pars dorsalis and medial parts of pars palatinum and pars dentalis, with arrow pointing to suprapalatal pit, in lingual view. Specimens at different scales: left (**A–C**) and right (**D**) scale bars = 1 mm.



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CHAPTER 3 — REASSESSMENT OF THE TYPE SPECIES OF ALBANERPETON ESTES AND HOFFSTETTER—A. INEXPECTATUM ESTES AND HOFFSTETTER FROM THE MIOCENE OF FRANCE[1]

INTRODUCTION

Estes and Hoffstetter (1976) described the new genus and species Albanerpeton inexpectatum for two large collections of isolated and occasional articulated skull and postcranial bones from middle and, possibly, lower Miocene fissure fills near La Grive-St. Alban, southeastern France. Subsequent work by Estes (1981), McGowan (1998a, b), and Rage and Hossini (2000) provided little new osteological information about the species, although the last authors did extend the geographical range of A. inexpectatum to the middle Miocene Sansan locality of southcentral France. Although A. inexpectatum lies outside the temporal and geographical scope of my study, the species is important for studies of North American albanerpetontids for four reasons. First, A. inexpectatum is the type species of Albanerpeton, the only albanerpetontid genus recognized from North America. Second, A. inexpectatum is the only congener identified from outside of North America and, as I argue herein, the last survivor of a subgeneric clade whose origins can be traced back to the Early–Late Cretaceous boundary in North America. Third, as the type species of the type genus, A. inexpectatum is an important reference taxon and has played a central role in our interpretations of albanerpetontid morphology and paleobiology. Numerous Middle Jurassic–Paleocene albanerpetontid fossils and taxa have since been reported, and A. inexpectatum needs to be reconsidered in light of these subsequent discoveries. Finally, although numerous albanerpetontid fossils are now known, in terms of the number and quality of specimens A. inexpectatum is arguably represented by some of the best collections yet available for any albanerpetontid species.

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[1] A version of this chapter has been published. Gardner 1999. Annales de Paléontologie. 85: 57–84.

My objectives here are to (1) provide a revised diagnosis and expanded redescription for A. inexpectatum based primarily on jaws and frontals, (2) document and interpret intraspecific variation in these elements, and (3) comment on the phylogeny, paleobiogeography, and functional morphology of the species.

GEOLOGICAL SETTING AND LOCALITIES

Specimens of Albanerpeton inexpectatum described herein come from terrigenous fissure fills in elevated outcrops of Middle Jurassic (Bajocian in age; Freudenthal and Mein, 1989) limestone near the village of La Grive-St. Alban, department of Isère, southeastern France. About a dozen fossiliferous fissure fills of various ages have been identified in this area since the middle part of the nineteenth century (Freudenthal and Mein, 1989). Mammal fossils support ages of MN 5, MN 6, or MN 7/8 for individual fissure fills (Rage and Holman, 1984; Freudenthal and Mein, 1989; Bruijn et al., 1992) and indicate that infilling occurred over a relatively short span of about 6 million years from the late early to late middle Miocene (see Steininger et al., 1996:figs. 2.1, 2.2). One of the albanerpetontid-bearing fissures—Fissure M in Milliet Quarry—is the reference locality for the MN 7/8 zone (Bruijn et al., 1992). A taxonomically diverse assortment of mammals (see faunal list in Bruijn et al. 1992:112–113), birds (Ballman, 1969), squamates (Hoffstetter, 1946a, b, 1969; Hoffstetter and Rage, 1972; Rage and Holman, 1984), salamanders (Estes and Hoffstetter, 1976), frogs (Bailon and Hossini, 1990; Hossini, 1992), and albanerpetontids (Estes and Hoffstetter, 1976; Gardner, 1999) is known from the La Grive-St. Alban fissure fills. Because many older collections from these fissures lack reliable locality data, the age of specimens often cannot be determined more precisely than early or middle Miocene.

Rage and Hossini (2000) recently reported Albanerpeton inexpectatum from the Sansan locality, located further to the southwest in the department of Gers, France. This locality consists of terrigenous silt- and sandstones and calcareous intercalations (Steininger et al., 1996) and is dated as MN 6 (early middle to middle middle Miocene) by mammals (Bruijn et al., 1992; Steininger et al., 1996) and magnetostratigraphic correlations (Sen, 1996). Sansan is the reference locality for the MN 6 zone.

SYSTEMATIC PALEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order ALLOCAUDATA Fox and Naylor, 1982
Family ALBANERPETONTIDAE Fox and Naylor, 1982
Genus ALBANERPETON Estes and Hoffstetter, 1976

ALBANERPETON INEXPECTATUM Estes and Hoffstetter, 1976
(Figs. 3-1 to 3-4)

Holotype—MNHN.LGA 176, fused axis and first trunk vertebra (Estes and Hoffstetter, 1976:fig. 1C, D, F and pl. 6, figs. 5, 9, 15).

Holotype Horizon and Locality—Unknown fissure fill near La Grive-St. Alban, department of Isère, southeastern France; MN 5, MN 6, or MN 7/8 (early or middle Miocene) in age. The holotype is from fissure M (MN 7/8 or late middle Miocene; Bruijn et al., 1992; Steininger et al., 1996) in Milliet Quarry, according to Estes and Hoffstetter (1976) and Estes (1981) based on the preservation of the bone, but this is unproven (J.-C. Rage, pers. comm. 1998).

Referred Specimens—Until 1997, specimens listed by Estes and Hoffstetter (1976:table 3) under the heading "Collection Paris" and figured by these authors were in R. Hoffstetter's uncatalogued research collection. These specimens are now in the MNHN.LGA collection and include the following, all of which I have seen firsthand: MNHN.LGA 1205–1209, 1227 and 1228, isolated premaxilla; MNHN.LGA 1210 and 1211, fused premaxillae; MNHN.LGA 1212, 1213 and 1230–1232, maxilla; MNHN.LGA 1226, articulated maxilla, lacrimal, and prefrontal; MNHN.LGA 1201–1204, 1248, 1249, 1251 and 1252, dentaries; MNHN.LGA 1244–1247 and 1250, mandibles; MNHN.LGA 1214–1222, fused frontals; MNHN.LGA 1223, composite fused frontals and paired parietals; MNHN.LGA 1229, quadrate; MNHN.LGA 1236, atlas; MNHN.LGA 1241, first trunk vertebra; MNHN.LGA 1238-1240, 1242 and 1243, more posterior trunk vertebrae; MNHN.LGA 1235, sacral vertebra; MNHN.LGA 1233 and 1234, caudal vertebrae; MNHN.LGA 1255 and 1256, humeri; MNHN.LGA 1254, femur. Uncatalogued specimens in the MNHN.LGA collection include an articulated premaxilla,

maxilla, and lacrimal (all three elements incomplete), numerous jaws, frontals, trunk and caudal vertebrae, humeri and femora, and several atlantes and axes. I was not able to examine the following referred specimens: a neurocranium (MNHN.LGA 1253; see Estes and Hoffstetter, 1976:pl. 8, fig. 4 and pl. 9. figs. 1–4), uncatalogued MNHN.LGA atlantes and axes reported by McGowan (1998b), uncatalogued UCBL skull and postcranial bones (Estes and Hoffstetter, 1976:table 3; Estes, 1981:20), and uncatalogued MCZ mandibles (Estes, 1981:20), all from La Grive-St. Alban; and catalogued MNHN dentaries, maxillae and a humerus from Sansan (Rage and Hossini, 2000).

The provenance of specimens listed above in the collection of the MNHN.LGA is uncertain (J.-C. Rage, pers. comm. 1998). The ages of these specimens are consequently problematic: they may be MN 5, MN 6, or MN 7/8 in age or some combination thereof (J.-C. Rage, pers. comm. 1998). Estes and Hoffstetter (1976) proposed that most of the specimens in the MNHN.LGA collection came from fissure M (MN 7/8 in age; Bruijn et al., 1992; Steininger et al., 1996) in Milliet Quarry based on the preservation of the fossils, but this is unproven. Labels accompanying some of the upper jaws (MNHN.LGA 1205–1213) and all of the catalogued frontals (MNHN.LGA 1214–1222) included in my study claim that these specimens came from Peyre and Beau Quarry, but this information is not particularly instructive because fissure fills in this quarry range in age from MN 5 to MN 7/8 (Rage and Holman, 1984; Rage and Hossini, 2000; J.-C. Rage, pers. comm. 1998). Some of the uncatalogued A. inexpectatum specimens not available to me in the collection of the UCBL from La Grive-St. Alban are reliably known to have been collected from fissure M in Milliet Quarry and fissure L7 in Lechartier Quarry (J.-C. Rage, pers. comm. 1998). Deposits in both of these fissures are MN 7/8 or late middle Miocene in age (Bruijn et al., 1992; Steininger et al., 1996).

Distribution—Middle and ?early Miocene, France: fissure M in Milliet Quarry and fissure L7 in Lechartier Quarry, both MN 7/8 or late middle Miocene, and unknown fissure(s) (MN 5, MN 6, and/or MN 7/8 or late early to late middle Miocene) in Peyre and Beau Quarry, all near La Grive-St. Alban, department of Isère; and Sansan locality (MN 6 or early middle to middle middle Miocene), department of Gers.

Revised Diagnosis (modified from Gardner, 1999)—Medium-sized species of Albanerpeton differing from all congeners in the following autapomorphies: pustulate labial ornament on premaxilla; large maxillae and dentaries ornamented labially; dentary dorsally bears low process behind tooth row; azygous frontals broad, with length less than or equal to width; and ventrolateral crest on large frontals relatively broad, with ratio of VCW:FW^2 greater than 0.60, and ventral face of crest deeply concave dorsally. Differs further from most congeners, but resembles A. nexuosus Estes and unnamed Paskapoo species in the following derived character states: premaxilla robustly constructed, variably fused medially, and bearing pars dorsalis that is dorsoventrally short and strongly sutured dorsally with nasal; maxilla with anteroposteriorly short premaxillary lateral process; and frontals with narrow, spike-like or acuminate internasal process. More closely resembles Paskapoo species than A. nexuosus in three synapomorphies—premaxilla with entire labial face of pars dorsalis ornamented in large specimens, premaxillae lacks dorsal boss, and maxilla with anterior end of tooth row in line with leading edge of nasal process—but differs further from the former species in primitively retaining a prominent vomerine process on the premaxilla and inferred larger body size.

Description

Albanerpeton inexpectatum is known from isolated and occasional articulated vertebrae and skull elements and isolated long bones. The nasal, jugal, squamosal, and palatal bones have yet to be identified; most of these elements remain undescribed for albanerpetontids as a whole. Estes and Hoffstetter's (1976:fig. 4) cranial reconstruction for A. inexpectatum has been widely accepted and reproduced (Carroll and Holmes, 1980:fig. 12; Estes, 1981:fig. 4; Fox and Naylor, 1982:fig. 5; Trueb and Cloutier, 1991; Milner, 1994:fig. 1.6A, B). This reconstruction is generally accurate, although the lack of a jugal and presence of a posteriorly open maxillary arcade are incorrect (see Fig. 2-1A and account below for maxilla). Figure 3-1 depicts a composite, incomplete skull for A. inexpectatum. As this composite skull utilizes elements from comparable-sized, but probably certainly different individuals, articulations between some of the bones are imprecise. Nevertheless, I believe this reconstruction adequately shows the pattern of bones in the anterior part of the skull and it confirms many aspects of Estes and Hoffstetter's (1976) original reconstruction (Gardner, 2000). My descriptions below focus on the taxonomically and systematically informative jaws and frontals. Unless stated otherwise, these descriptions are composites.

Premaxilla (Fig. 3-1, 3-2A–I; Table 3-1)—The premaxilla is robustly constructed and the largest specimens are about 3.0 mm high (Table 3-1). Small premaxillae are isolated, whereas most of the large premaxillae are fused medially. Premaxillae thus appear to have fused ontogenetically, but overlap in the sizes of unfused and fused specimens implies that there was considerable variation in the timing of this event. Fused premaxillae, such as MNHN.LGA 1211 (Fig. 3-2A) and 1210 (Fig. 3-2B, C), are more strongly fused labially than lingually. Isolated premaxillae medially bear a dorsoventrally elongate flange and grooves that, in life, articulated with complementary structures on the opposite premaxilla. The medial flange is moderately long and extends along the medial face of the bone, typically down about the ventral one-half of the pars dorsalis onto the dorsal part of the pars dentalis (Fig. 3-2D). The pars dorsalis is moderately low and wide (Table 3-1). The dorsal edge of the process was strongly sutured to the anterior end of the nasal, even in small individuals. The lacrimal notch is moderately deep and wide, in both absolute and relative terms (Table 3-1). The labial surface of the pars dentalis is perforated by tiny, scattered external nutritive foramina. The entire labial face of the process on large premaxillae is covered with closely-packed pustules and short, anastomosing ridges. In each of the two smallest premaxillae at hand, MNHN.LGA 1205 (not figured) and 1206 (Fig. 3-2E), the labial ornament is less prominent and it is restricted more medially and dorsally. No premaxilla has a boss on the pars dorsalis.

In lingual view, the suprapalatal pit is elliptical in lingual outline, moderate in absolute size (Table 3-1), and occupies about four to seven percent of the lingual surface area of the pars dorsalis (Fig. 3-2B, G, H). The suprapalatal pit is located about one-third to one-half of the distance across the pars dorsalis from the medial edge and typically low on the process, with the ventral rim of the pit in line with, or just dorsal to, the dorsal surface of the pars palatinum (Fig. 3-2H). The suprapalatal pit is displaced more dorsally, to varying degrees, on some specimens that have a small- to moderate-sized foramen located just ventromedial to the pit, at the junction between the pars dorsalis and pars palatinum (Fig. 3-2B). This unnamed foramen is present in 14 of the 18 isolated premaxillae and five of the eight fused pairs at hand. The foramen is clear of sediment on both sides in MNHN.LGA 1210. In this specimen, a canal extends lingually from the foramen into the base of the pars dorsalis and opens inside the suprapalatal pit.

In about one-half of the available premaxillae, a tiny foramen of unknown function perforates the pars dorsalis above, and slightly medial to, the suprapalatal pit. Two weakly developed internal struts are present, one medial and one lateral to the suprapalatal pit. Both struts are narrow mediolaterally and the base of neither strut extends any appreciable distance lingually across the dorsal surface of the pars palatinum. One or two tiny foramina typically perforate the lateral wall of the more lateral strut, but in MNHN.LGA 8 (unfigured) one larger foramen is present and can be seen to open medially inside the suprapalatal pit.

The pars palatinum is a lingually broad and horizontal shelf, developed into a lingually elongate, triangular-shaped vomerine process medially and a broad maxillary process laterally (Fig. 3-2C). The lingual face of both processes is indented with a shallow facet. In life, these facets evidently contacted the vomer (Fox and Naylor, 1982), an element that remains undescribed for albanerpetontids. In paired premaxillae, the vomerine processes were sutured medially with one another, whereas in fused premaxillae available to me the medial edges of these processes are at best only weakly fused. The dorsal surface of the maxillary process typically bears low knobs and ridges for contact with the ventral surface of the complementary process on the maxilla. Along its lingual edge, the maxillary process dorsally bears a low, labiolingually compressed rim. In life, this rim would have abutted against the lingual edge of the premaxillary dorsal process of the maxilla when the premaxilla and maxilla were articulated. On the underside of the maxillary process is a low, drumlin-shaped process. The function of this unnamed process is unclear, but its shape and slightly roughened ventral surface suggests that it may have articulated with a palatal bone or ligament. The palatal foramen is subcircular to elliptical in outline and moderate in size, with a diameter less than that of the more medial teeth. The palatal foramen opens ventrally about one-third of the distance lingually across the pars palatinum and dorsally in the floor of the suprapalatal pit at, or just labial to, the opening of the pit. A hair pushed through the palatal foramen in MNHN.LGA 1207 (Fig. 3-2F) shows that the canal between the ventral and dorsal openings passes vertically through the pars palatinum. In most premaxillae, a smaller unnamed foramen penetrates the bone at the junction between the pars palatinum and pars dentalis. This foramen is usually medial, but occasionally lateral, to the ventral opening of the palatal foramen. A hair inserted into this unnamed foramen in MNHN.LGA 1207

(Fig. 3-2G–I) extends dorsomedially through the bone and emerges in the floor of the suprapalatal pit, labial to the dorsal opening of the palatal foramen. This canal may also have carried a duct from the presumed gland in the suprapalatal pit.

Maxilla (Figs. 3-1, 3-2J–N, 3-3)—MNHN.LGA 1232 (Fig. 3-2M, N), the largest and most nearly complete specimen, is about 5.2 mm long; the smallest available specimens were probably about two-thirds as large when complete. In labial view the pars facialis is low and tapers posteriorly, the nasal process is triangular, and the ventral edge of the pars dentalis is nearly straight. The anterior one-third or so of the labial face of the bone is perforated with up to about six small external nutritive foramina. On large maxillae, this region is sparsely ornamented with low, short, discontinuous ridges and occasional pustules (Estes and Hoffstetter, 1976:pl. 5, fig. 1; here:Fig. 3-2J). Near the posterior end of the bone, the pars facialis labiodorsally bears a shallow, elongate, and anteriorly-tapered scar for articulation with the jugal. The latter element is unknown for Albanerpeton inexpectatum and other congeners, but it has recently been reported in skeletons of Celtedens McGowan and Evans from the Spanish Barremian (McGowan and Evans, 1995). These skeletons confirm Fox and Naylor's (1982) prediction that the maxillary arcade in albanerpetontids was complete posteriorly, not open as shown in Estes and Hoffstetter's (1976:fig. 4) cranial reconstruction for A. inexpectatum.

The premaxillary lateral process is short (i.e., length subequal to height at base) and pointed anteriorly in labial or lingual outline. In life, this process labially overlapped and fit into a complementary facet, of similar dimensions and shape, on the premaxilla. The pattern of premaxillary-maxillary contact is more complex lingually and served to strengthen the contact between the two bones. A vertical ridge, with a bulbous knob midway down its length, extends down the lingual face of the premaxillary lateral process on the maxilla, just anterior to the tooth row (Fig. 3-2K). A vertical slot formed in the junction between this ridge and the lingual face of the process received the posterior end of the pars dentalis on the premaxilla. When the maxilla and premaxilla were thus articulated, the knob on the former bone would have lingually overlapped the premaxillae in the junction between the pars dentalis and pars palatinum, thereby preventing the premaxilla from being displaced lingually. The premaxillary dorsal process is a lingually broad and anteriorly short flange that, in life, dorsally overlapped the maxillary process on the premaxilla and formed the floor of the external naris. Ventrally, the posterior edge of the premaxillary dorsal process bears a transverse ridge that abutted against the posterior edge of the maxillary process on the premaxilla. This transverse ridge is developed lingually into a low, heel-like knob that is most prominent on large maxillae such as MNHN.LGA 1232 (Fig. 3-2M, N). The shallowly convex and slightly roughened ventral surface of this knob suggests that it articulated with a palatal bone or ligament.

The pars palatinum is broad lingually and narrows posteriorly (Fig. 3-2L, N). The internal narial margin is approximately concave in dorsal or occlusal outline and spans four to six tooth positions. Posterior from the internal narial margin, a shallow trough perforated by several foramina extends along the dorsolingual surface of the pars palatinum. In life, this trough received the medial edge of one or more palatal bones (palatine, epipterygoid, or pterygoid). MNHN.LGA 1226 (Estes and Hoffstetter, 1976:pl. 5, fig. 2; here:Fig. 3-3) shows that when the unknown palatal bone(s) and maxilla were articulated, the anterior end of the former element(s) would have been overlain dorsally by the base of the lacrimal. This configuration would have undoubtedly strengthened the palatal–maxillary joint. MNHN.LGA 1226 and an articulated premaxilla, maxilla, and lacrimal (unnumbered and unfigured MNHN.LGA specimen) also show the complex pattern of lacrimal–maxillary contact: the base of the lacrimal articulates across the saddle-shaped, bony patch on the dorsal surface of the maxillary pars palatinum, extends dorsally up the lingual face of the nasal process, then overlaps labially along the posterior edge of the nasal process and more posteriorly onto the adjacent part of the pars facialis.

Dentary and Postdentary Bones (Fig. 3-4A–F)—The largest available dentary, part of the mandible MNHN.LGA 1250 (Estes and Hoffstetter, 1976:pl. 7, fig. 7), is about 8.7 mm long. Dentaries are relatively robust in construction and become more so with increased size. The dental parapet is perforated externally by either a single row of about six external nutritive foramina or up to ten foramina arranged into two somewhat parallel rows. The external nutritive foramina are typically confined to the anterior one-half of the dentary, but in some dentaries the posteriormost foramen approaches the level of the posterior end of the tooth row. In large dentaries, such as MNHN.LGA 1201 (Fig. 3-4D), the labial surface of about the anterior one-third of the bone is weakly ornamented with short, low ridges similar to those on comparable-sized maxillae. The dorsal edge of the dental parapet is relatively straight in labial or lingual outline. Immediately behind the tooth row is a low and triangular dorsal process that contributes labially to the coronoid process. Referred dentaries of Albanerpeton inexpectatum from Sansan (Rage and Hossini, 2000:fig. 2) also have this unnamed process. On some large dentaries (Fig. 3-4D), the posterior one-third of the bone is indented labially with a faint, broad scar that evidently marks the area of insertion for the external adductor muscle. Ventrally, the anterior one-half to two-thirds of the bone bears an anteroposteriorly elongate scar, bounded labially by a low ridge, for attachment of the intermandibularis muscles.

In dorsal view, the dentary is broadly curved and the symphyseal eminence is prominently developed. Nineteen dentaries preserve intact symphyseal prongs. These specimens show that, as in other albanerpetontids, paired or single prongs occur with about equal frequency on both the left and right dentaries. The structure of the remainder of the lingual surface is also consistent with that seen in other albanerpetontid dentaries, as follows: dental parapet high; subdental shelf low, narrow and gutter-shaped dorsally, becoming deeper and labiolingually narrower posteriorly; Meckelian groove closed anteriorly; and broad area posteriorly for attachment of postdentary bones.

Five mandibles preserve the postdentary bones in articulation with the dentary (see Estes and Hoffstetter, 1976:pl. 7, figs. 1–4, 7; here:Fig. 3-4E, F). I concur with Estes and Hoffstetter (1976) and Estes (1981) that the postdentary bones consist of a fused angular and articular ventrally and a prearticular dorsally. However, I could not see the line of fusion that these authors reported between the angular and articular. The prearticular is labiolingually flattened and in the shape of an inverted "V." The apex of this bone overlaps the unnamed dorsal process on the dentary lingually and posteriorly to form a prominent coronoid process. The posterior face of the prearticular contribution to the coronoid process is shallowly concave, faces posterolingually, and has a roughened surface, presumably for insertion of the tendon from the superficialis head of the internal adductor muscle.

Dentition (Figs. 3-2A–K, M, N, 3-3, 3-4A–F)—Marginal teeth exhibit the characteristic albanerpetontid pattern of attachment and structure in being highly pleurodont, non-pedicellate and straight, with crowns that are labiolingually compressed, chisel-like, and have three mesiodistally aligned cuspules. On the premaxilla, teeth increase in size medially along the tooth row. Teeth are weakly heterodont in size anteriorly on the other jaws, with the longest teeth occupying the third–sixth positions on the maxilla and the eighth–eleventh positions on the dentary. The teeth are closely spaced, with the number of loci ranging from eight–ten (n = 22) on the premaxilla, 20–22 (n = 3) on the maxilla, and 24–33 (n = 13) on the dentary. The number of tooth positions on the dentary increases with the size of this bone (Estes and Hoffstetter, 1976); this presumably was the case for the upper jaws as well. The anterior end of the tooth row on the maxilla is in line with the leading edge of the nasal process. Most jaws have one or several empty tooth slots for replacement teeth. Several of the specimens at hand bear evidence of tooth replacement. For example, one maxilla (MNHN.LGA 1213; Fig. 3-2K) has a nearly functional replacement tooth, the crown of which barely extends past the ventral margin of the pars dentalis, at the seventh locus.

Frontals (Fig. 3-1, 3-4G–M)—Frontals at hand range from about 3.4–5.0 mm (n = 8) in midline length and 3.4–5.6 mm (n = 9) in width across the posterior edge of the frontal roof. In each of the two smallest specimens, MNHN.LGA 1214 (Fig. 3-4G, H) and MNHN.LGA 1215 (not figured), the two halves are incompletely fused posteriorly, indicating that the frontals fuse ontogenetically. Larger frontals are more solidly fused, although many retain a faint median line of fusion ventrally. In dorsal outline, the fused frontals are typically broader than long (ratio of FL:FW[1] = 0.87–1.00, n = 8, $\bar{x}$ = 0.92±0.04) and approach the shape of an equilateral triangle. The internasal process is narrow and spike-like or acuminate in dorsal or ventral outline. The lateral face of the process has the characteristic groove for tongue-in-groove contact with the nasal. The anterolateral process is smaller and projects more laterally. An anteroposteriorly narrow shelf extending between the bases of the internasal and anterolateral processes forms the ventral edge of the slot for receipt of the nasal. In life, this shelf braced the nasal from below. Posterior to the anterolateral process, the lateral edge of the frontal diverges at about 30° from the midline. The dorsal and ventral margins of the slot for receipt of the prefrontal are excavated medially. In dorsal and ventral views, the orbital margin is shallowly concave and the posterior edge of the frontal roof is slightly concave to either side of the midline. The posterior face of the frontal roof is smooth in small frontals, indicating that these bones abutted against the anterior edge of the paired parietals. In large individuals, the frontals were strongly sutured with the parietals. The posterior end of the ventrolateral crest projects beyond the posterior edge of the frontal roof. In life, the posterior end of the crest underlapped the lateral wing of the parietal and medially received an anteriorly-directed tab from the parietal. The pattern of frontal-parietal contact is accurately depicted in MNHN.LGA 1223 (see Estes and Hoffstetter, 1976:pl. 8, figs. 2, 3), despite the fact that this specimen is a composite consisting of fused frontals and a left and right parietal that may not be from the same individual. The dorsal ornament of pits and ridges changes ontogenetically (cf., Fig. 3-4G, I, K). On small frontals, the dorsal surface is indented with a mosaic of shallow, polygonal pits. In medium-sized frontals, the pits are enclosed by low, narrow ridges that coalesce to form a reticulate pattern. With further growth, the ridges become wider and taller, the pits become concomitantly deeper, and both become more irregular in dorsal outline.

In ventral view, the ventrolateral crest is broad (ratio of $VCW{:}FW^2 = 0.34–0.66$, $n = 9$, $\bar{x} = 0.51 \pm 0.10$), and becomes relatively and absolutely broader as frontal size increases (cf., Fig. 3-4H, J, L). The crest is approximately triangular in transverse view, being dorsoventrally deepest medially and shallowest laterally. The ventral surface of the crest faces ventrolaterally and is strongly concave dorsally in the orbital region. Comparisons with extant salamanders (see Carroll and Holmes, 1980) suggest that the internal adductor muscles probably originated from the ventral surface of the ventrolateral crest, at least along the more posterior part of the crest. The ventrolateral crest grades anteriorly into the anterolateral process. This process is bordered ventrolaterally by a ventrally directed flange (Fig. 3-4M) that contributes medially to a facet for articulation with the underlying neurocranium and laterally to the slot for receipt of the prefrontal. With increased frontal size, the flange deepens ventrally and extends towards the distal end of the anterolateral process.

Tiny foramina penetrate the frontals laterally along the orbital margin (Fig. 3-4M) and inside the slot for receipt of the prefrontal, in the ventral face of the ventrolateral crest—most prominently medial to the slot for receipt of the prefrontal (Fig. 3-4H, J, L)—and in the posterior end of the crest. These previously unreported foramina occur in all other species of Albanerpeton for which frontals are available. In general, I have not been able to confidently trace the canals that extend from these foramina into the bone, largely because the canals are narrow and plugged with sediment. Frontals broken across the ventrolateral crest expose a prominent canal that runs anteroposteriorly through the interior of the crest. Comparisons with anurans (see Roček, 1980:fig. 28) suggest that the canal through the ventrolateral crest may have held the orbitonasal artery.

Other Elements (Figs. 3-1, 3-3)—Estes and Hoffstetter (1976) also described and figured for Albanerpeton inexpectatum a prefrontal, quadrate, neurocranium, lacrimals, parietals, vertebrae, humeri, and femora from La Grive-St. Alban. Estes (1981) redescribed all of these elements, except for the neurocranium, and McGowan (1998b) commented on the structure of the atlanto-axial complex. As I generally concur with these authors' descriptions and interpretations, I limit my comments here to the four points below.

(1) Estes and Hoffstetter (1976) and Estes (1981) reported that a pair of small foramina perforate the lacrimal in MNHN.LGA 1226, in what would have been the anterior margin of the orbit (see Estes and Hoffstetter, 1976:fig. 4 and pl. 5, figs. 1, 2). Further preparation of this specimen by myself reveals that the septum between the two supposed foramina is not bone, but dried preservative that bisected a larger foramen (Fig. 3-3). The position of this foramen suggests that it carried the nasolacrimal duct of the nasal organ. This organ is typically well-developed in extant lissamphibians, particularly in terrestrial species for which olfaction is important in detecting prey, conspecifics, or both (Duellman and Trueb, 1986:232, 385–387). The large size of the foramen for the nasolacrimal duct in MNHN.LGA 1226 implies that the nasal organ and, hence, olfaction were similarly well-developed in Albanerpeton inexpectatum, if not in albanerpetontids in general.

(2) MNHN.LGA 1226 confirms Estes and Hoffstetter's (1976) and Estes' (1981) claim that Albanerpeton inexpectatum retains a prefrontal. The prefrontal is definitely present in the specimen, albeit relatively small and solidly fused ventrally and ventrolaterally with the larger lacrimal. The line of fusion between the two bones can readily be traced across the inner surface (Fig. 3-3), as Estes and Hoffstetter (1976:312) and Estes (1981:21) observed, and onto the anterior and posterior margins. This line of fusion cannot confidently be traced across the external face of MNHN.LGA 1226 owing to the extensive ornament. It is unclear whether fusion of the lacrimal and prefrontal is an ontogenetic phenomenon in A. inexpectatum or if these bones were fused in other species.

(3) Although not apparent in Estes and Hoffstetter's reconstruction, it is clear from their descriptions (1976:313; see also Estes, 1981:21) that they believed the posterior end of the prefrontal contacted the frontals by fitting into a slot just in front of the orbital margin. MNHN.LGA 1226 demonstrates that this too is correct (contra

McGowan 1998a). The only free articular surface on the specimen for contact with the frontal extends across the posterior end and onto the posteromedial edge of the prefrontal (Fig. 3-3)—the underlying lacrimal has no such articular surface. Manipulation of MNHN.LGA 1226 and comparable-sized frontals from conspecific individuals confirms that, in life, the posterior end of the prefrontal would have fit into the complementary slot in the frontal in a mortise and tenon fashion (Fig. 3-1), as in other albanerpetontids. McGowan's (1996, 1998a; McGowan and Ensom, 1997) contention that this slot instead received the lacrimal in Albanerpeton and Celtedens follows from his unproven belief that the prefrontal is absent in albanerpetontids. If the lacrimal was involved in contacting the frontal in A. inexpectatum, it did so only at the anterolateralmost point of contact and would, at best, have contributed minimally to the joint.

(4) Estes and Hoffstetter (1976) and Estes (1981) identified a foramen in the base of the neural arch in the atlas of Albanerpeton inexpectatum as the spinal foramen. I concur with their identification. The foramen occurs in the junction between the posterior surface of the anterior cotyles and the base of the neural arch, in the same position as the foramen for exit of the first spinal nerve in urodeles (Edwards, 1976) and gymnophionans (Norris and Hughes, 1918; Jenkins and Walsh, 1993). McGowan's (1998b) remarks (p. 118) and figure of an uncatalogued MNHN.LGA atlas (1998:fig. 1a) imply that this foramen was missing in atlantes of A. inexpectatum that he examined. Despite McGowan's (1998b:118) claim to the contrary, a tiny spinal foramen is indeed present and clearly visible in Estes and Hoffstetter's figure (1976:pl. 6, fig. 14) of a referred atlas (MNHN.LGA 1236). As I have not seen the specimens that McGowan (1998b) examined, I cannot explain the apparent discrepancy between our observations, other than to suggest that he probably overlooked the foramen.

Remarks

Estes and Hoffstetter (1976) diagnosed Albanerpeton inexpectatum on the structure and contacts of the first three vertebrae. It is now apparent that the first three vertebrae are similarly modified in all albanerpetontids (e.g., Estes, 1981; Fox and Naylor, 1982; McGowan, 1998b); hence, this character complex is diagnostic only at the familial level.

Subsequent diagnoses for Albanerpeton inexpectatum by Estes (1981), McGowan

(1998a), and Rage and Hossini (2000) used 14 attributes in total. As discussed below (see next paragraph), two of these features are reliably diagnostic because they are unique to A. inexpectatum: dentary bears dorsal process behind tooth row (Estes, 1981; Rage and Hossini, 2000) and frontals relatively broad (McGowan, 1998a; Rage and Hossini, 2000). Five other features differentiate A. inexpectatum from one or more, but not all, congeners: pars dorsalis on premaxilla relatively short (Rage and Hossini, 2000) and ornamented labially (Rage and Hossini, 2000); suprapalatal pit moderate in size (Rage and Hossini, 2000); dentary teeth weakly heterodont in size anteriorly (Estes, 1981; Rage and Hossini, 2000); and internasal process on frontals narrow and spike-like (McGowan, 1998a). The orbital margin accounting for about one-half the total length of the frontals (McGowan, 1998a) is diagnostic at the generic level (Chapter 2). The ninth character, closed notochordal canal in atlas (Estes, 1981), differentiates A. inexpectatum only from an indeterminate Middle Jurassic albanerpetontid species known by an atlantal centrum that primitively retains an open notochordal pit (see Seiffert, 1969). The proportions of the lacrimal notch and the length of the medial flange on the premaxilla (Rage and Hossini, 2000) and the pattern of dorsal ornament on the frontals (McGowan, 1998a) are diagnostically unreliable, because all three characters vary markedly within and among species of Albanerpeton. Nor is the relative size of the pars palatinum on the upper jaws (Estes, 1981; Rage and Hossini, 2000) useful for differentiating species of Albanerpeton, because this shelf is consistently well developed (i.e., broad labiolingually; extends across labial face of premaxilla). The final character, shape of the femur (Estes, 1981), can be discounted because the femur upon which this character was founded is from an indeterminate salamander, not A. nexuosus (contra Estes, 1981). McGowan (1998b:118) suggested that fusion of the axis and first trunk vertebra may be diagnostic for A. inexpectatum, but the reliability of this character cannot be determined until examples of these vertebrae are available for other congeners.

In my opinion, Albanerpeton inexpectatum is reliably diagnosed by five autapomorphies. These character states are as follows: (1) pustulate labial ornament on premaxilla (premaxillary ornament in other albanerpetontids consists of anastomosing ridges or, less commonly, continuous ridges arranged in a more regular polygonal pattern); (2) maxilla and dentary in large individuals weakly ornamented labially (unornamented regardless of size in other albanerpetontids); (3) dentary bears low dorsal process that contributes labially to coronoid process (process absent on dentaries of other albanerpetontids); (4) azygous frontals broad, with midline length less than or approximately equal to width across posterior edge (relatively narrower and in the form of an anteriorly elongate isosceles triangle in other albanerpetontids); and (5) ventrolateral crest on large frontals wide, with ratio of $VCW:FW^2 > 0.60$, and ventral face of crest deeply concave dorsally (ratio of $VCW:FW^2$ does not exceed 0.45 and ventral face of crest convex to shallowly concave on large frontals of other albanerpetontids). Combinations of synapomorphies and symplesiomorphies listed in the revised diagnosis above further differentiate A. inexpectatum from its congeners.

VARIATION IN ALBANERPETON INEXPECTATUM

As most albanerpetontid species have been named and described based on relatively few specimens, variation in the group is poorly understood. Consequently, the reliability of most features historically used to differentiate species has not been adequately demonstrated. Albanerpeton inexpectatum is known by numerous, well-preserved jaws and frontals of various sizes that provide an excellent opportunity to document patterns of variation in these informative elements.

The size and construction (e.g., bone well ossified; processes, articular surfaces and ornament prominently developed) of the available jaws and frontals of Albanerpeton inexpectatum indicate that these specimens came from moderate- to large-sized individuals in late juvenile/subadult to adult stages of growth. Considerable ontogenetic variation is seen in these elements, to the extent that all but one of the autapomorphies for the species (dorsal process behind tooth row on dentary) are influenced to some extent by growth. On small premaxillae, the pustulate ornament on the labial face of the pars dorsalis is weakly developed and confined dorsomedially on the process. With further growth of the bone, ornament becomes more prominent and spreads ventrally and laterally to cover the entire labial face of the pars dorsalis. Premaxillae appear to fuse somewhat later in ontogeny, although there is considerable variation in the timing of this event. With growth of the maxilla, the nasal process becomes relatively lower and more blunt. Although there is no direct evidence that the number of tooth positions on the upper jaws increases with growth, this seems likely given that tooth counts on the dentary increase ontogenetically. Other ontogenetic trends seen in the dentary include the bone becoming more robust, the dental parapet increasing in relative height, and muscle scars and symphyseal eminence becoming more pronounced. Ornament develops on the labial surfaces of the maxilla and dentary late in the ontogenies of these bones. Pronounced ontogenetic changes occur in the frontals. Medial fusion of the frontals occurs early in ontogeny, as evidenced by the observation that the smallest available frontals are almost completely fused. With further growth, the frontals broaden, the dorsal ornament becomes more pronounced and irregular, the internasal process becomes relatively shorter, the ventrolateral crest widens and its ventral surface becomes increasingly concave, the flange below the more posterior lateral slot expands anteriorly and ventrally, the paired facets for articulation with the neurocranium become more pronounced, and the posterior edge of the frontal roof sutures with the paired parietals.

In the absence of any convincing evidence for geographic, temporal, or sexual variation, I suggest that other instances of variation in the jaws and frontals of Albanerpeton inexpectatum are best attributed to individual differences. In the premaxilla, variation of this sort is evident in numerous features that I consider taxonomically uninformative, including the relative depth and width of the lacrimal notch (Table 3-1), the number and size of the foramina in the lateral wall of the more lateral internal strut, and the presence of a tiny foramen just dorsal to the suprapalatal pit and of a larger foramen ventromedial to the suprapalatal pit. The relative height of the pars dorsalis on the premaxilla varies in A. inexpectatum and other congeners, but intraspecific variation in this character does not obscure phylogenetically significant differences among species. One or two symphyseal prongs occur with about equal frequency on either the left or right dentary and the arrangement and number of external nutritive foramina in this bone varies among individuals.

The axis and first trunk vertebra are fused in some individuals of Albanerpeton inexpectatum (Estes and Hoffstetter, 1976; Estes, 1981; McGowan, 1998b), but too few specimens are available to determine whether this fusion is ontogenetic or due to other sources of variation.

Albanerpeton inexpectatum is informative for showing that, at least in this species, other characters I consider taxonomically and phylogenetically informative for albanerpetontid species are subject to relatively little intraspecific variation. These characters include the following: the position, size, shape and orientation of the suprapalatal pit, the size of the palatal foramen, the orientation of the canal between the dorsal and ventral openings of the palatal foramen and the form of the vomerine process on the premaxilla; the shape and proportions of the premaxillary lateral process on the maxilla; the degree of heterodonty along the tooth row on the maxilla and dentary; and the shape and proportions of the internasal process on the frontals.

PHYLOGENY AND PALEOBIOGEOGRAPHY

My phylogenetic analysis of relationships within Albanerpeton (see Chapter 7) allies A. inexpectatum with the geologically younger North American species A. nexuosus (Campanian and Maastrichtian) and the Paskapoo species (late Paleocene) in the robust-snouted clade based on the following six cranial synapomorphies: (1) premaxilla robust in construction (primitively more gracile); (2) premaxillae variably fused in each species, presumably fusing with growth (primitively paired); (3) pars dorsalis on premaxilla relatively short, with ratio of PDH:PDW^2 less than about 1.5 (process primitively taller, with ratio of PDH:PDW^2 greater than about 1.5); (4) pars dorsalis on premaxilla strongly sutured dorsally with nasal (process primitively abuts against or weakly sutured with nasal); (5) premaxillary lateral process on maxilla short, with anteroposterior length of process subequal to height at base (process primitively longer than height at base); and (6) internasal process on frontals narrow and spike-like (process primitively broader and more acute. Within this clade the Tertiary congeners are identified as sister-species based on two unambiguous premaxillary synapomorphies: ornament covers entire labial face of pars dorsalis on large premaxillae (ornament primitively restricted more dorsally) and boss absent (primitively present). A third synapomorphy of the two Tertiary species is convergent with the Judithian species named in Chapter 6—anterior end of maxillary tooth row in line with leading edge of nasal process (primitively extends several loci anterior to process).

Albanerpeton inexpectatum is biogeographically interesting because it is the geologically youngest albanerpetontid and the only species of Albanerpeton known from outside of North America. The only other record of a Tertiary albanerpetontid is that of the Paskapoo species from the late Paleocene of Alberta. A substantial temporal gap of about 35 million years (Berggren et al., 1995) separates the two inferred sister-species. In the absence of any pre-Miocene records of Albanerpeton in the Old World, the presence of A. inexpectatum in the Miocene of France is best explained by an unknown species of the robust-snouted clade having emigrated in the early or middle Tertiary from North America into Europe across either of two high latitude overland routes (see Woodburne and Swisher, 1995; Beard, 1998): eastward across the De Geer Land Bridge or westward across Beringia and through Asia. This hypothesized ancestor probably resembled A. inexpectatum and the Paskapoo species in having the entire labial surface of the pars dorsalis sculpted on large premaxillae and in lacking a premaxillary boss. More systematically informative Upper Cretaceous and Tertiary fossils are needed from Eurasia to test this scenario and to establish the timing and route of dispersal.

FUNCTIONAL MORPHOLOGY

The robustly constructed skull, highly modified anterior vertebrae, weakly constructed trunk vertebrae, and small limbs of albanerpetontids have long been interpreted as evidence that these animals used their snout for burrowing (Estes and Hoffstetter, 1976; Estes, 1981; Fox and Naylor, 1982; McGowan, 1998b). This inference is well supported by comparisons with such extant head-first burrowers as caecilians, amphisbaenids, uropeltid snakes, and certain salamanders and mammals, all of which have similarly robust skulls composed of bones that are heavily built, ornamented externally, and fused or complexly sutured with one another (see Schwenk and Wake, 1993 and references therein). Strengthening of the skull among albanerpetontids appears to have been particularly extreme in Albanerpeton inexpectatum. I suggest that this condition was related, in part, to the need to reinforce the skull for burrowing in rocky soils of the Miocene karst landscape near present day La Grive-St. Alban. Many of the cranial apomorphies of interest here are synapomorphies at more inclusive levels within the genus. Six of these are synapomorphies for the robust-snouted clade, a group for which strengthening of the snout was a key evolutionary trend. The four premaxillary synapomorphies for the clade (premaxilla robustly constructed, variably fused, and pars dorsalis low and strongly sutured with nasal) collectively reinforced the snout, whereas the shortened premaxillary lateral process on the maxilla was probably more resistant to breakage when the snout was subjected to mechanical stress. The functional significance of a spike-like internasal process on the frontals is unclear to me. The presence of extensive labial ornament on the premaxillary pars dorsalis in A. inexpectatum and its inferred, Paleocene sister-species presumably compensated for the loss of the boss, a structure that when primitively present must have strengthened the more dorsal part of the pars dorsalis. The skull was further strengthened in A. inexpectatum by the development of prominent pustulate ornament on the premaxilla and the ontogenetic appearance of ornament on the maxilla and dentary. Additional adaptations to burrowing in A. inexpectatum are seen in the form of the skull. The relatively low premaxillary pars dorsalis and broad frontals imply that the skull was low and wide, probably more so than in Estes and Hoffstetter's (1976:fig. 4) cranial reconstruction for the species. This skull form is typical of terrestrial salamander taxa that burrow (e.g., ambystomatids) or inhabit rocky crevices (e.g., some plethodontids; Larson et al., 1981). Such crevices would have been common on the karst landscape inhabited by A. inexpectatum.

Albanerpetontids almost certainly fed on hard-bodied or otherwise resilient prey (Estes and Hoffstetter, 1976; Naylor, 1979; Estes, 1981; Fox and Naylor, 1982), as evidenced by such features as their relatively solid jaws, interlocking intermandibular joint, and strong, chisel-like teeth. While the jaw apomorphies discussed in the previous paragraph undoubtedly strengthened the skull of Albanerpeton inexpectatum for burrowing, I suggest that these character states also reinforced the jaws for feeding. Other autapomorphies of A. inexpectatum may have further enhanced feeding in different ways. The markedly broad frontals indicate that the head and, by implication, the gape of the jaws were relatively wider than in other species. This would have permitted the consumption of larger prey. The taking of larger and more active prey was also facilitated by enlargement of the adductor muscles, which resulted in a stronger bite. Enlarged adductor muscles in A. inexpectatum can be inferred from two autapomorphies: (1) the broad and deeply concave ventral face of the ventrolateral crest increased the area for attachment of the internal adductor muscles and (2) the unnamed dorsal process on the dentary labially braced the coronoid process for insertion of a ligament from the internal adductor muscle. The labial scar on the posterior part of some large dentaries for insertion of the external adductor muscle further attests to the large size of the adductor musculature in the species.

CONCLUSIONS

Albanerpeton inexpectatum is important for studies of North American albanerpetontids because it is the type species of the type genus and the only member of Albanerpeton from outside of North America. Examination of specimens in the collection of the MNHN.LGA and comparisons with other albanerpetontid fossils yields the following findings:

(1) Albanerpeton inexpectatum can be diagnosed and reliably differentiated from all other albanerpetontid species by character states of the jaws and frontals, including a suite of five autapomorphies.

(2) Jaws and frontals of Albanerpeton inexpectatum vary with growth and among individuals. Many of the diagnostic characters for the species are influenced to some extent by ontogeny.

(3) Synapomorphies of the upper jaws and frontals place Albanerpeton inexpectatum within the Euramerican Late Cretaceous–Miocene robust-snouted clade, as the sister-taxon of the unnamed Paskapoo species from the late Paleocene of Alberta. Based on the inferred relationships of A. inexpectatum and the absence of any reliable pre-Miocene occurrences of the genus outside of North America, I suggest that the presence of A. inexpectatum in the Miocene of France is the result of an early or middle Tertiary dispersal of an unknown ancestral species from North America into Europe.

(4) Albanerpeton inexpectatum represents an extreme case of skull strengthening among albanerpetontids. Strengthening of the skull and other cranial attributes in the species appear to be related to burrowing in rocky substrate and the consumption of larger or more resilient prey.

TABLE 3-1. Straight line measurements and ratios for premaxillae of Albanerpeton inexpectatum Estes and Hoffstetter; Miocene, Peyre and Beau Quarry, La Grive-St. Alban, France. Columns are: "Measurement or Ratio;" "n," number of specimens (left and right sides in fused premaxillae measured separately); "R," range; and "$\bar{x}$" and "SD," mean and standard deviation, respectively. Measurements follow Figure 1-2.

Measurement or Ratio	n	R	$\bar{x}$ and SD
PmH (height of premaxilla; mm)	9	2.16–3.00	2.62±0.28
PDH (height of pars dorsalis; mm)	9	1.44–1.68	1.56±0.10
PDW^1 (width of pars dorsalis across base of lacrimal notch; mm)	7	0.84–1.39	1.15±0.17
PDW^2 (width of pars dorsalis across suprapalatal pit; mm)	9	1.06–1.58	1.30±0.15
LaND (depth of lacrimal notch; mm)	7	0.60–0.77	0.68±0.07
LaNW (width of lacrimal notch; mm)	7	0.41–0.58	0.51±0.49
SPH (height of suprapalatal pit; mm)	9	0.31–0.48	0.39±0.05
SPW (maximum width of suprapalatal pit; mm)	9	0.29–0.55	0.42±0.08
$PDH:PDW^2$ (relative height of pars dorsalis)	9	1.04–1.47	1.21±0.14
LaND:PDH (relative depth of lacrimal notch)	7	0.38–0.50	0.44±0.04
$LaNW:PDW^1$ (relative width of lacrimal notch)	7	0.24–0.67	0.44±0.13
SPH:PDH (relative height of suprapalatal pit)	9	0.19–0.35	0.26±0.04
$SPW:PDW^2$ (relative width of suprapalatal pit)	9	0.25–0.38	0.32±0.05

FIGURE 3-1. Composite, incomplete skull of Albanerpeton inexpectatum Estes and Hoffstetter, in dorsal view; Miocene, unrecorded fissure fills near La Grive-St. Alban, France. This reconstruction uses three specimens from comparable-sized, but probably different, individuals: MNHN.LGA 1211, fused premaxillae; MNHN.LGA 1222, fused frontals; and MNHN.LGA 1226, right maxilla articulated with a fused prefrontal and lacrimal. Specimens at same scale: scale bar = 1 mm.

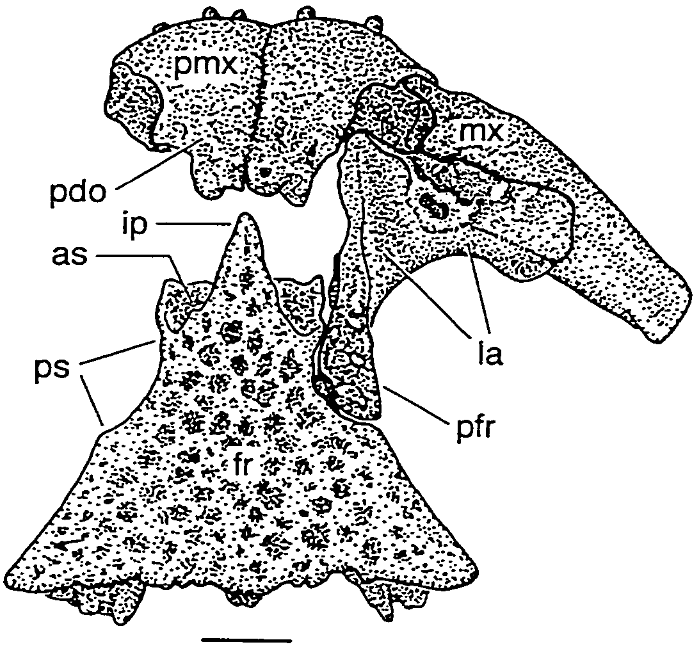
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FIGURE 3-2. Upper jaws of Albanerpeton inexpectatum Estes and Hoffstetter; Miocene, unrecorded fissure fill(s) near La Grive-St. Alban, France. Premaxillae (A–I): **A**, MNHN.LGA 1211, fused premaxillae, in labial view; **B**, **C**, MNHN.LGA 1210, fused premaxillae, in (**B**) lingual and (**C**) occlusal views; **D**, MNHN.LGA 1209, left premaxilla, in medial view; **E**, MNHN.LGA 1206, right premaxilla, in labial view; **F**, MNHN.LGA 1207, right premaxilla with hair extending dorsoventrally through canal between ventral and dorsal openings of palatal foramen, in lingual and slightly occlusal view; **G–I**, MNHN.LGA 1207, right premaxilla with hair extending ventromedially–dorsolaterally through canal between unnamed dorsal foramen in floor of suprapalatal pit and unnamed ventral foramen in junction between pars palatinum and pars dentalis, in (**G**) linguodorsal and slightly lateral, (**H**) lingual, and (**I**) linguomedial and slightly occlusal views (hair darkened to enhance contrast with bone). Maxillae (J–N): **J–L**, MNHN.LGA 1213, right maxilla, in (**J**) labial, (**K**) lingual, and (**L**) dorsal views; **M**, **N**, MNHN.LGA 1232, left maxilla, in (**M**) lingual and (**N**) occlusal views. Specimens at same scale: scale bar = 1 mm.

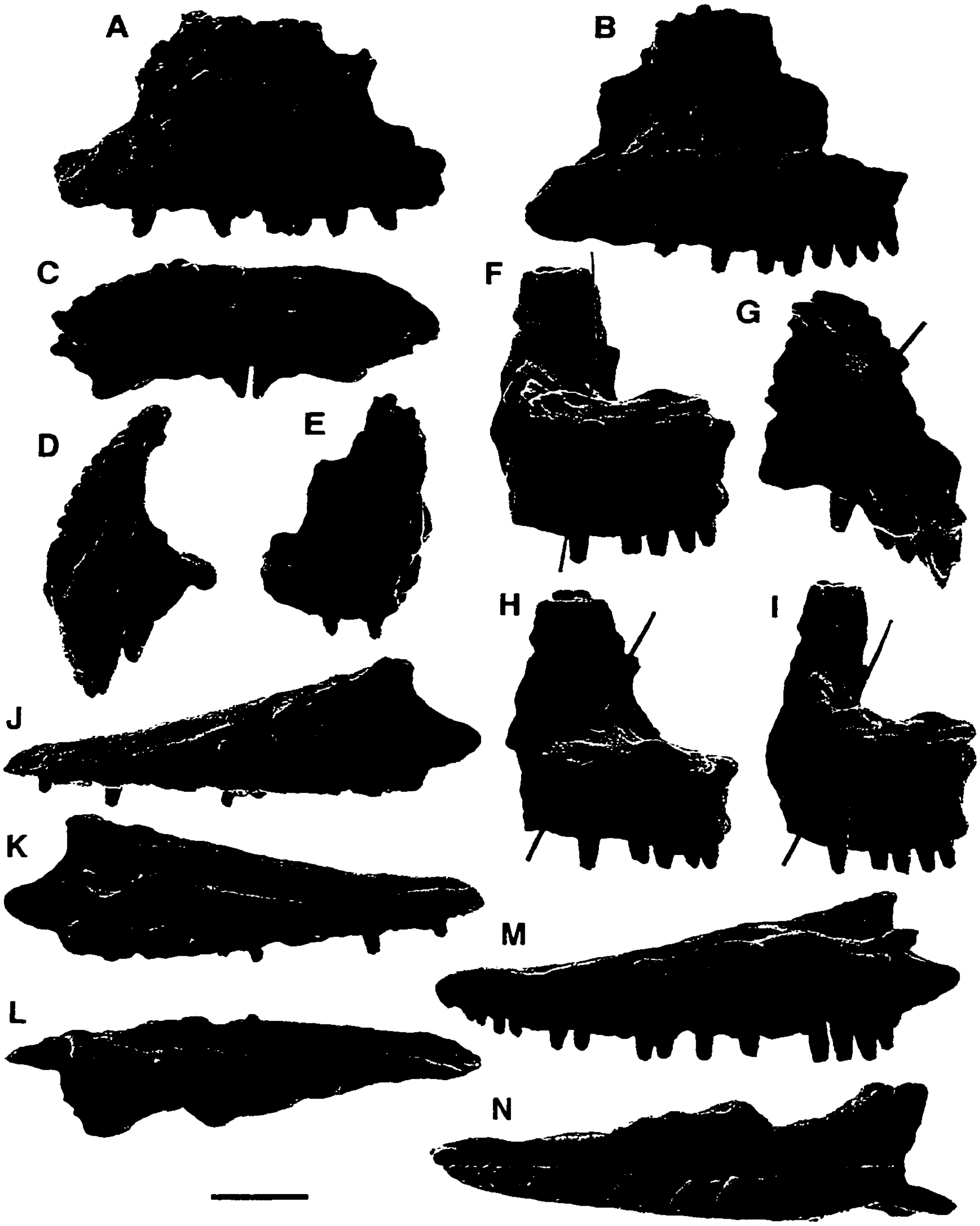
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FIGURE 3-3. Right maxilla articulated with fused prefrontal and lacrimal (MNHN.LGA 1226) of Albanerpeton inexpectatum Estes and Hoffstetter, in internal view; Miocene, unknown fissure fill near La Grive-St. Alban, France. Note line of fusion (arrow) between prefrontal and lacrimal and large lacrimal foramen (lafo). Scale bar = 1 mm.

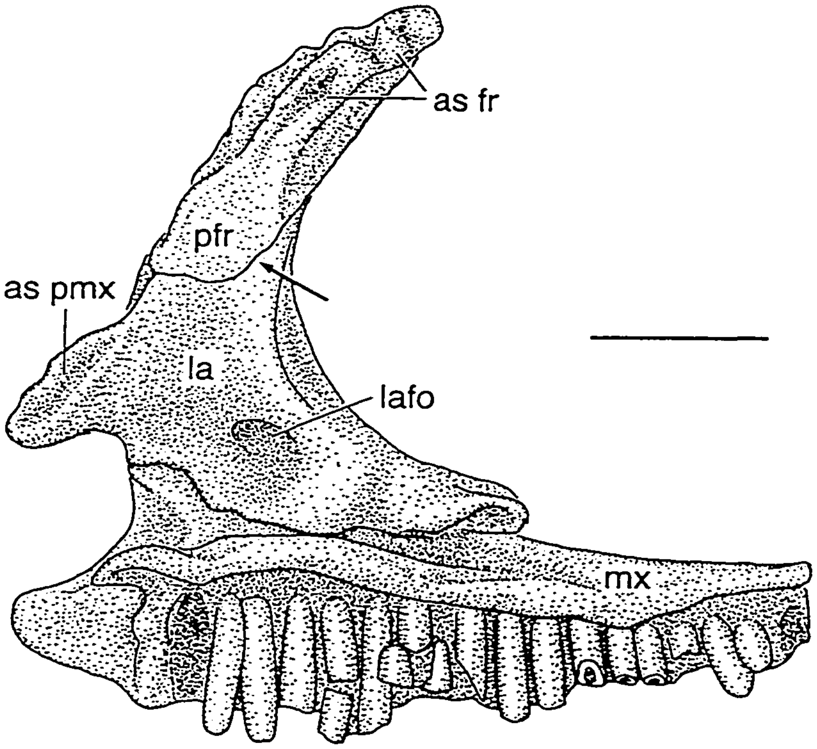
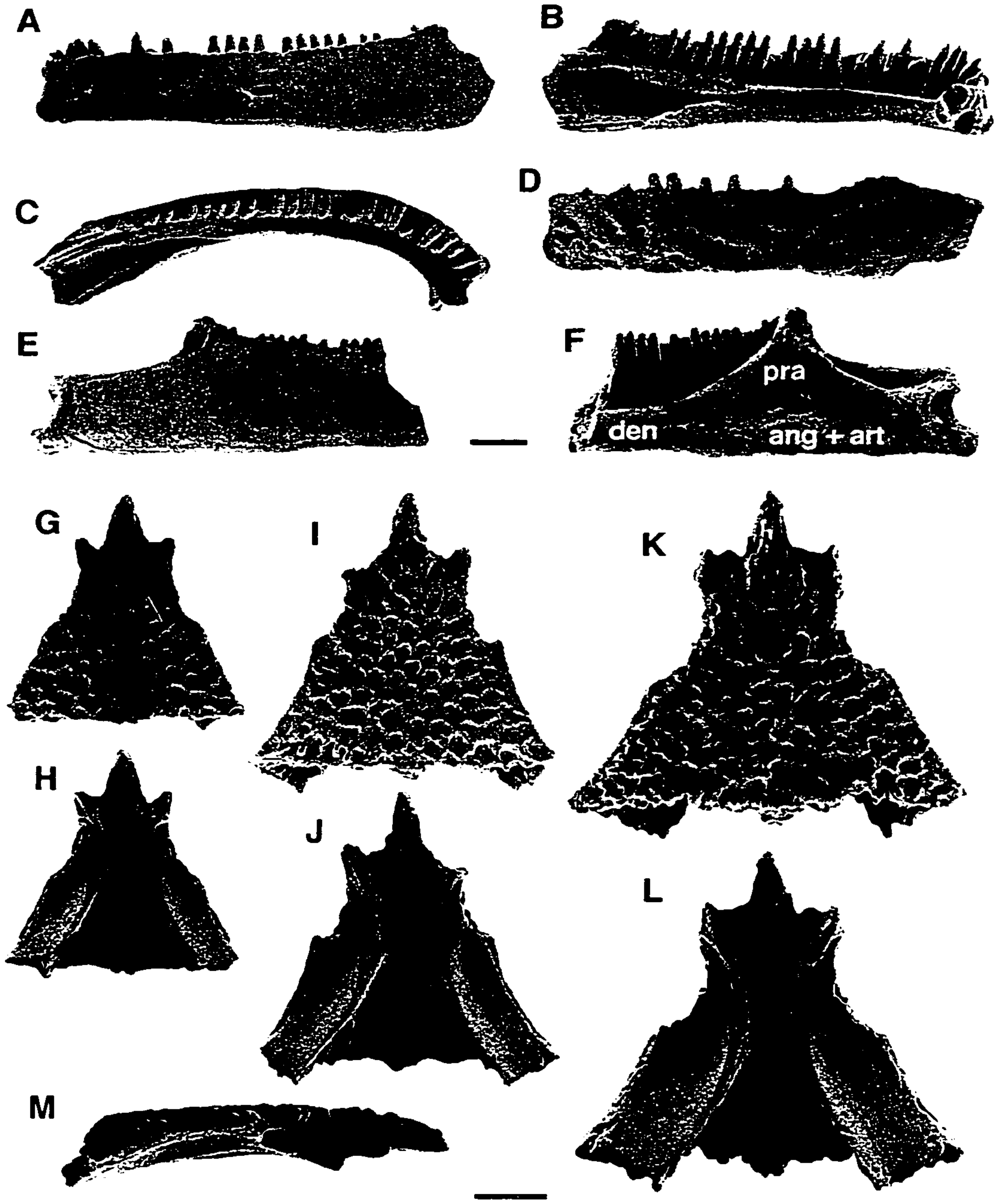


FIGURE 3-4. Mandibles and frontals of Albanerpeton inexpectatum Estes and Hoffstetter; Miocene, unrecorded fissure fill(s) near, La Grive-St. Alban, France. Dentaries (A–F): A–C, MNHN.LGA 1248, left dentary missing posteriormost end, in (A) labial, (B) lingual, and (C) occlusal views; D, MNHN.LGA 1201, left dentary missing posteriormost end and dorsal process behind tooth row, in labial view; E, F, MNHN.LGA 1244, incomplete right mandible consisting of posterior end of dentary (den), prearticular (pra), and fused angular and articular (ang+art), in (E) labial and (F) lingual views. Fused frontals (G–M): G, H, MNHN.LGA 1214, small fused frontals, in (G) dorsal and (H) ventral views; I, J, MNHN.LGA 1216, medium-sized fused frontals, in (I) dorsal and (J) ventral views; K, L, MNHN.LGA 1222, large fused frontals, in (K) dorsal and (L) ventral views; M, MNHN.LGA 1220, medium-sized fused frontals, in right lateral view. Specimens at different scales: top (A–F) and bottom (G–M) scale bars = 1 mm.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CHAPTER 4 — NEW MATERIAL AND REDESCRIPTION OF ALBANERPETON ARTHRIDION FOX AND NAYLOR, WITH COMMENTS ON THE APTIAN-ALBIAN BIOGEOGRAPHY OF ALBANERPETONTIDS[1]

INTRODUCTION

Albanerpeton arthridion Fox and Naylor is of interest because it is the oldest and one of the most poorly known species within Albanerpeton Estes and Hoffstetter. Fox and Naylor (1982) described A. arthridion based on the incomplete holotype premaxilla and three referred, incomplete dentaries from outcrops of the upper Antlers Formation (early-middle Albian) exposed at Greenwood Canyon, Texas, USA. These four jaws, along with isolated trunk vertebrae, an atlas, and a humerus from the Antlers Formation, had earlier been referred by Estes (1969, 1981) to Prosiren elinorae Goin and Auffenberg, a prosirenid salamander named on a trunk vertebra from the same formation. No other fossils have since been described for A. arthridion. In the absence of more diagnostic specimens, doubts have been raised about the validity of the species (McGowan, 1994) and its generic identity (Rage and Hossini, 2000). McGowan subsequently (1998a) ignored A. arthridion, without explanation, in his recent treatment of Albanerpeton.

Here I present a revised diagnosis and expanded description for Albanerpeton arthridion based on the four previously reported jaws and on additional specimens—including the first maxillae, frontals, atlantes, and humeri identified for the species—from Greenwood Canyon and other sites in the Antlers Formation of Texas and Oklahoma. These specimens collectively provide critical new information about the osteology and relationships of this hitherto poorly known species. Material from Oklahoma additionally extends the range of A. arthridion back into the latest Aptian-earliest Albian. I also report on paracontemporaneous albanerpetontid jaws from the Cloverly Formation of Wyoming and comment on the identity of a supposed

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[1] A version of this chapter has been published. Gardner 1999. Palaeontology. 42: 529-544.

Albanerpeton-like atlas (Winkler et al., 1990) from the Paluxy Formation of Texas. Albanerpetontid fossils reported herein from the Antlers and Cloverly formations are the oldest records (Aptian–Albian) of the family in North America. I finish this chapter by examining the biogeographical implications of these occurrences.

GEOLOGICAL SETTING AND LOCALITIES

Antlers and Paluxy Formations

The Antlers Formation (sensu Hill, 1901; Fisher and Rodda, 1966, 1967) is a thick package of terrestrial clastics that crops out in east- and north-central Texas, southeastern Oklahoma, and southwestern Arkansas (Frederickson and Redman, 1965; Fisher and Rodda, 1967; Hart and Davis, 1981; Hobday et al., 1981; Darling and Lock, 1984). Fisher and Rodda (1967) informally divided the Antlers Formation in Texas into a lower sand, a middle clay, and an upper sand. These units are broadly correlative to the south and east with their more nearshore equivalents—the Twin Mountains, Glen Rose, and Paluxy formations, respectively (see Fisher and Rodda, 1967:figs. 4, 5)—all of which crop out in central Texas. The Antlers and Paluxy formations consist of fine-grained fluvial, deltaic, and floodplain clastics deposited on a broad coastal plain along the western and northern margins of the East Texas Embayment (Fisher and Rodda, 1967; Caughey, 1977; Hobday et al., 1981). Deposition of both formations pre-dates the northward transgression of marine waters from the proto-Gulf of Mexico onto the North American continent (Winkler et al., 1995) and the establishment in the late Albian (Williams and Stelck, 1975; Kauffman and Caldwell, 1993) of a continuous Western Interior Seaway.

OMNH V706, a microsite in a prison compound in Atoka County, southeastern Oklahoma (Fig. 4-1), appears to lie within the middle part of the Antlers Formation (Cifelli et al., 1997; Brinkman et al., 1998). The age of this site can only be estimated with reference to north-central Texas, where the middle clay unit of the Antlers Formation correlates further still to the east and south with the Glen Rose Formation. The latter unit is dated by marine invertebrates as latest Aptian–earliest Albian (Scott, 1940; Young, 1967, 1974, 1986; Amsbury, 1974; Perkins, 1974).

The Forestburg and Butler Farm sites and SMU locality 108-2 lie further to the south in Texas (Fig. 4-1) and are slightly younger. The first two localities are in north-central Texas, within the upper sand unit of the Antlers Formation as mapped by Fisher and Rodda (1967:fig. 1) and Caughey (1977:fig. 3). SMU locality 108-2 is located further to the southeast in Erath County, where it lies at the base of the Paluxy Formation (Winkler et al., 1990:figs. 1, 4). Age estimates of latest Aptian–earliest Albian for the underlying Glen Rose Formation (Scott, 1940; Young, 1967, 1974, 1986; Amsbury, 1974; Perkins, 1974) and middle Albian for the overlying Walnut Formation (Young, 1974, 1986) based on marine invertebrates constrain the ages of the intervening Paluxy Formation and the laterally equivalent upper sand unit of the Antlers Formation to the early–middle Albian (Winkler et al., 1990; Jacobs et al., 1991). Here I use the name "Forestburg" for three localities reported by Patterson (1956) near the town of Forestburg in Montague County: (1) Greenwood Canyon (= SMU locality 21; Winkler et al., 1989), on Denton Creek, four km southwest of Forestburg; (2) an unnamed site located an unreported distance northeast of Forestburg, along Willawalla Creek; and (3) an unnamed site located an unreported distance south of Forestburg, near the ghost town of Uz. The first two sites lie about 27 and 43 m, respectively, below the top of the formation (Patterson, 1956); the stratigraphic position of the last site is unknown. Fossils at Greenwood Canyon, the most productive of the Forestburg sites (Winkler et al., 1989), were collected from fossiliferous pockets within a laterally continuous layer, up to 1 m thick, and consisting predominantly of sand and clay (Patterson, 1950–51, 1951, 1956). It should be appreciated that because this fossiliferous layer is exposed for an unreported, but evidently laterally extensive, distance around the entrance to the canyon (Patterson, 1950–51, 1956), the name "Greenwood Canyon" denotes an area, rather than a discrete site per se. Many of the albanerpetontid fossils in the collection of the FMNH were collected from Greenwood Canyon, as shown by labels accompanying specimens that read "Greenwood Canyon," "Turtle Gulley," and "Triconodont Gully"—the latter two names refer to parts of the "Greenwood Canyon Gully system" (Goin and Auffenberg, 1958:450). Other specimens in the collection are simply labelled "Forestburg" and could have been collected from any of the three Forestburg sites. The Butler Farm locality (= SMU locality 20; Winkler et al., 1989), located further to the north in Wise County, lies about 30 m below the top of the formation (Slaughter, 1965, 1968, 1971; Winkler et al., 1989). Greenwood Canyon and Butler Farm have produced the majority of the nonmarine vertebrate fossils recovered from the Antlers Formation (Winkler et al., 1989, 1990, and references therein), including teeth and jaws of mammalian taxa that define Russell's (1975) Paluxian North American Land Mammal Age. Given the importance of these sites, it is unfortunate that both are currently inaccessible (Winkler et al., 1989).

Cloverly Formation

The Cloverly Formation (sensu Moberly, 1960; Ostrom, 1970) is best exposed as scattered outcrops in the Bighorn Basin of south-central Montana and north-central Wyoming. The formation consists largely of floodplain and lacustrine bentonitic claystones and fluvial sandstones deposited on a broad, low-lying alluvial plain prior to the transgression of the Western Interior Seaway across the present day western United States (Moberly, 1960; Ostrom, 1970; Furer, 1970; Winslow and Heller, 1987). Limited magnetostratigraphic (Douglass and Johnson, 1984) and fission-track (Chen and Lubin, 1997) analyses and biostratigraphic correlations involving dinosaurs (e.g., Ostrom, 1970; Weishampel, 1990; Jacobs et al., 1991) and ostracods and charophytes (Peck and Craig, 1962) favor an Aptian–Albian or somewhat older age for the formation. Jacobs et al. (1991) suggested that the Cloverly Formation may be slightly younger than fossiliferous horizons of the Antlers and Paluxy formations in Texas, but this is unproven. Fragmentary albanerpetontid elements have been collected from one locality, OMNH V62, in the Cloverly Formation. This microsite is in Bighorn County, north-central Wyoming (Fig. 4-1), in the lower part of the formation in Ostrom's (1970) unit V (= "Little Sheep Mudstone Member" of some authors). Fission-track dates of 113 ± 8 million years reported by Chen and Lubin (1997) for samples from the top of unit V place the unit within the Aptian–Albian, according to the time scale of Gradstein et al. (1995).

SYSTEMATIC PALAEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order ALLOCAUDATA Fox and Naylor, 1982
Family ALBANERPETONTIDAE Fox and Naylor, 1982
Genus *ALBANERPETON* Estes and Hoffstetter, 1976

ALBANERPETON ARTHRIDION Fox and Naylor, 1982

(Figs. 4-2 to 4-4)

Prosiren elinorae Goin and Auffenberg, 1958 [in part: premaxilla, dentaries, and humerus referred by Estes 1969:87, fig. 2a–j; 1981:18, fig. 3B–E].

Albanerpeton? *arthridion* (Fox and Naylor, 1982) Rage and Hossini, 2000.

Holotype—FMNH PR805, incomplete right premaxilla missing pars palatinum and having two intact teeth, one broken tooth, and empty slots for four teeth (Estes, 1969:fig. 2c–e; Fox and Naylor, 1982:fig. 1c; here:Figs. 4-2A, B, 4-3A, B).

Holotype Horizon and Locality—Early–middle Albian, upper sand unit, Antlers Formation; Turtle Gully, Greenwood Canyon, Montague County, Texas, USA.

Referred Specimens—Upper sand unit, Antlers Formation, numerous localities, Texas: Turtle Gully, Greenwood Canyon: FMNH PR806, PR807, dentaries; Triconodont Gully, Greenwood Canyon: FMNH PR2025, premaxilla; FMNH PR2046–PR2050, dentaries; FMNH PR2026, PR2027, fused frontals; unrecorded gully, Greenwood Canyon: FMNH PR1891, dentary; unrecorded Forestburg locality(ies): FMNH PR2023, PR2024, premaxillae; FMNH PR2031–PR2045, PR2051, dentaries; Butler Farm locality: SMU 61041, humerus. Middle clay unit, Antlers Formation, OMNH V706, Oklahoma: OMNH 32344, 33282, 33287, 34067, premaxillae; OMNH 33284, 34072, maxillae; OMNH 32337, 32340–32342, 32348, 32350, 32362, 32365, 32368, 33283, 33285, 33286, 33336, 33337, 33339, 33342, 33344, 33345, 33347, 34056, 34058–34066, 34068–34071, dentaries; OMNH 32397–32400, fused frontals; OMNH 32371, 32372, atlantal centra; OMNH 33516, humerus.

Distribution—Latest Aptian–middle Albian: middle clay and upper sand units, Antlers Formation; Texas and Oklahoma.

Revised Diagnosis (modified from Gardner, 1999)—Species of Albanerpeton with no recognized apomorphies. Differs from congeners in having premaxilla primitively retaining suprapalatal pit that is small, occupying about one percent of lingual surface area of pars dorsalis, and located well dorsal to pars palatinum. Differs further from congeners in the following primitive character states: from A. galaktion Fox and Naylor, A. cifellii Gardner, and the new Judithian species in having suprapalatal pit oval in lingual outline; and from A. inexpectatum Estes and Hoffstetter, A. nexuosus Estes, and the unnamed Paskapoo species in having premaxilla unfused medially, relatively gracile in build, and bearing pars dorsalis that is relatively tall and not strongly sutured with nasal and in having frontals with internasal process acute in dorsal outline. Resembles Paskapoo species in one derived feature, estimated snout-pelvic length (SPL) less than about 40 mm, but differs further in having premaxilla primitively retaining a boss and, evidently, a prominent vomerine process.

Description

Unless explicitly stated otherwise, descriptions below are composites.

Premaxilla (Figs. 4-2A–E, 4-3A–C)—The eight premaxillae at hand are incomplete, but collectively they document most of this element's morphology. Premaxillae are delicate and tiny. The largest specimen, the holotype (Fig. 4-2A, B, 4-3A, B), is only about 1.6 mm high. The pars dorsalis is complete on FMNH PR805 and nearly complete on OMNH 33287 (Fig. 4-2C) and FMNH PR2023 (Fig. 4-2D). On each specimen, the process is relatively tall and narrow (Table 4-1). The dorsal edge of the pars dorsalis on FMNH PR805 is smooth, indicating that this surface abutted against the anterior end of the nasal. The lacrimal notch on FMNH PR805 and OMNH 33287 is relatively narrow and deep (Table 4-1). All eight premaxillae are unfused. In several specimens, including the holotype, the medial flange extends down the medial edge of the pars dorsalis and onto the upper part of the medial edge of the pars dentalis, but in FMNH PR2025 (not figured) and OMNH 33287 the flange is restricted to the basal part of the pars dorsalis and uppermost part of the pars dentalis (cf., Fig. 4-2A, C). Labially, the dorsal part of the pars dentalis and ventral two-thirds of the pars dorsalis are perforated with scattered, tiny external nutritive foramina. The dorsal one-third of the pars dorsalis on the holotype bears a low boss that is ornamented with indistinct, anastomosing ridges. The presence of a boss cannot be determined for the remaining specimens, because these all lack the dorsal end of the pars dorsalis.

Opening in the lingual face of the pars dorsalis, the suprapalatal pit lies slightly greater than one-half the distance from the medial edge of the process and well dorsal to the pars palatinum. The pit is ovoid to elliptical in lingual outline and remarkably tiny (Table 4-1), occupying in the holotype about only one percent of the lingual surface area of the pars dorsalis. The pit is bounded laterally by a labiolingually low internal strut and medially by a less prominent internal strut. Both struts arise just dorsal to the dorsal margin of the suprapalatal pit and extend ventrolaterally down the internal face of the pars dorsalis. The base of neither strut extends any significant distance lingually onto the dorsal surface of the pars palatinum. Several premaxillae, including FMNH PR805 (see Estes, 1969:fig. 2e) have a tiny, sediment-infilled foramen in the lateral face of the more lateral internal strut.

The pars palatinum is most nearly complete in FMNH PR2023 (Fig. 4-2D). This and other referred premaxillae show that the pars palatinum is as well-developed as in other albanerpetontids (contra Estes, 1981). FMNH PR2024 (Figs. 4-2E, 4-3C) preserves the base of an evidently well-developed and lingually directed vomerine process. FMNH PR2023 preserves a broad maxillary process that is smooth dorsally and bears along its lingual edge a low dorsal rim. The palatal foramen is tiny (i.e., foramen diameter one-half to one-third the diameter of the bases of the more medial of the premaxillary teeth) and subcircular in occlusal outline. The foramen opens dorsally in the junction between the dorsal surface of the pars palatinum and the lingual face of the pars dorsalis, between the bases of the internal struts, well ventral and slightly lateral to the suprapalatal pit. Ventrally, the palatal foramen opens about one-third of the distance lingually across the pars palatinum, in line with the third to fourth loci. The canal connecting the dorsal and ventral openings of the palatal foramen is exposed in the broken face of the pars palatinum on the holotype and clearly extends dorsoventrally through the shelf (Figs. 4-2B, 4-3B). One or two smaller foramina open more labially in the junction between the ventral surface of the pars palatinum and the pars dentalis. I have not been able to identify the dorsal openings of these more labial foramina, but homologous foramina in other albanerpetontid premaxillae open dorsally in the floor of the suprapalatal pit.

Maxilla (Figs. 4-2F, G, 4-3D–I)—Previously unknown for Albanerpeton arthridion, two incomplete maxillae are now available from OMNH V706. OMNH 33284 (Fig. 4-2F, G, 4-3D–G) is the posterior two-thirds of a left maxilla that is broken transversely between the internal narial opening and posteriormost part of the nasal process. OMNH 34072 (Fig. 4-3H, I) is a less nearly complete right maxilla. The latter specimen is broken posteriorly just behind the internal narial margin and anteriorly it is missing the premaxillary dorsal process, the anterior end of the premaxillary lateral process, and, possibly, the anteriormost end of the tooth row. OMNH 33284 and 34072 are delicate, small, and would have been no longer than about 2.5 mm and 1.8 mm, respectively, when complete. Both specimens are unornamented labially, except for four tiny external nutritive foramina on OMNH 34072. The pars facialis is low and tapers posteriorly. OMNH 34072 preserves an intact nasal process that is triangular in labial outline. The posterior edge of the process and adjacent part of the pars facialis are bevelled where the maxilla was overlapped dorsally and slightly labially by the lacrimal. The posterior end of the maxilla is complete in OMNH 33284 and labiodorsally has a shallow facet for contact with the anterior end of the jugal. Both specimens show that the pars palatinum is broad lingually, with a shallow trough dorsolingually for articulation with an unknown palatal bone. OMNH 33284 further shows that the pars palatinum tapers posteriorly. More nearly intact in OMNH 34072, the internal narial margin is shallowly concave in dorsal outline and spans at least five tooth positions. The ventral margin of the pars dentalis is straight in lingual or labial view, although breakage in OMNH 34072 creates the impression that the margin was shallowly convex ventrally. The anterior end of the tooth row in OMNH 34072 extends at least two loci anterior to the leading edge of the base of the nasal process.

Dentary (Fig. 4-2H–M)—None of the 57 dentaries are complete. Each specimen is delicate, slender, and small. The most nearly complete of these, FMNH PR806 (Estes, 1969:fig. 2g, i, j; here:Fig. 4-2H–J), has an intact tooth row, but lacks the posteriormost end of the bone and the ventral edge of the area for attachment of the postdentary bones. FMNH PR806 is 4.3 mm long; the other specimens were comparable in size when complete. The dorsal margin of the dental parapet is horizontal and essentially straight in labial view. The labial face is smooth, except for a row of up to six small external nutritive foramina that extends along the anterior one-half to two-thirds of the bone. Ventrally and ventrolaterally is an anteroposteriorly elongate scar, bounded laterally by a low rim or groove (Fig. 4-2K), for attachment of the intermandibularis muscles. This scar is indistinct on some specimens, including the three dentaries that Fox and Naylor (1982) described. The symphyseal eminence is moderately well-developed. Nine dentaries preserve intact symphyseal prongs: five of the six right dentaries, including FMNH PR806, each bear a single symphyseal prong; the other right dentary and each of the three left dentaries have a pair of symphyseal prongs. As in other albanerpetontids, the subdental shelf deepens posteriorly, the Meckelian canal is closed anteriorly and the posterior one-third of the dentary bears scars for attachment of the postdentary bones. The dorsal edge of the dentary behind the tooth row lacks a dorsally-directed process. Several dentaries preserve the anterior tip of the angular in situ within the opening for the Meckelian canal (Fig. 4-2L).

Dentition (Fig. 4-2A–M, 4-3A–E, G–I)—As is characteristic for albanerpetontids, the marginal teeth are highly pleurodont, non-pedicellate, and have crowns that are strongly compressed labiolingually, chisel-like, and faintly tricuspid. Teeth are straight, parallel along their lengths, and closely spaced. Maxillary and dentary teeth are weakly heterodont in size anteriorly, with the highest teeth on the dentary occupying the eighth to tenth loci. The only premaxilla (OMNH 33282; not figured) and dentary (FMNH PR806; Fig. 4-2H–J) that convincingly preserve a complete tooth row have nine and 33 loci, respectively. Neither maxilla has an intact tooth row: OMNH 33284 preserves the posteriormost 14 loci; OMNH 34072 preserves 12 loci along the anterior part of the tooth row, but the anteriormost end of the row may be absent. Judging by the overlap between OMNH 33284 and 34072, I estimate that the maxilla held about 23 loci when complete. Most jaws preserve one or more empty tooth slots for replacement teeth. Further evidence of tooth replacement is seen in a maxilla (OMNH 34072; Fig. 4-3I) with a large lingual resorption pit in the base of the tooth at both the fourth and sixth loci and in a dentary (FMNH PR1891; Fig. 4-2M) with a replacement crown in situ in the tooth slot at the fourth and eleventh loci. A premaxilla (FMNH PR2023; Fig. 4-2D) and a dentary (FMNH PR2051; not figured) each exhibit an unusual dental anomaly consisting of two parallel rows of functional teeth.

Frontals (Figs. 4-2N, O, 4-4)—Previously unknown for Albanerpeton arthridion, six pairs of frontals are now available. The two pairs, FMNH PR2026 (Fig. 4-2N, O, 4-4) and FMNH PR2027 (not figured), from Greenwood Canyon are nearly complete and measure about 2.6 and 2.4 mm in midline length, respectively. The four pairs of frontals from OMNH V706 are fragmentary, but when complete these would have been about the same size as FMNH PR2026 and PR2027. Frontals are solidly fused along the midline, although several retain a faint median line of fusion ventrally. FMNH PR2026 and PR2027 are about 1.2 times longer than wide and, in dorsal outline, resemble an anteroposteriorly elongate isosceles triangle. The internasal and anterolateral processes and the slots for receipt of the nasal anteriorly and prefrontal more posteriorly are well-developed. The internasal process is anteriorly acute in dorsal outline, with the length subequal to the width, and has a groove along the lateral face for tongue-in-groove contact with the medial edge of the nasal. Posterior to the anterolateral process, the lateral wall of the frontal extends posterolaterally at about 15° from the midline. The dorsal and ventral edges of the more posterior slot are shallowly excavated medially and the orbital margin is shallowly concave in dorsal or ventral view. The posterior edge of the frontal roof is shallowly emarginated to either side of the midline and the posterior face is smooth, indicating that the frontal roof abutted against the paired parietals. The dorsal surface is indented with shallow, broad pits that are polygonal in dorsal outline. These pits are enclosed by low, round-topped ridges that coalesce to form a reticulate pattern. On some frontals, such as FMNH PR2026, the pits are shallower and more irregular in outline across the anterior one-third of the frontals.

Ventrally, the anterolateral process bears a shallow facet, evidently for articulation with the underlying neurocranium. Just posterior and medial to this facet, a tiny unnamed foramen penetrates the ventral surface of the bone. The ventrolateral crest is relatively narrow in ventral view, with the ratio of VCW:FW^2 about 0.4 in FMNH PR2026 and 0.3 in PR2027. In transverse view, the crest is developed into a thick, ventrally convex rim, the ventrolateral face of which is shallowly bevelled along the orbital margin. The crest projects beyond the posterior edge of the frontal where, in life, the posterior end of the crest underlapped the parietal and medially received an anteriorly projecting tab from the parietal.

Atlas (Fig. 4-2P–S)—OMNH 32371 (Fig. 4-2P) and 32372 (Fig. 4-2Q–S) are from OMNH V706. These are the only vertebrae known for Albanerpeton arthridion. Neither centrum preserves the neural arch, although from the broken bases of the neural arch walls it is evident that an arch was present. Both centra are about 1.3 mm wide across the outer edges of the anterior cotyles and about 0.7 mm long between the anterior edge of the odontoid process and the ventral edge of the posterior cotyle. The specimens resemble other albanerpetontid altantes (see Seiffert, 1969; Estes and Hoffstetter, 1976; Estes, 1981; Fox and Naylor, 1982; Estes and Sanchíz, 1982; McGowan, 1996, 1998b) as follows: centrum short; articular surface for contact with skull continuous across anterior cotyles and ventral surface of odontoid process; anterior cotyles kidney-shaped in anterior outline, with anterior face shallowly concave; odontoid process broad and gutter-like in anterior view, having lateral edges confluent to either side with dorsal margin of anterior cotyles; notch deep beneath odontoid process and separating medial edges of anterior cotyles; and posterior cotyle having dorsal and ventral edges deeply excavated anteriorly. Much of the posterior cotyle is broken on OMNH 32371, but OMNH 32372 preserves the characteristic, faint tripartite facets for articulation with the axis. Both centra lack an open notochordal pit. In this respect they resemble all other described albanerpetontid atlantes, except for an indeterminate centrum (Seiffert, 1969:fig. 1D) from the Middle Jurassic of France. A small foramen, of uncertain function, opens low on the posterior surface of the anterior cotyle. On either side and just behind the posterior face of the anterior cotyle, the broken base of the neural arch exposes a narrow groove extending transversely between the neural canal and the lateral surface of the bone. This groove is best exposed on the right side of OMNH 32372 (Fig. 4-2R). Comparisons with rare albanerpetontid atlantes from elsewhere that preserve a complete or nearly complete neural arch (see Estes and Hoffstetter, 1976:pl. 6, fig. 14; Fox and Naylor, 1982:fig. 1h; here:Fig. 6-8F–H) indicate that, when intact, the neural arch on OMNH 32371 and 32372 would have enclosed the groove dorsally to form a foramen. The position of this groove argues for it being the canal connecting the medial and lateral openings of the foramen for exit of the first spinal nerve.

Humerus (Fig. 4-2T, U)—The distal ends of two humeri are available: one left (OMNH 33516; Gardner and Averianov, 1998:fig. 4A; here:Fig. 4-2T, U) from OMNH V706 and one right (SMU 61041; Estes, 1969:fig. 2a, b) from Butler Farm. The latter specimen was originally referred by Estes (1969, 1981) to Prosiren elinorae, but was not considered by Fox and Naylor (1982) in their type description of Albanerpeton arthridion. Both humeri resemble the incomplete left humerus in the holotype skeleton of Celtedens megacephalus (Costa) and referred humeri of Albanerpeton inexpectatum (Estes and Hoffstetter, 1976:pl. 9, figs. 6–7), an indeterminate species of Celtedens McGowan and Evans (McGowan and Ensom, 1997:fig. 2b), and indeterminate European Cretaceous albanerpetontids (see Estes and Sanchíz, 1982:fig. 5J; Duffaud and Rage, 1999:fig. 1) as follows: shaft elongate, slender, and in line with radial condyle; distal end about two times as wide in ventral view as diameter of shaft; radial condyle developed into a prominent, hemispherical ball; ulnar condyle markedly smaller than radial condyle; and epicondylus lateralis humeri virtually absent. OMNH 33516 and SMU 61041 differ from referred humeri of A. inexpectatum and the humerus in the holotype skeleton of C. megacephalus in being smaller, and from some of the humeri described by Estes and Sanchíz (1982) from the Spanish Barremian and by McGowan and Ensom (1997) from the English Berriasian in having a completely ossified radial condyle.

Remarks

Albanerpetontid elements described above can be associated based on their structure, small size, and provenance. These indicate that only one taxon, namely Albanerpeton arthridion, can be identified in the Antlers Formation. The two nearly complete frontals from Greenwood Canyon are diagnostic for Albanerpeton in being triangular in dorsal outline and, thus, uphold Fox and Naylor's (1982) generic assignment of the species. As discussed below, two of the three premaxillary characters previously used to diagnose A. arthridion are unreliable for this purpose.

Estes (1981:20) stated that the pars palatinum on the premaxilla and maxilla is weakly developed in Prosiren elinorae (= jaws of Albanerpeton arthridion). The only upper jaw listed for A. arthridion by Estes (1969, 1981) and, therefore, the only one presumably known to him, was the premaxilla FMNH PR805. Estes (1981) evidently inferred from FMNH PR805 that the pars palatinum was also poorly developed on the maxilla. The pars palatinum on FMNH PR805 is not weakly developed, it is broken (Fox and Naylor, 1982), and only the lingualmost part remains as a horizontal ridge extending across the lingual face of the bone. The canal connecting the dorsal and ventral openings of the palatal foramen is evident in Estes' figure (1969:fig. 2c) of FMNH PR805 (cf., Fig. 4-2B, 4-3B), indicating that the pars palatinum was already broken and the canal exposed when he first described the specimen. Referred premaxillae and maxillae described above for A. arthridion convincingly show that the pars palatinum is as well-developed as in other albanerpetontid species.

Based again on FMNH PR805, Fox and Naylor (1982:120) diagnosed Albanerpeton arthridion as follows: "Differs from other Albanerpeton in elongate medial ridge [= "medial flange," here] extending along pars dentalis and pars facialis [= "pars dorsalis," here] of premaxillary, with long, deep paralleling grooves; and in raised boss on pars facialis dorsally." I do not consider the lengths of the medial flange and accompanying grooves diagnostically useful, because the sizes of these structures are more variable within and less variable among albanerpetontid species than Fox and Naylor (1982) suspected. Among premaxillae at hand for A. arthridion, the medial flange and associated grooves may extend along virtually the entire medial edge of the bone or may be restricted to the uppermost part of the pars dentalis and basalmost part of the pars dorsalis (cf., Fig. 4-2A, C). Similar variation is seen in other species for which adequate numbers of premaxillae are available. The presence of a premaxillary boss is diagnostic for A. arthridion only in combination with other features, because this structure is primitive for the genus and it occurs in all North American Cretaceous congeners.

Despite the problems outlined above, in my opinion, the premaxilla remains the most diagnostically informative element for Albanerpeton arthridion, as it does for other species in the genus. Although I have not been able to identify any autapomorphies or unique combinations of synapomorphies for A. arthridion, the species can be reliably differentiated from all congeners by two primitive character states of the suprapalatal pit: (1) pit occupies about 0.01 of the lingual surface area of the pars dorsalis (pit occupies 0.04 to nearly 0.25 of pars dorsalis in other congeners) and (2) pit is located high on the lingual face of the pars dorsalis, well dorsal to pars palatinum (pit opens lower on pars dorsalis, often with ventral edge of pit confluent with dorsal surface of pars palatinum in other congeners).

Albanerpeton arthridion also lacks other derived character states of the premaxilla (e.g., premaxillae fused medially; boss enlarged or absent; suprapalatal pit triangular or slit-shaped in lingual outline) and frontals (e.g., ventrolateral crest relatively broader and flat or concave in transverse view; internasal process acuminate in outline) that occur, in some combination, in all geologically younger congeners. Many of the premaxillary character states that I interpret as primitive for the genus also occur in premaxillae of non-Albanerpeton albanerpetontids. This distribution of character states argues for A. arthridion being the most basal of the species currently included within Albanerpeton, an interpretation that is supported by my phylogenetic analysis of the genus presented in Chapter 7.

Albanerpeton arthridion is diagnosed by one putative apomorphy—inferred small body size. Albanerpetontids as a whole were relatively small animals, as evidenced by skeletons of Celtedens megacephalus and C. ibericus McGowan and Evans that have SPLs of about 50 mm (McGowan and Evans, 1995; pers. obs., 1997). Judging by the sizes of their isolated bones, most other albanerpetontid species attained comparable or somewhat larger body sizes. By contrast, none of the bones at hand for A. arthridion are more than half the size of the largest homologous bones available for most other albanerpetontid species. A depositional, taphonomic, or collecting bias towards smaller, presumably subadult, bones of A. arthridion can be dismissed because the specimens in question were collected along with small and larger bones of other taxa at several geographically and stratigraphically distinct microsites. Despite their small absolute size, I interpret the available specimens of A. arthridion as having come from mature individuals based on the following observations: each bone is solidly ossified, with well-formed processes and articular surfaces; jaws have fully formed, functional teeth that were being actively replaced; several dentaries (e.g., FMNH PR2046; Fig. 4-2K) have a roughened labial surface and prominent scar for the intermandibularis muscles; the holotype premaxilla has a relatively well-developed boss; frontals are solidly fused; and the radial condyle is completely ossified on both humeri. Given that 77 bones are now available for A. arthridion, I suggest that the largest of these can be used with some confidence to estimate maximum body size for the species. This obviously will underestimate the true maximum body size, but I believe the difference to be negligible.

Based on FMNH PR2026, the largest and most nearly complete of the six pairs of frontals at hand for Albanerpeton arthridion, I estimate a head-body length of only about 30 mm for the species. This approaches the lower limit of body size (measured as snout-vent length) for tailed amphibians (see Clarke, 1996:tables 1, 2, and references therein). The Paleocene Paskapoo species is known by jaws and a pair of frontals that are not much larger than those of A. arthridion, suggesting that the former species is also relatively small. However, derived premaxillary character states (e.g., premaxillae fused; pars dorsalis short; boss absent) in the Paskapoo species argue against a close relationship between the two congeners. This implies that small body size (i.e., SPL less than about 40 mm) developed at least twice within Albanerpeton (Chapter 7). This trend is not surprising, considering that reduced body size has arisen independently, and occasionally repeatedly, in many lineages of extant lissamphibians (see review by Clarke, 1996). Clarke (1996) noted that small body size conveys several advantages to extant amphibians, most notably allowing a greater range of microhabitats and variety of prey to be exploited. Individuals of A. arthridion presumably enjoyed similar benefits by virtue of their small size.

Genus and Species Indeterminate

Specimens—OMNH 33517, premaxilla; OMNH 33518, maxilla; OMNH 33519–33522, dentaries; OMNH 33423, lot of six fragmentary dentaries.

Horizon and Locality—Aptian–Albian; unit V, Cloverly Formation; OMNH locality V62, Bighorn County, Wyoming.

Remarks—Unfigured albanerpetontid jaws from the Cloverly Formations are fragmentary and none can be identified below the familial level. The premaxilla preserves no notable features, but the maxilla and several dentaries have intact teeth that are diagnostic for the Albanerpetontidae in being highly pleurodont, non-pedicellate, and chisel-like. Other characteristic albanerpetontid features seen in the dentaries are the prominent ventral scar for attachment of the intermandibularis muscles, the labial row of external nutritive foramina, symphyseal prongs, a deep dental parapet, and an anteriorly closed Meckelian canal. These jaws are the first amphibian fossils reported from the Cloverly Formation.

Order CAUDATA? Scopoli, 1777

Family, Genus, and Species Indeterminate

Caudata?, gen. et sp. indet., Winkler et al. (1990:table 1).

Specimen—SMU 72153, atlantal centrum lacking neural arch (Winkler et al., 1990:fig. 6A).

Horizon and Locality—Early-middle Albian; Paluxy Formation; SMU locality 108-2, Erath County, Texas.

Remarks—Winkler et al. (1990:104) briefly described SMU 72153 and suggested that this atlantal centrum may pertain to *Albanerpeton*. Judging by their published photograph (Winkler et al., 1990:fig. 6A) of SMU 72153 in anterior view, this atlantal centrum appears to differ from unequivocal albanerpetontid atlantes, such as those I described above for *A. arthridion*, in having the anterior cotyles more subcircular in anterior outline, the median notch between anterior cotyles broader and shallower, and the odontoid process relatively narrower and thicker, with a nearly flat dorsal surface. I suspect based on the structure of the anterior cotyles and odontoid process that SMU 72153 is a salamander atlas, but I would have to see the specimen firsthand to confirm this.

THE EARLY BIOGEOGRAPHY OF NORTH AMERICAN ALBANERPETONTIDS

As discussed by Gardner and Averianov (1998), attempts to decipher the biogeographical history of the Albanerpetontidae continue to be hampered by the group's limited fossil record. The oldest occurrences of albanerpetontids are in the Jurassic of western Europe and consist of the following: an indeterminate centrum (Seiffert, 1969; Estes and Hoffstetter, 1976; Estes, 1981) from the early Bathonian (Kriwet et al., 1997) of France; isolated elements, including specimens of the undescribed Kirtlington species (Chapter 2), from late Bathonian sites in England (Evans and Milner, 1994; McGowan, 1998a; Gardner, 2000); and undescribed elements, including diagnostic *Celtedens* frontals (McGowan, 1998a), from Kimmeridgian or Oxfordian sites in Portugal (Estes, 1981; Milner, 1994; McGowan, 1996). Early Cretaceous albanerpetontids are represented in

Europe by the following: isolated bones of *Celtedens* from the Berriasian of England (McGowan and Ensom, 1997); two skeletons of *C. ibericus* (McGowan and Evans, 1995), frontals of *Celtedens* (McGowan, 1998a), and indeterminate skull and postcranial bones (Estes, 1981; Estes and Sanchíz, 1982) from Barremian sites in Spain; and the holotype skeleton of *C. megacephalus* from the early Albian (Bravi, 1994) of Italy (Costa, 1864; D'Erasmo, 1914; Estes, 1981). The oldest reliable records elsewhere in the Old World are undescribed jaws and frontals of the undescribed Anoual species from the Berriasian of Morocco (Sigogneau-Russell et al., 1998) and indeterminate dentaries from the Cenomanian of Uzbekistan (Gardner and Averianov, 1998).

The oldest North American albanerpetontid fossils yet documented are the specimens reported above from the Cloverly and Antlers formations. These specimens provide a minimum age of latest Aptian–earliest Albian for the establishment of the albanerpetontids in North America. Given the presence of older (i.e., Bathonian–Barremian) albanerpetontids in the Old World and the distribution of land masses during this time (Smith et al., 1994), I suspect that albanerpetontids were in North America substantially before the latest Aptian, but no fossils are presently known from the continent that confirm this was the case. Fossil occurrences and paleogeographical reconstructions (Gardner and Averianov, 1998:fig. 5) suggest four scenarios for the establishment of albanerpetontids in North America: (1) dispersal from Asia; (2) dispersal from Europe; (3) albanerpetontids were present on the proto-North American continent before the breakup of Laurasia and subsequent isolation of North America; or (4) some combination of these. The Asian dispersal scenario is weakened by the fact that the oldest unequivocal albanerpetontid fossils (Cenomanian) from Asia postdate the establishment of the Bering Land Bridge in the Albian (Gardner and Averianov, 1998), while the oldest North American occurrences (this study) antedate the establishment of the land bridge. The remaining scenarios are somewhat better supported by the available evidence, but none can be favored at present.

Regardless of precisely when or how albanerpetontids became established in North America, fossils from the Cloverly and Antlers formations demonstrate that these amphibians were on the continent before (Fig. 4-5A) the Western Interior Seaway opened briefly in the early late Albian (Fig. 4-5B) and then continuously from about the latest Albian–middle Maastrichtian (Williams and Stelck, 1975; Kauffman and Caldwell, 1993).

This timing is significant, because it means that the seaway, which effectively divided North America into eastern and western subcontinents for most of the Late Cretaceous, would not initially have barred the east–west movement of albanerpetontids across the continent. The record of nonmarine Cretaceous microvertebrates to the east of the Western Interior Seaway is sparse, to the extent that lissamphibians are known only from the Campanian age Ellisdale locality in New Jersey, USA (Denton and O'Neill, 1998). The apparent lack of diagnostic albanerpetontid fossils at this locality is surprising, as the Ellisdale lissamphibian assemblage otherwise resembles contemporaneous, albanerpetontid rich-assemblages in the Western Interior.

CONCLUSIONS

Albanerpetontid fossils reported herein from the Early Cretaceous (Aptian–Albian) of the Western Interior are the geologically oldest records for the family in North America and permit the following observations:

(1) Based on previously described and new specimens from the Antlers Formation of Texas and Oklahoma, I argue that Albanerpeton arthridion is a valid species of Albanerpeton and the basalmost species in the genus.

(2) Fossils of Albanerpeton arthridion and of an indeterminate albanerpetontid from the paracontemporaneous Cloverly Formation of Wyoming establish the presence of albanerpetontids in North America by at least the latest Aptian, well before the opening of the Western Interior Seaway. Consequently, this marine barrier would not initially have limited the movement of albanerpetontids across the continent. The failure to identify albanerpetontid specimens in deposits to the east of the seaway is probably due to the sparse record of Cretaceous microvertebrates in eastern North America.

(3) Occurrences of albanerpetontids in the Old World and paleogeographical reconstructions, coupled with the sparse pre-Albian record of lissamphibians in North America, imply that a date of latest Aptian or earliest Albian almost certainly underestimates the antiquity of albanerpetontids on the continent. Further insights into the early history of North American albanerpetontids thus await the discovery of even older fossils.

TABLE 4-1. Straight line measurements and ratios for premaxillae of Albanerpeton arthridion Fox and Naylor; latest Aptian–middle Albian, Antlers Formation, Texas and Oklahoma, USA. "Value" is measurement or ratio for one specimen; other column headings follow Table 3-1. Measurements follow Figure 1-2.

Measurement or Ratio	Value	n	Range	$\bar{x}$ and SD
PmH (height of premaxilla; mm)	1.63	1	—	—
PDH (height of pars dorsalis; mm)	0.96	1	—	—
PDW^1 (width of pars dorsalis across base of lacrimal notch; mm)	—	2	0.48–0.50	—
PDW^2 (width of pars dorsalis across suprapalatal pit; mm)	—	7	0.41–0.53	0.48±0.04
LaND (depth of lacrimal notch; mm)	0.43	1	—	—
LaNW (width of lacrimal notch; mm)	—	2	0.07–0.16	—
SPH (height of suprapalatal pit; mm)	—	7	0.07–0.12	0.08±0.02
SPW (maximum width of suprapalatal pit; mm)	—	7	0.05–0.07	0.06±0.02
PDH:PDW^2 (relative height of pars dorsalis)	1.8	1	—	—
LaND:PDH (relative depth of lacrimal notch)	0.45	1	—	—
LaNW:PDW^1 (relative width of lacrimal notch)	—	2	0.15–0.33	—
SPH:PDH (relative height of suprapalatal pit)	0.08	1	—	—
SPW:PDW^2 (relative width of suprapalatal pit)	—	7	0.10–0.15	0.13±0.02

FIGURE 4-1. Map of southern part of the western USA showing locations of Lower Cretaceous (Aptian–Albian) microsites mentioned in the text. Symbols: circle, Antlers Formation; triangle, Paluxy Formation; and square, Cloverly Formation.

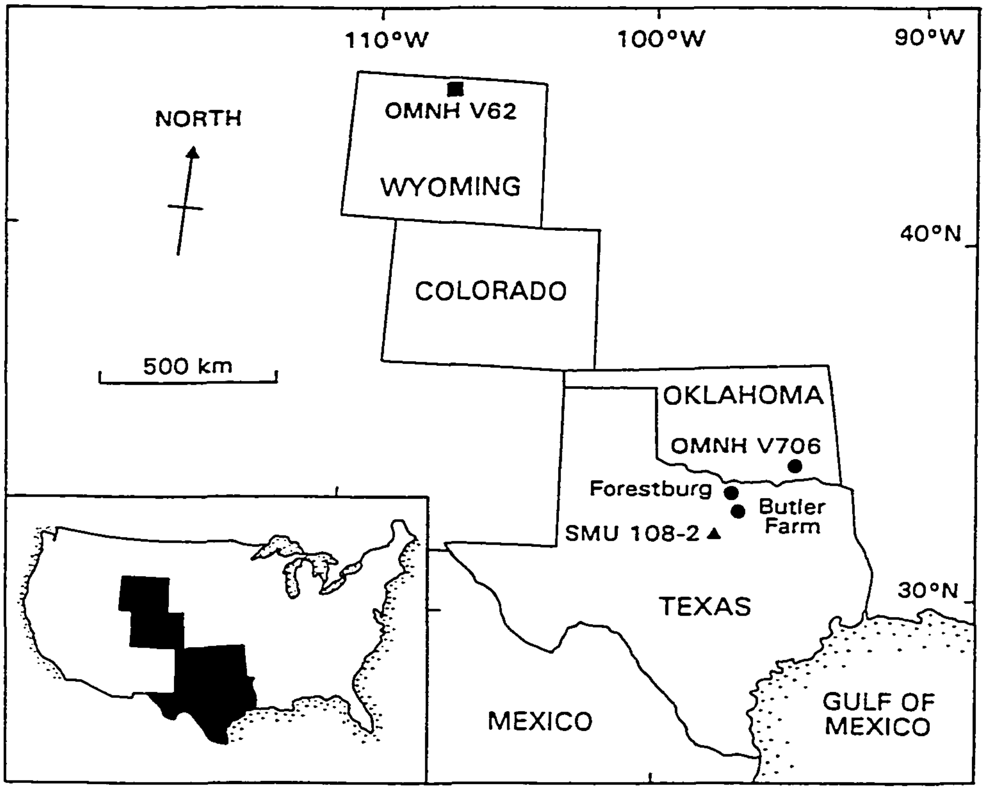
110°W
100°W
90°W
NORTH
OMNH V62
WYOMING
40°N
COLORADO
500 km
OKLAHOMA
OMNH V706
Forestburg
Butler Farm
SMU 108-2
TEXAS
30°N
MEXICO
GULF OF MEXICO

FIGURE 4-2. Cranial and postcranial elements of Albanerpeton arthridion Fox and Naylor; latest Aptian–middle Albian, Antlers Formation, Texas and Oklahoma. Premaxillae (**A–E**): **A**, **B**, FMNH PR805, holotype, right premaxilla, in (**A**) labial and (**B**) lingual views; **C**, OMNH 33287, left premaxilla, in labial view; **D**, FMNH PR2023, right premaxilla, in lingual view; **E**, FMNH PR2024, left premaxilla, in occlusal view. Maxilla (**F**, **G**): OMNH 32284, posterior two-thirds of left maxilla, in (**F**) lingual and (**G**) occlusal views. Dentaries (**H–M**): **H–J**, FMNH PR806, right dentary, in (**H**) labial, (**I**) lingual, and (**J**) occlusal views; **K**, FMNH PR2046, anterior part of left dentary, in labial view; **L**, FMNH PR2036, posterior part of left dentary with anterior end of angular (arrow) in articulation, in lingual view. **M**, FMNH PR1891, anterior one-half of left dentary, in occlusal view. Fused frontals (**N**, **0**): FMNH PR2026, in (**N**) dorsal and (**O**) ventral views. Atlantal centra (**P–S**): **P**, OMNH 32371, in anterior view; **Q–S**, OMNH 32372, in (**Q**) posterior, (**R**) dorsal, and (**S**) ventral views. Humerus (**T**, **U**): OMNH 33516, distal one-half of left humerus, in (**T**) ventral and (**U**) dorsal views. Provenances: FMNH and OMNH specimens are from, respectively, the Forestburg localities, Texas, and OMNH V706, Oklahoma. Specimens at different scales: top right (**A–E**) and bottom right (**F–U**) scale bars = 1 mm.

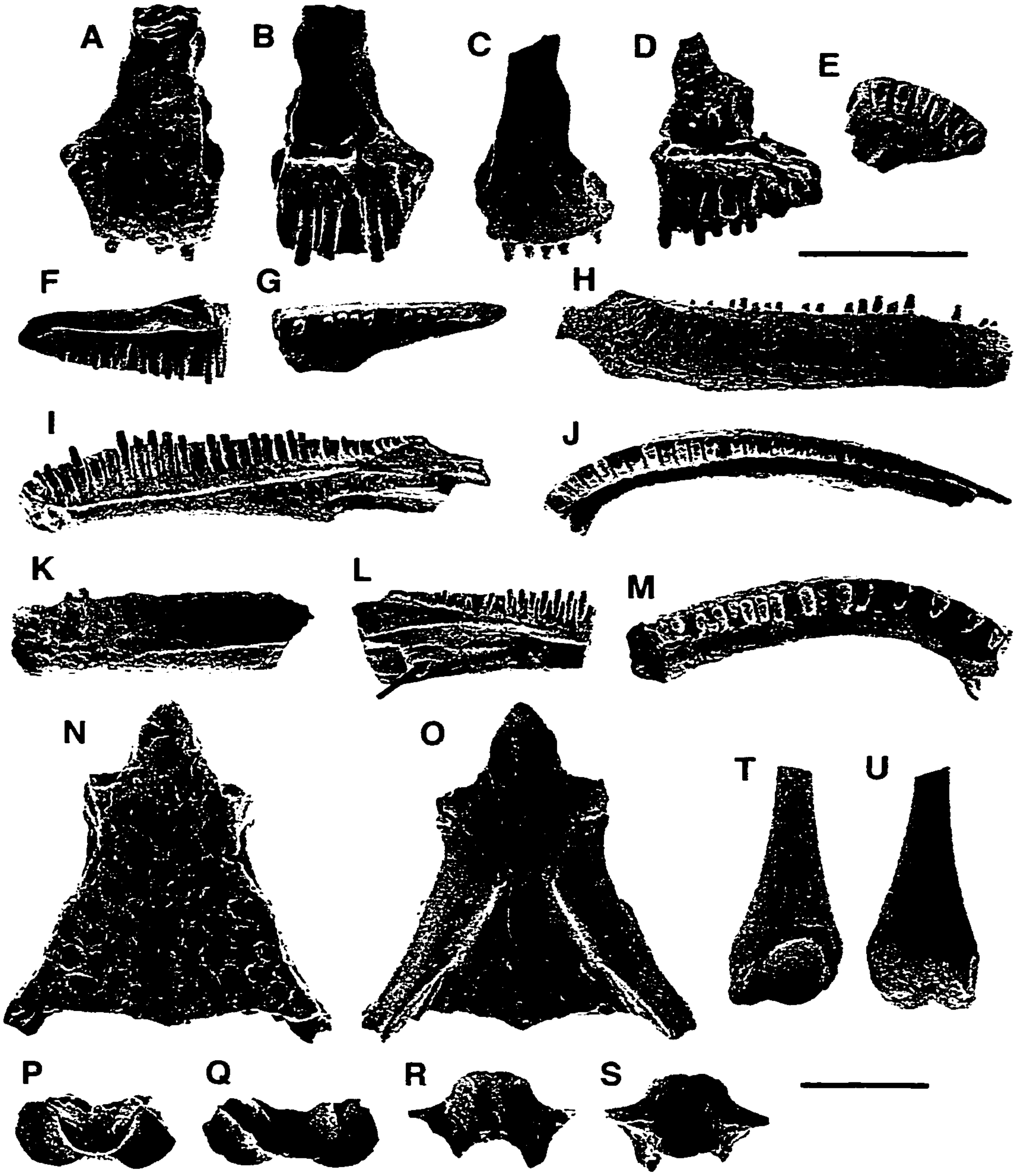
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FIGURE 4-3. Upper jaws of Albanerpeton arthridion Fox and Naylor; latest Aptian–middle Albian, Antlers Formation, Texas and Oklahoma. Premaxillae (A–C): **A**, **B**, FMNH PR805, holotype, right premaxilla, in (A) labial and (B) lingual views; **C**, FMNH PR2024, left premaxilla, in occlusal view with labial margin to top of page. Maxillae (D–I): **D–G**, OMNH 33284, posterior two-thirds of left maxilla, in (D) labial, (E) lingual, (F) dorsal, and (G) occlusal views; **H**, **I**, OMNH 34072, anterior one-third of right maxilla, broken anteriorly, in (H) labial and (I) lingual views. Provenances: FMNH and OMNH specimens are from, respectively, the Forestburg localities, Texas, and OMNH V706, Oklahoma. Cross hatches denote broken surfaces. Specimens at same scale: scale bar = 1 mm.

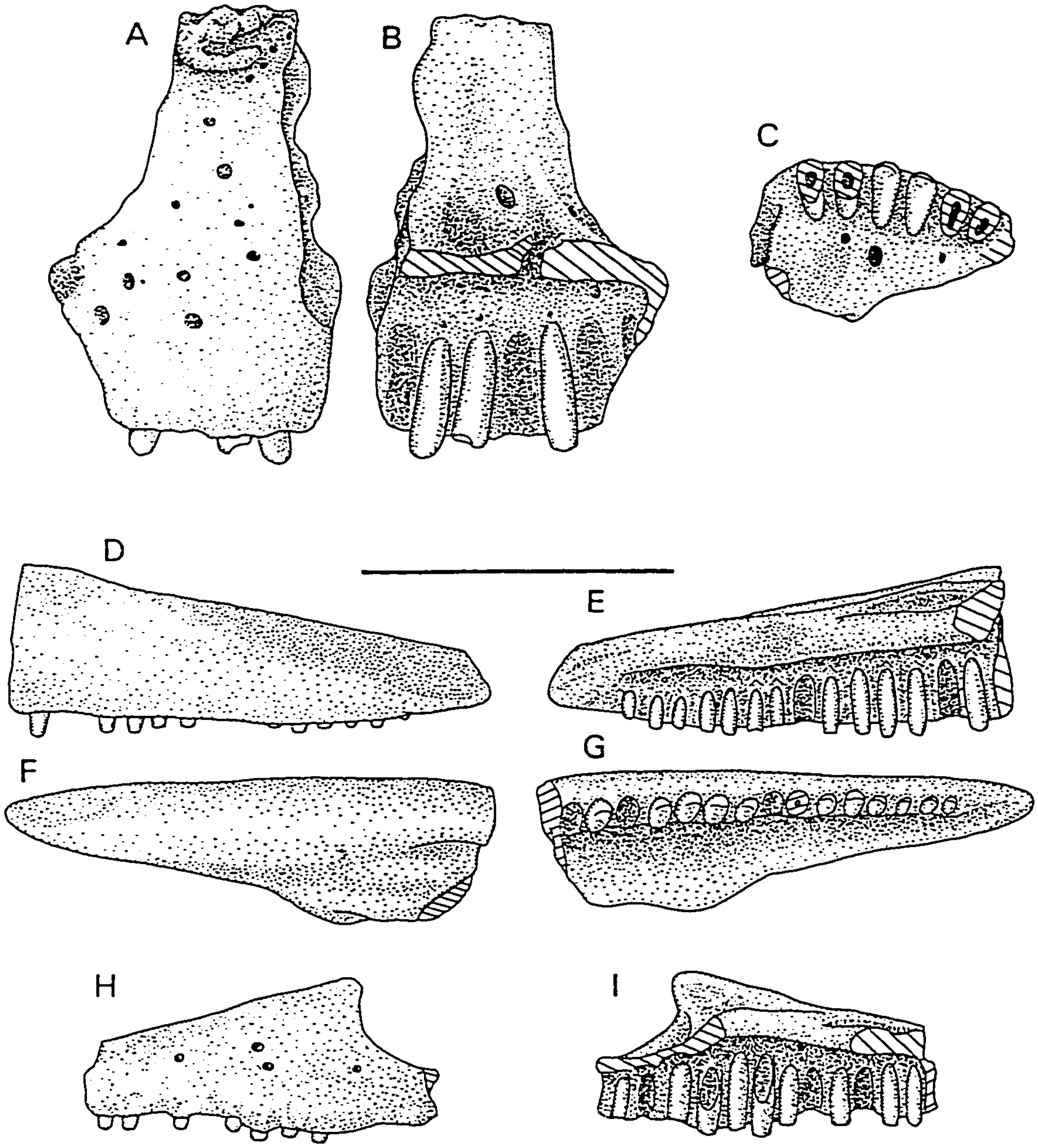
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FIGURE 4-4. Fused frontals of Albanerpeton arthridion Fox and Naylor; early–middle Albian, Greenwood Canyon locality, Antlers Formation, Texas. **A**, **B**, FMNH PR2026, fused frontals, in (**A**) dorsal and (**B**) ventral views. Scale bar = 1 mm.

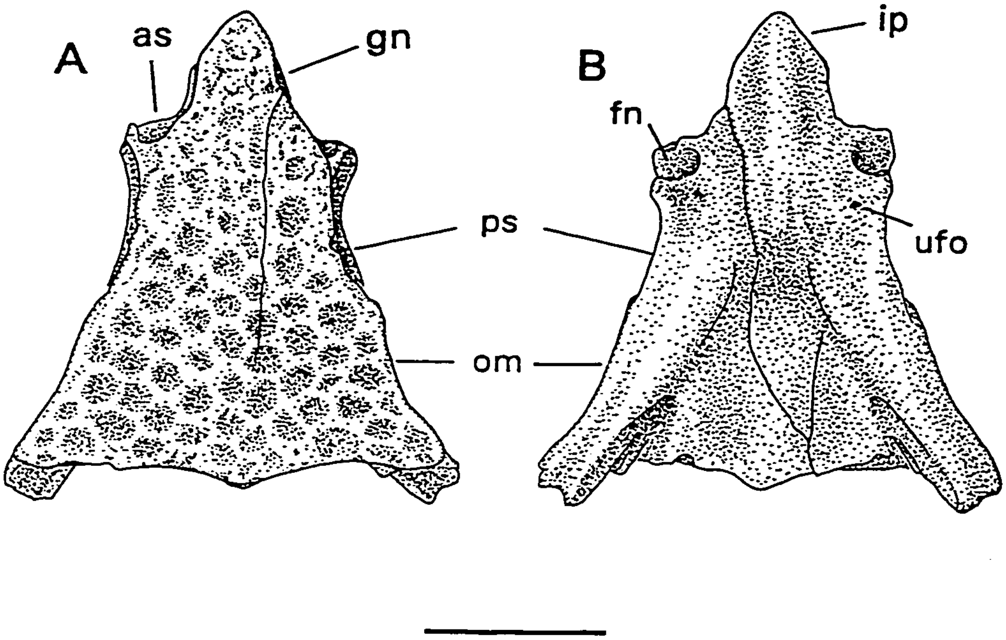
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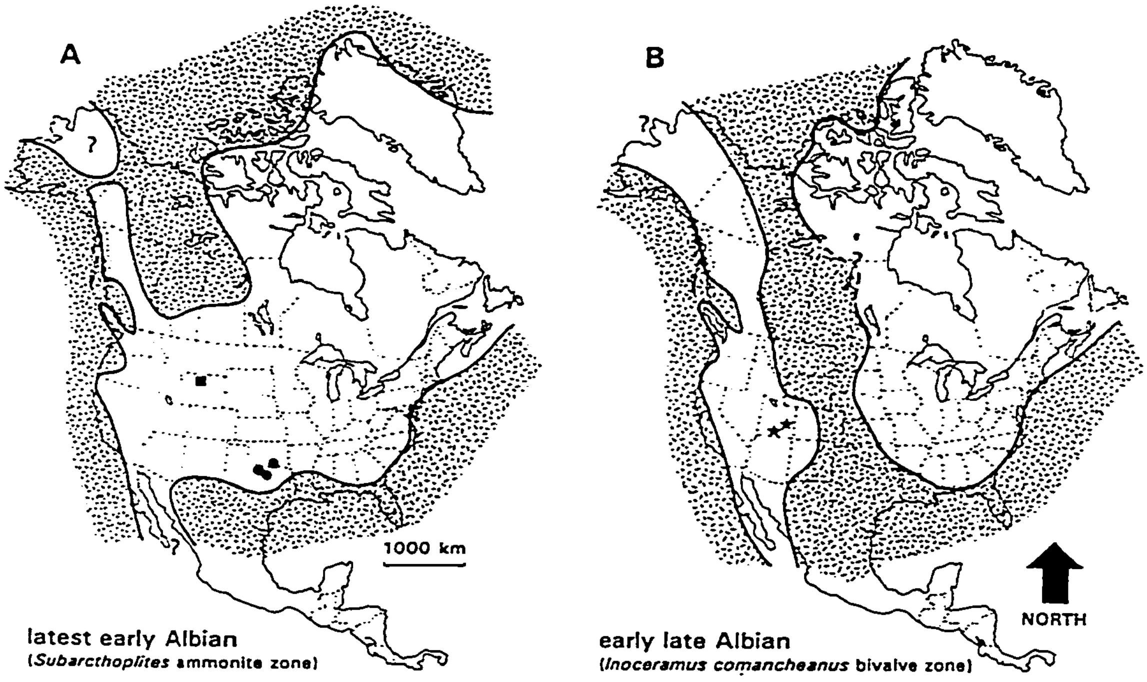
FIGURE 4-5. Paleogeographical maps of North America during the late Early Cretaceous (modified from Williams and Stelck, 1975:text-figs. 2, 3) showing the opening of the Western Interior Seaway and pre-Campanian occurrences of albanerpetontids on the continent. **A**, latest early Albian, prior to opening of seaway. **B**, early late Albian, during first brief opening of seaway; the seaway was again continuous from the latest Albian–middle Maastrichtian. Symbols: square, Cloverly Formation (Aptian–Albian), Wyoming; circle, upper sand unit (latest Aptian–middle Albian) of Antlers Formation, Texas and Oklahoma; and star, Mussentuchit Member (latest Albian–earliest Cenomanian) of Cedar Mountain Formation and middle part (Turonian–Coniacian) of Straight Cliffs Formation, both in Utah (see Chapter 5). Marine waters indicated by cross-hatching.



latest early Albian
(*Subarcthoplites* ammonite zone)

early late Albian
(*Inoceramus comancheanus* bivalve zone)

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CHAPTER 5 — NEW ALBANERPETONTIDS FROM THE LATEST ALBIAN TO CONIACIAN OF UTAH, USA[1]

INTRODUCTION

Albanerpetontid fossils are well represented in the Aptian–middle Albian (Fox and Naylor, 1982; Gardner, 1999a, here:Chapter 4) and Campanian–Maastrichtian (Estes, 1981; Fox and Naylor, 1982; Rowe et al., 1992; Gardner, 1996, in press; here:Chapter 6) of the North American Western Interior, but until recently were unavailable from deposits of intermediate age on the continent. Differences in premaxillary structure between pre-late Albian and post-Santonian albanerpetontids imply that considerable evolutionary change occurred during the intervening 15 million year (Gradstein et al., 1995) hiatus. Albanerpetontid fossils from elsewhere are uninformative for elucidating the pattern and timing of these changes, as these records are limited to five indeterminate dentaries from Uzbekistan (Gardner and Averianov, 1998). Here I report on new collections of isolated and rare articulated bones from microvertebrate sites in Utah (Fig. 5-1) that help fill this stratigraphic gap in the Cretaceous albanerpetontid record and provide new insights into the history of the family and, especially, the type genus Albanerpeton Estes and Hoffstetter.

GEOLOGICAL SETTING AND LOCALITIES

Cedar Mountain Formation

The Cedar Mountain Formation consists of terrigenous sediments deposited during the Barremian–early Cenomanian (Kirkland et al., 1997) across a broad alluvial plain (Eaton et al., 1990), before and during the establishment of the Western Interior Seaway,

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[1] A version of this chapter has been published: Gardner 1999. Journal of Vertebrate Paleontology. 19: 632–638.

but well inland to the west. Exposures of the formation in central and eastern Utah have historically been divided into the basal Buckhorn Conglomerate Member and a thicker, unnamed upper shale member consisting of floodplain mudstones and minor fluvial sandstones (Stokes, 1952; Peterson et al., 1980; Cifelli et al., 1999). Kirkland et al. (1997) recently proposed four new members to replace Stoke's (1952) unnamed shale member. In ascending order, these new units are the Yellow Cat, Poison Strip, Ruby Ranch, and Mussentuchit members. Microvertebrate sites in a stratigraphically restricted level 10–20 m below the top of the smectitic mudstone-dominated Mussentuchit Member, in exposures along the western flank of the San Rafael Swell in Emery County, east-central Utah, have yielded a diverse, nonmarine vertebrate assemblage (Cifelli et al., 1999) of latest Albian–earliest Cenomanian age (Cifelli et al., 1997). Albanerpetontid fossils have been collected in this horizon from six localities (Fig. 5-1B): OMNH V235, V239, V240, V695, V696, and V801.

Straight Cliffs Formation

As exposed on the Kaiparowits Plateau in south-central Utah, the Straight Cliffs Formation is a sandstone-dominated complex of nonmarine and brackish beds that was deposited along the episodically transgressing and regressing western edge of the Western Interior Seaway during the middle Turonian–early Campanian (Peterson, 1969; Eaton, 1991). In ascending order, the Straight Cliffs Formation consists of the Tibbet Canyon, Smoky Hollow, John Henry, and Drip Tank members (Peterson, 1969). Albanerpetontid bones reported herein were collected in Garfield County, Utah (Fig. 5-1C), from OMNN V4 and V60 in the middle of the Smoky Hollow Member and from OMNH V856 in the lower part of the overlying John Henry Member. The Smoky Hollow Member is nonmarine in origin and dated as late Turonian based on mollusks in the over- and underlying members (Peterson, 1969; Eaton, 1991). The John Henry Member is a complex of brackish water and nonmarine beds (Peterson, 1969; Eaton, 1991) and mollusks support an early Coniacian–late Santonian age (Eaton, 1991) for the unit. The depositional environment of OMNH V856 is uncertain, but its position near the base of the member implies that the site is probably early or middle Coniacian in age.

SYSTEMATIC PALEONTOLOGY

Subclass LISSAMPHIBIA Haekel, 1866
Order ALLOCAUDATA Fox and Naylor, 1982
Family ALBANERPETONTIDAE Fox and Naylor, 1982
Genus ALBANERPETON Estes and Hoffstetter, 1976

Remarks–For the purposes of this chapter, recall that I interpret the second of the two kinds of premaxillae described by Fox and Naylor (1982:124) for A. galaktion Fox and Naylor as belonging instead to A. nexuosus Estes (see Chapter 6). Figure 5-2 repeats a simplified cladogram of my phylogeny for Albanerpeton (see Chapter 7) and the three major premaxillary patterns in the genus.

ALBANERPETON sp., cf. A. NEXUOSUS Estes, 1981
(Fig. 5-3A–E)

Specimens—OMNH 26222, fused and incomplete premaxillae; OMNH 27413, incomplete right dentary.

Horizon and Localities—Latest Albian–earliest Cenomanian; Mussentuchit Member, Cedar Mountain Formation; two localities: OMNH V239 (OMNH 26222) and V695 (OMNH 27413), both in Emery County, Utah.

Description

Premaxilla (Fig. 5-3A, B)—The only available specimen is OMNH 26222, a solidly fused pair of incomplete premaxillae. Parts of the dorsal end of the pars dorsalis are missing from both sides, but intact sections show that bone was about 3.0 mm high when complete and strongly sutured dorsally with the nasal. The pars dorsalis is relatively short and broad, with the height of the process about 1.2 (left side) and 1.3 (right side) times greater than the width of the process across the suprapalatal pit. A distinct lacrimal notch is absent. Instead, the lateral margin of the dorsal half of the pars dorsalis is inclined medially at about 10° from the vertical, with the lateral face flattened and roughened for contact with the lacrimal. Lingually, the pars dentalis and ventral one-half of the pars dorsalis are perforated by scattered, external nutritive foramina. The more dorsal part of the pars dorsalis is covered by a pronounced, raised boss that is continuous across the two halves and prominently ornamented with anastomosing, narrow ridges.

The suprapalatal pit lies midway across the lingual face of the pars dorsalis, just dorsal to the pars palatinum. The pit is oval in lingual outline and moderate in size, measuring 0.40 mm high and 0.34 mm wide, and occupying about five percent of the lingual surface area of the pars dorsalis. Lateral to the suprapalatal pit is a mediolaterally broad internal strut. This strut arises just dorsal to the pit and expands lingually as it extends ventrolaterally down the inner face of the pars dorsalis. The strut is perforated laterally by a tiny, sediment-infilled foramen. As the pars palatinum is broken and only the labialmost part remains, neither the structure of the shelf nor the extent to which the base of the internal strut extended across the dorsal surface of the shelf can be determined. Just medial to the preserved base of the lateral strut, and best seen on the right side (Fig. 5-3B, C), the broken face of the pars palatinum exposes the canal between the dorsal and ventral openings of the palatal foramen. This canal is narrow and extends dorsoventrally through the pars palatinum. The pars dentalis is broken laterally and only the medialmost six tooth positions remain on each side. In total, six empty tooth slots and six broken teeth are preserved. The teeth are highly pleurodont, non-pedicellate, and were evidently relatively elongate when complete. No tooth preserves a crown.

Dentary (Fig. 5-3D, E)—OMNH 27413 is the anterior part of a robustly constructed, right dentary. The specimen is 5.1 mm long as preserved and was from an individual comparable in size to that represented by OMNH 26222. The distal ends of the symphyseal prongs are broken, but the dentary preserves a well-developed symphyseal eminence, a ventral scar for attachment of the intermandibularis muscle, and a row of five external nutritive foramina. The dental parapet is relatively high and its dorsal edge is moderately convex dorsally in labial outline. About 16 tooth positions are preserved, consisting of four empty tooth slots, the bases of about seven teeth, and five intact, highly pleurodont, non-pedicellate teeth with chisel-like crowns. Judging by the preserved teeth and empty slots, the teeth were moderately heterodont anteriorly, with the largest located about one-third of the distance from the anterior end of the tooth row.

Remarks

I associate OMNH 26222 and 27413 in part on their provenance and large size, but mainly on their resemblance to jaws that I (see Chapter 6) attribute to Albanerpeton nexuosus, a large-bodied species that was widespread in the Western Interior during the Campanian and Maastrichtian. OMNH 26222 resembles referred premaxillae of A. nexuosus (Fox and Naylor, 1982:fig. 2d, e; here:Figs. 5-2C, 6-5A, B) in the following five derived character states: robust build; fused medially; and pars dorsalis relatively short, strongly sutured dorsally with nasal, and dorsal half of labial face covered with a prominent boss. The first four of these apomorphies are diagnostic for a subgeneric clade (see below, "Discussion" and Chapter 6) and support assigning OMNH 26222 to Albanerpeton. The fifth character state is important for assessing the specific identity of OMNH 26222, because elsewhere among albanerpetontids a similarly large boss is seen only in Campanian and Maastrichtian premaxillae of A. nexuosus. A second diagnostic premaxillary feature of A. nexuosus—tall flange on lingual edge of maxillary process—cannot be determined for OMNH 26222 because the specimen lacks the relevant part of the pars palatinum. OMNH 26222 differs from Campanian and Maastrichtian premaxillae of A. nexuosus in having a somewhat smaller foramen in the lateral face of the internal strut, more irregular ornament on the boss, and more elongate teeth; the taxonomic significance of these differences is unclear. Albanerpeton nexuosus is also diagnosed by two apomorphies of the dentary (see Estes, 1964:figs. 43e, 44c): teeth strongly heterodont anteriorly and dorsal margin of dental parapet strongly convex or angular dorsally in labial outline. Although seen in OMNH 27413, neither of these features is as pronounced as in unequivocal dentaries of A. nexuosus. As OMNH 26222 and 27413 cannot confidently be referred to A. nexuosus, I identify these jaws as pertaining to A. sp., cf. A. nexuosus. This conservative approach is also prudent because jaws from the Mussentuchit Member are about 15 million years (Gradstein et al., 1995) older than the oldest specimens of A. nexuosus from the early Campanian Milk River Formation of Alberta (Chapter 6).

ALBANERPETON CIFELLII Gardner, 1999b
(Fig. 5-3F, G)

"Albanerpeton species A" Gardner, 1999c:63.
"unnamed upper Turonian species" Gardner, 1999b:533.

Holotype—OMNH 25400, incomplete right premaxilla (Fig. 5-3F, G).

Holotype Horizon and Locality—Late Turonian; Smoky Hollow Member, Straight Cliffs Formation; OMNH V4, Garfield County, Utah, USA.

Etymology—After Richard L. Cifelli, whose collecting efforts in the Cretaceous of Utah resulted in discoveries of the albanerpetontid fossils reported in this paper.

Distribution—Known only from the holotype locality.

Diagnosis (from Gardner, 1999b)—Species of Albanerpeton most similar to A. galaktion and the new Judithian species in having premaxilla with suprapalatal pit triangular- to slit-like in lingual outline, but differs from these and all other congeners in having premaxilla with lingual face of pars dorsalis bearing a facet dorsomedially, the ventrolateral margin of which is formed by a dorsal expansion of the more lateral internal strut.

Description—OMNH 25400 (Fig. 5-3F, G), the holotype and only specimen, is an incomplete right premaxilla lacking the vomerine and maxillary processes on the pars palatinum and about the lateral quarter of the pars dentalis. The premaxilla is gracile in build and moderate in size, with a height of 2.07 mm. An elongate medial flange extends down the basal three-quarters of the pars dorsalis onto the dorsal part of the pars dentalis, indicating that OMNH 25400 was broadly sutured medially to its opposite in life. The pars dorsalis is relatively tall and narrow, with the height 1.95 times the width across the suprapalatal pit. Instead of a distinct lacrimal notch, the lateral margin of the pars dorsalis above the external narial margin is inclined medially at about 25° from the vertical and the lateral face is slightly roughened for contact with the lacrimal. The dorsal end of the pars dorsalis is essentially smooth. The labial face of the pars dentalis laterally preserves the anterior end of a facet that was overlain labially in life by an anteriorly directed process from the maxilla. Except for a few tiny external nutritive foramina, the remainder of the pars dentalis and about the lower two-thirds of the pars dorsalis are smooth. The dorsal third of the pars dorsalis bears a low, indistinct boss that is weakly ornamented with low ridges and shallow pits. This weakly developed boss may indicate that the holotype is not from a fully mature individual.

In lingual view, the suprapalatal pit is located in the lateral half of the pars dorsalis and low on the process, such that the floor of the pit is formed by the dorsal surface of the pars palatinum. The pit is moderate in absolute size (0.30 mm high; 0.21 mm wide) and occupies about seven percent of the lingual surface area of the pars dorsalis. The lingual outline of the pit approaches that of a dorsoventrally elongate, narrow, and right-angled triangle. The suprapalatal pit is bordered laterally by a mediolaterally narrow, but otherwise prominent internal strut that is perforated laterally by two tiny, sediment-infilled foramina. The strut expands lingually as it extends ventrolaterally down the pars dorsalis, and the base of the strut extends about half the distance lingually across the dorsal face of the pars palatinum. The strut extends dorsomedially up the lingual face of the pars dorsalis, well past the dorsal edge of the suprapalatal pit. At its dorsal end, the strut flares mediolaterally and is developed into a lingually raised rim that is concave ventrolaterally in lingual view. This rim forms the ventrolateral margin of a shallow, but prominent facet located more dorsomedially on the lingual face of the pars dorsalis.

Although broken medially and laterally, the pars palatinum preserves an intact palatal foramen. This foramen is elliptical in outline, with the long axis extending labiolingually, and is moderate in size—i.e., diameter of foramen along long axis subequal to diameter of the bases of the more medial teeth. The foramen opens dorsally into the floor of the suprapalatal pit and ventrally in the ventral surface of the pars palatinum, just lingual to the pars dentalis. The canal connecting these openings extends dorsoventrally through the pars palatinum. No other foramina perforate the pars palatinum. The pars dentalis is deep and perforated above the tooth row by several small foramina. The tooth row preserves the medial six tooth positions, consisting of two empty tooth slots and the bases of four highly pleurodont, gracile, and evidently elongate teeth. No tooth preserves a crown.

Remarks—OMNH 25400 is unique among albanerpetontid premaxillae that I have seen in having a dorsomedial facet, bordered ventrolaterally by the expanded dorsal end of the more lateral internal strut, on the lingual face of the pars dorsalis. This differs from the typical albanerpetontid condition, in which (1) the lingual face of the pars dorsalis is smooth dorsally and lacks a facet, (2) neither of the internal struts extends any appreciable distance dorsal to the suprapalatal pit, and (3) the dorsal end of each internal strut is unexpanded and instead grades into the lingual face of the pars dorsalis. In these premaxillae, the dorsal edge of the pars dorsalis is smooth or bears low ridges and knobs, indicating that the dorsal end of the process either abutted against, or sutured with, the anterior end of the nasal. The structure of OMNH 25400 is strikingly different and suggests a different pattern of contact with the nasal. Specifically, the anterior end of the nasal lingually underlapped the dorsal end of the premaxillary pars dorsalis, where it fit into the facet on the inner face of the process and was braced ventrolaterally by the expanded dorsal end of the internal strut. The unique structure of the pars dorsalis in OMNH 25400 and inferred pattern of contact with the nasal indicate that this late Turonian premaxilla represents a previously unrecognized species, for which I propose the name Albanerpeton cifellii.

Although diagnostic frontals are unknown for Albanerpeton cifellii, the species can be assigned to the type genus based on the triangular to slit-shaped suprapalatal pit. This character state is derived within the genus (Chapter 7) and occurs in two other North American congeners, A. galaktion and the new Judithian species (Figs. 6-4B, 6-7B, respectively). All other known albanerpetontids primitively retain an oval suprapalatal pit (Chapter 7).

Albanerpetontids exhibit various features—such as complex contacts between elements, extensive cranial ornament, and solidly constructed bones—that strengthened the skull for burrowing, feeding, or both (Estes and Hoffstetter, 1976; Fox and Naylor, 1982; Gardner, 1999c, 2000; here:Chapters 3, 8). The unique pattern of nasal-premaxillary contact inferred for Albanerpeton cifellii represents a novel strategy within the genus for reinforcing the snout, and one that evidently compensated for the more gracile build of the premaxilla and the taller, presumably weaker pars dorsalis.

Genus and Species Indeterminate

(Fig. 5-3H–M)

Horizons, Localities, and Voucher Specimens—Latest Albian–earliest Cenomanian horizons: Mussentuchit Member, Cedar Mountain Formation; six localities, Emery County, Utah: OMNH V235: OMNH 26958, maxilla; OMNH V239: OMNH 26210, jaw fragments; OMNH V240: OMNH 27094, dentary; OMNH V695: OMNH 27375, premaxilla; OMNH 26802, maxilla; OMNH 26738, 26739, 26803, 27378, 27409, dentaries; OMNH V696: OMNH 27019, dentary; OMNH V801: OMNH 27978–27980, premaxilla; OMNH 27973, maxilla; OMNH 27972, dentary. Late Turonian horizon: Smoky Hollow Member, Straight Cliffs Formation; two localities, Garfield County, Utah: OMNH V4: OMNH 25403, premaxillae; OMNH 25391, 25393, maxillae; OMNH 23706, 25397, 25399, dentaries; OMNH V60: OMNH 25880, premaxillae; OMNH 25875, 25878, 25881, 25882, maxillae; OMNH 24426, 24427, 25872–25874, 25884, 25885, 25916, dentaries; OMNH 25859, atlantal centrum. Early or middle Coniacian horizon: John Henry Member, Straight Cliffs Formation; OMNH V856, Garfield County, Utah: OMNH 31149, maxilla; OMNH 31148, indeterminate jaw fragment; OMNH 31091, fragmentary frontal.

Remarks—Specimens listed above are too fragmentary to be identified below the familial level. Most of the jaws from the Mussentuchit Member of the upper Cedar Mountain Formation are uninformative, beyond showing that albanerpetontids were relatively abundant in the region during the latest Albian and earliest Cenomanian. The three most nearly complete premaxillae (OMNH 27375, 27979, 27980) lack the dorsal part of the pars dorsalis, the more lateral part of the pars dentalis, and much of the pars palatinum. Judging by the broken base of the pars dorsalis on OMNH 27375 (Fig. 5-4H) and 27979, the process was probably taller than wide when complete. All three specimens primitively resemble premaxillae of *A. arthridion* (Figs. 4-2B, D, 4-3B) and non-*Albanerpeton* albanerpetontids in having the suprapalatal pit relatively small (width about 0.10 mm and 0.15 mm in OMNH 27980 and 27375, respectively), subcircular in lingual outline, and located well dorsal to the pars palatinum. OMNH 26738, the anterior part of a small, right dentary (Fig. 5-3I) preserves the base of a symphyseal prong and the anteriormost seven tooth positions, including three broken and four intact teeth. This dentary also exhibits character states (labial surface unornamented; dorsal edge of the dental parapet nearly straight in labial view; teeth only weakly heterodont anteriorly) that are primitive for albanerpetontids. The presence of both large and small jaws in the unit raises the possibility that these may be from different-sized individuals of the same species. I consider this unlikely, because the jaws differ in features (e.g., form of internal struts and relative size, shape, and position of suprapalatal pit in premaxilla; profile of dorsal edge of dental parapet on dentary) that do not vary ontogenetically in albanerpetontids, but do differ among species (Gardner, 2000; here:Chapter 2).

None of the jaws from the holotype locality (OMNH V4) of Albanerpeton cifellii, in the Smoky Hollow Member of the Straight Cliffs Formation, can be confidently referred to this species. The posterior end of a left maxilla (OMNH 25391; Fig. 5-3J) from OMNH V4 has teeth that are markedly stouter than those on the holotype premaxilla of A. cifellii, which suggests that the two specimens may not be from conspecific individuals. Of further interest is the fact that the maxilla preserves several replacement tooth crowns, evidently in situ—one such crown is just visible on the pars dentalis, above the base of the sixth tooth from the posterior end of the row. The most notable specimen from the second locality (OMNH V60) in the Smoky Hollow Member is an atlantal centrum (OMNH 25859; Fig. 5-3K). The specimen lacks an open notochordal pit and exhibits such characteristic albanerpetontid features as the tripartite facets in the posterior cotyle, a broad and dorsally concave odontoid process, and a pair of shallow, kidney-shaped anterior cotyles. Although the neural arch is broken, the base of the arch on both sides preserves a foramen for exit of the first spinal nerve. A fragmentary left frontal (OMNH 31091; Fig. 5-3L, M) from the overlying John Henry Member exhibits the characteristic slot for receipt of the prefrontal, polygonal dorsal ornament, and a prominent ventrolateral crest.

Albanerpetontids have also been reported in faunal lists for the late Cenomanian part of the Dakota Formation (Eaton et al., 1997; Kirkland et al., 1997:table 4) and the Turonian part of the Straight Cliffs Formation (Eaton et al., 1997), both from southwestern Utah. As the specimens in question are undescribed, unfigured, and I have not seen them, I cannot comment on these reports other than to note that the presence of albanerpetontid fossils in these units would not be surprising considering the specimens reported herein.

DISCUSSION

Prior to this report, the only confirmed records of Cenomanian albanerpetontids were of four indeterminate dentaries, one being the holotype of Nukusurus insuetus Nessov nomen dubium, from the early Cenomanian Khodzhakul Formation of Uzbekistan (Nessov, 1981, 1988, 1997; Gardner and Averianov, 1998). Latest Albian–earliest Cenomanian jaws reported here from the upper Cedar Mountain Formation pertain to two albanerpetontid species, one indeterminate below the familial level and the second identified as Albanerpeton sp., cf. A. nexuosus. These occurrences constitute the geologically oldest record of sympatry among albanerpetontids. Fragmentary premaxillae of the former species primitively resemble those of geologically older albanerpetontids in the relative size and position of the suprapalatal pit. By contrast, premaxillae of A. sp., cf. A. nexuosus and all geologically younger congeners are more derived in having the suprapalatal pit relatively larger and located lower on the pars dorsalis (see Fig. 5-2 and Chapter 7). The only documented stratigraphic overlap between these two kinds of premaxillae is in the Mussentuchit Member of the Cedar Mountain Formation. This implies that the transition from a primitive to a more derived premaxillary pattern in albanerpetontids and, hence, the origin of the post-middle Albian clade within Albanerpeton, occurred no later than the Early/Late Cretaceous boundary.

Albanerpeton sp., cf. A. nexuosus can provisionally be allied with A. nexuosus, the unnamed Paskapoo species, and A. inexpectatum Estes and Hoffstetter in the subgeneric robust-snouted clade (Fig. 5-2 and Chapter 7) on the strength of premaxillary synapomorphies (bone robust; premaxillae fused; pars dorsalis relatively short and strongly sutured dorsally with nasal) associated with strengthening the snout. A minimum date of latest Albian or earliest Cenomanian for the origin of this clade is provided by A. sp., cf. A. nexuosus.

Fossils from the Smoky Hollow Member of the Straight Cliffs Formation document the only confirmed occurrences of albanerpetontids from the Turonian stage. Besides representing a previously unrecognized species with an unusual pattern of premaxillary–nasal contact, Albanerpeton cifellii is notable for being the oldest Albanerpeton species having a triangular or slit-like suprapalatal pit in the premaxilla. This is a derived condition within the genus that unites A. cifellii, A. galaktion, and the new Judithian species in the gracile-snouted clade, which is the sister-group of the robust-snouted clade (Fig. 5-2 and Chapter 7). The gracile-snouted clade is known only from the Late Cretaceous of the North American Western Interior and A. cifellii provides a minimum age of late Turonian for the origin of the clade.

The two fragmentary jaws and incomplete frontal from the overlying John Henry Member of the Straight Cliffs Formation are uninformative, beyond showing that albanerpetontids remained in North American during the Coniacian. The only other albanerpetontid fossil reported from this stage is the fragmentary holotype dentary of Nukusurus sodalis Nessov nomen dubium from the Bissekty Formation of Uzbekistan (Nessov, 1997; Gardner and Averianov, 1998).

CONCLUSIONS

Fossils reported herein from the latest Albian to early or middle Coniacian of Utah help fill a gap of some 15 million years in the North American Cretaceous record of the Albanerpetontidae and provide the basis for the following observations:

(1) Jaws from the upper part of the Cedar Mountain Formation suggest that the Early/Late Cretaceous boundary marks (a) the last occurrence of albanerpetontids with a primitive non-Albanerpeton and A. arthridion level of premaxillary organization, (b) the first appearance of a more advanced level of premaxillary organization (suprapalatal pit larger and located lower on pars dorsalis) that diagnoses a subgeneric clade containing all Albanerpeton species except A. arthridion, and (c) the first appearance of the less inclusive Euramerican Late Cretaceous–Miocene robust-snouted clade.

(2) The recently recognized species Albanerpeton cifellii is named on a premaxilla exhibiting a unique pattern of articulation with the nasal, from the late Turonian part of the Straight Cliffs Formation. A. cifellii documents the first appearance of the gracile-snouted clade, a North American Late Cretaceous group that is the sister to the robust-snouted clade.

(3) While it is evident that the latest Early to middle Late Cretaceous was an important interval in the history of North American albanerpetontids, discoveries of contemporaneous fossils from elsewhere are needed to assess whether the evolutionary events I have postulated here were limited to the Western Interior or were part of a

geographically more widespread radiation of albanerpetontids.

FIGURE 5-1. Maps showing locations of North American latest Albian to Coniacian localities mentioned in the text. **A**, map of Utah showing positions of Emery and Garfield counties (blackened). **B**, map of Emery County showing distribution of Cedar Mountain Formation in outcrop (cross-hatched) and OMNH microsites (redrawn from Cifelli and Madsen, 1998:fig. 1). **C**, map of Garfield County showing distribution of Straight Cliffs Formation in outcrop (stippled; from Doelling, 1974) and OMNH microsites.

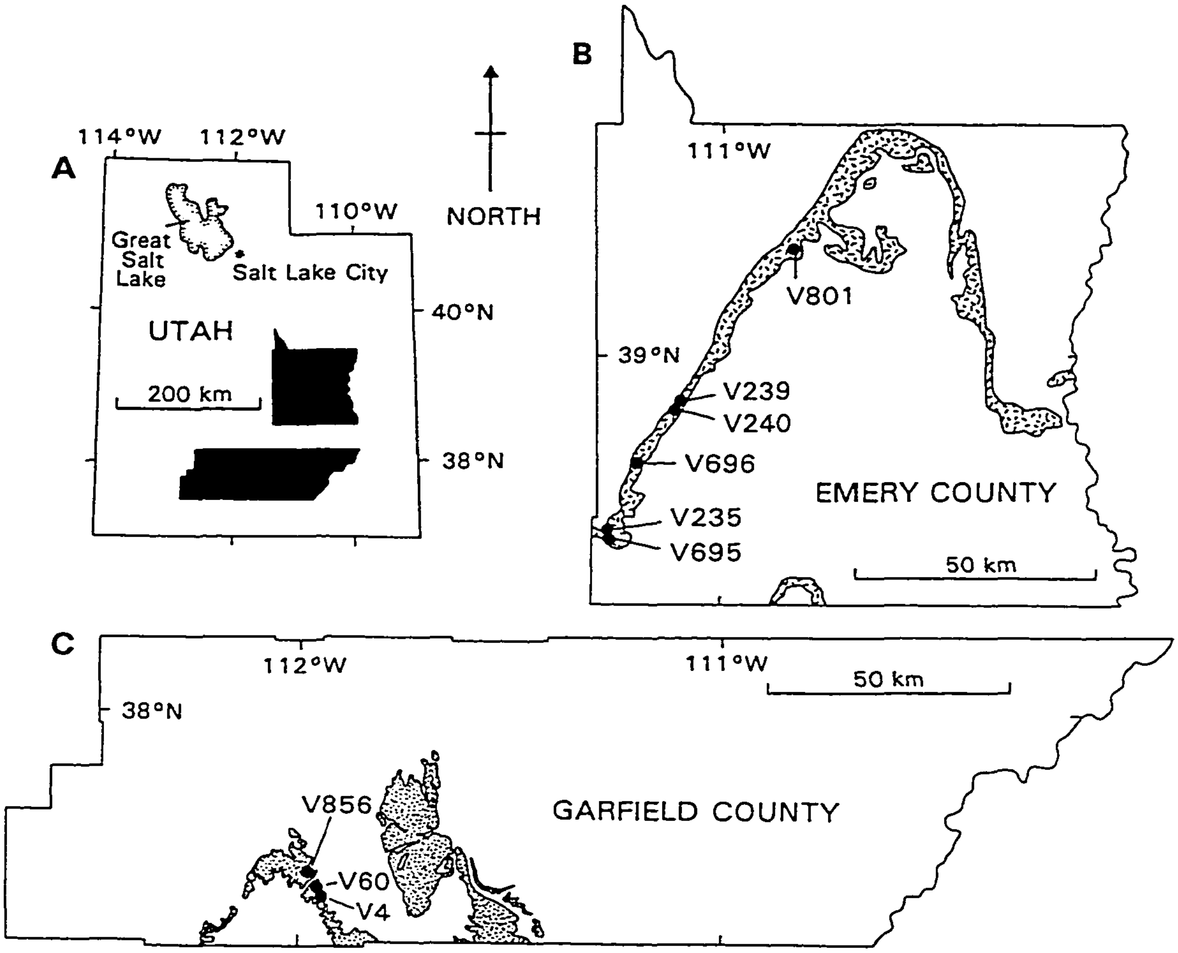

A
114°W
112°W
110°W
Great Salt Lake
Salt Lake City
UTAH
40°N
38°N
200 km
NORTH
B
111°W
39°N
V801
V239
V240
V696
V235
V695
EMERY COUNTY
50 km
C
112°W
111°W
38°N
50 km
V856
V60
V4
GARFIELD COUNTY

FIGURE 5-2. Reconstructed premaxillae, in lingual view, of select North American species of Albanerpeton superimposed on a simplified phylogeny to illustrate major patterns of premaxillary evolution in the genus (from Fig. 2-5). **A**, right premaxilla of A. arthridion Fox and Naylor, representative of the primitive albanerpetontid level of organization; based on FMNH PR805 (holotype) and FMNH PR2023 from the upper Antlers Formation (early–middle Albian), Texas. **B**, left premaxilla of A. galaktion Fox and Naylor, representative of the gracile-snouted clade; based on UALVP 16203 (holotype), 16204, and 16212 from the Milk River Formation (early Campanian), Alberta. **C**, fused premaxillae of A. nexuosus Estes, representative of the robust-snouted clade; based on UALVP 16206 and 39955 from the Milk River Formation (early Campanian), Alberta. Arrows point to suprapalatal pit. Specimens not to scale. See Chapter 7 for details of this phylogeny.

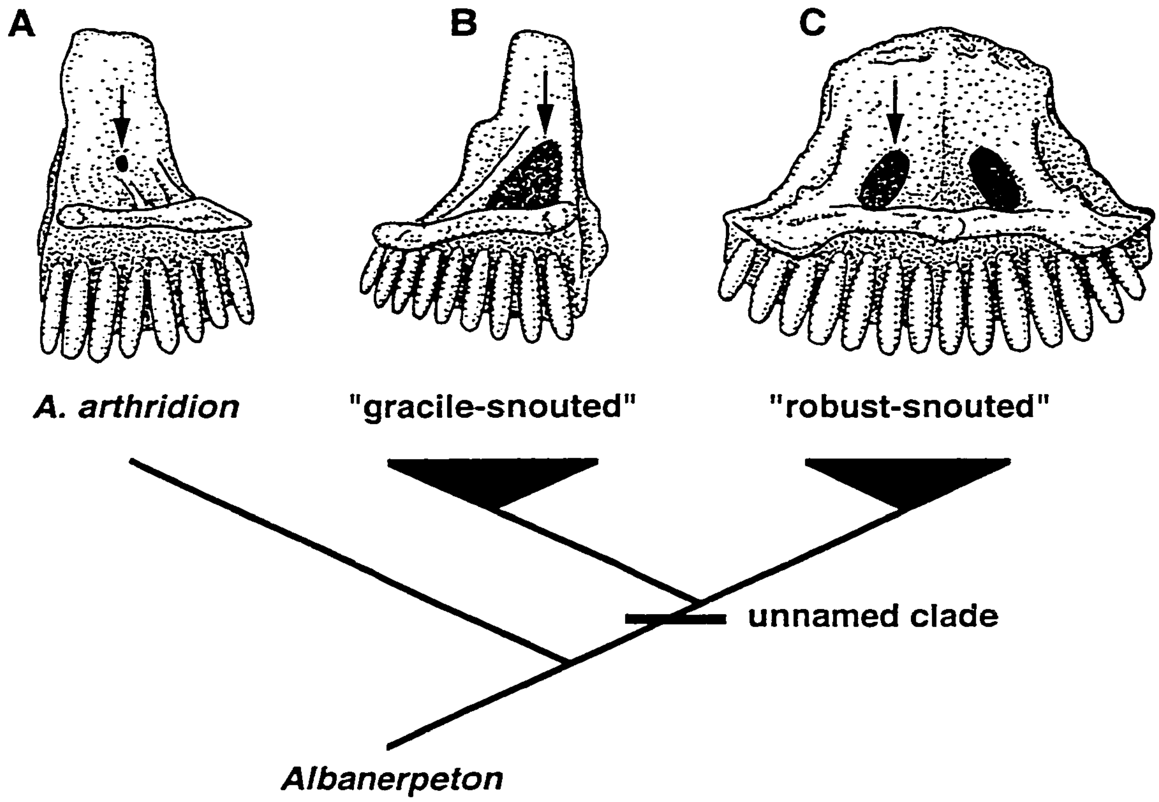
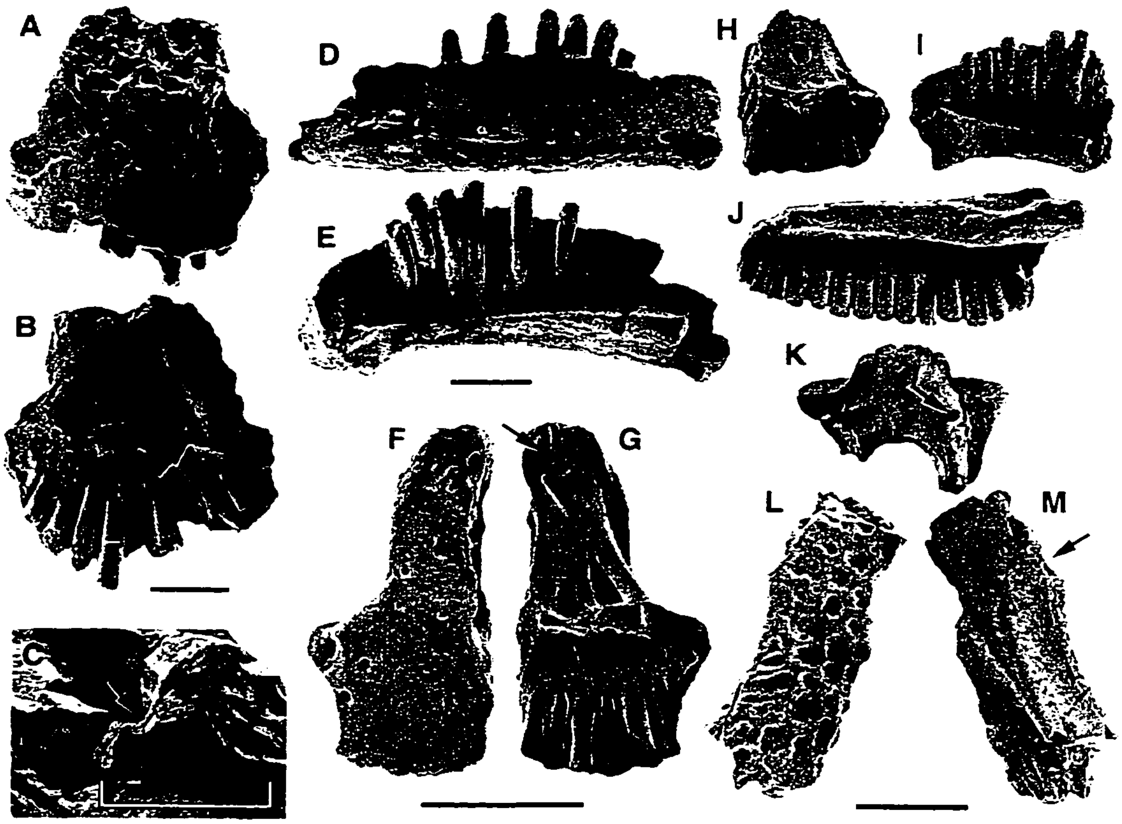

A
B
C
A. arthridion
"gracile-snouted"
"robust-snouted"
unnamed clade
Albanerpeton

FIGURE 5-3. Jaws of albanerpetontids; latest Albian–Coniacian, Utah. Albanerpeton sp., cf. A. nexuosus Estes (**A–E**): **A**, **B**, OMNH 26222, fused pair of incomplete premaxillae, in (**A**) labial and (**B**) lingual views, with arrow indicating canal exposed in broken face of pars palatinum between dorsal and ventral openings of palatal foramen; **C**, OMNH 26222, detail of right side in occlusolingual view, with arrow indicating canal exposed in broken face of pars palatinum between dorsal and ventral openings of palatal foramen; **D**, **E**, OMNH 27413, anterior end of right dentary, in (**D**) labial and (**E**) lingual and slightly dorsal views. Albanerpeton cifellii Gardner (**F**, **G**): OMNH 25400, holotype, right premaxilla, in (**F**) labial and (**G**) lingual views, with arrow indicating facet for receipt of anterior end of nasal. Albanerpetontid genus and species indeterminate (**H–M**): **H**, OMNH 27375, fragmentary right premaxilla, in lingual view; **I**, OMNH 26738, anterior end of right dentary, in lingual view; **J**, OMNH 25391, posterior half of left maxilla, in lingual view; **K**, OMNH 25859, atlantal centrum, in dorsal view, with arrow indicating medial opening of spinal foramen on right side; **L**, **M**, OMNH 31091, lateral part of left frontal, in (**L**) dorsal and (**M**) ventral views, with arrow indicating slot immediately anterior to orbital margin for receipt of dorsal end of prefrontal. Provenances: OMNH 26222, 26738, 27375, 27413, Mussentuchit Member (latest Albian–earliest Cenomanian), Cedar Mountain Formation; OMNH 25400, 25391, 25859, Smoky Hollow Member (late Turonian), Straight Cliffs Formation; OMNH 31091, John Henry Member (early or middle Coniacian), Straight Cliffs Formation. Specimens and figures at different scales: middle left (**A**, **B**), middle upper (**D**, **E**), bottom center (**F**, **G**), and bottom right (**H–M**) scale bars = 1 mm; bottom left (**C**) scale bar = 0.5 mm.


A
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C
D
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CHAPTER 6 — ALBANERPETONTIDS FROM THE CAMPANIAN AND MAASTRICHTIAN OF NORTH AMERICA[1]

INTRODUCTION

Sixteen non-marine formations of Campanian and Maastrichtian age (Fig. 6-1, Table 6-1) in the North American Western Interior have yielded albanerpetontid elements. Two species in the type genus Albanerpeton Estes and Hoffstetter have previously been identified from these horizons—A. nexuosus Estes and A. galaktion Fox and Naylor. Estes (1981) named the former species on a distinctive dentary from the late Maastrichtian (Lancian) Lance Formation of Wyoming and described the species based on the holotype dentary, 11 topotypic jaws (dentaries, maxillae, and premaxillae), and a topotypic femur. Estes (1964, 1969) had earlier referred these specimens to Prodesmodon copei Estes, a salamander named on a diagnostic atlas and known by additional atlantes and trunk vertebrae, all from the Lance Formation. On the strength of stratigraphical occurrences and morphology, Naylor (1979) convincingly argued that referred jaws of Prodesmodon Estes pertained instead to an Albanerpeton-like taxon, a genus then known only by the type species A. inexpectatum Estes and Hoffstetter from the Miocene of France. Estes (1981) agreed with Naylor's (1979) findings and accordingly erected the new species A. nexuosus to accommodate jaws and the femur originally referred to Prodesmodon. Estes (1981) also referred to A. nexuosus, without comment, additional specimens from the Hell Creek Formation (Lancian in age) of Montana, Judith River Formation of Montana and Oldman Formation of Alberta (both Judithian in age), and Milk River Formation (Aquilan in age) of Alberta. Fox and Naylor (1982) re-assigned albanerpetontid jaws, frontals, parietals, and atlantes from the Milk River Formation to their new species A. galaktion, which they named on a distinctive premaxilla.

No substantial new information has been presented for either species since their original descriptions. In the absence of additional material for Albanerpeton nexuosus,

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[1] A version of this chapter has been accepted for publication. Gardner. Geodiversitas. 22: XXX-XXX.

both the specific (McGowan, 1998a) and generic (Rage and Hossini, 2000) status of the species have been questioned. Although no further albanerpetontid material has been collected from the Milk River Formation, numerous undescribed specimens are available from over a half dozen localities—the 39 catalogued specimens listed by Fox and Naylor (1982) for A. galaktion sample only a fraction of the specimens available from the formation. An intriguing, but consistently overlooked, aspect of Fox and Naylor's (1982:124, 125) account for A. galaktion is their report of two distinctive premaxillary and dentary morphs. One of the dentary morphs closely resembles figured dentaries of A. nexuosus and this raises the possibility, as Fox and Naylor (1982) acknowledged, that more than one species may be represented. Both species clearly need to be re-examined, not only for the reasons noted above, but also because numerous albanerpetontid specimens and taxa have since been identified from North America and elsewhere.

Associations of elements for Albanerpeton galaktion and A. nexuosus have not previously been challenged and it is widely accepted that the species are stratigraphically separate, with the former restricted to the Aquilan and the latter to the Judithian–Lancian (Fox and Naylor, 1982; Breithaupt, 1982; Bryant, 1989; McGowan, 1998a; Duffaud and Rage, 1999; Rage and Hossini, 2000). I believe that some specimens originally referred to both species were incorrectly associated: Estes' (1981) topotypic collection for A. nexuosus includes dentaries of this species, indeterminate albanerpetontid dentaries and upper jaws, and a femur from an indeterminate salamander, whereas the large collection of albanerpetontid bones reported on by Fox and Naylor (1982) includes jaws and frontals of both A. galaktion and A. nexuosus, along with parietals and atlantes that cannot be referred to either species. Below I present evidence for re-associating jaws and frontals of the two species, then provide revised diagnoses and descriptions for each. Several collections from Judithian horizons in Alberta, Utah, and Texas include distinctive jaws and frontals that cannot be assigned to either A. galaktion or A. nexuosus, and I accordingly describe these specimens as belonging to a new Judithian species of Albanerpeton. I also document notable instances of indeterminate and mis-identified specimens, then finish by examining the biogeography and sympatry of Campanian and Maastrichtian albanerpetontids in the Western Interior.

IDENTIFICATION AND ASSOCIATION OF JAWS AND FRONTALS OF ALBANERPETON NEXUOSUS AND A. GALAKTION

As articulated skeletons are not available for Albanerpeton nexuosus or A. galaktion, evidence for associating isolated elements of these species instead relies on morphology, provenance (Table 6-1), and frequencies. Specimens from the Milk River Formation in the collection of the UALVP are critical for this purpose, because two distinctive morphs are evident among the dentaries, maxillae, premaxillae, and frontals. These morphs differ in characters that typically vary at the specific level among other albanerpetontids (Gardner, 2000; here:Chapter 2) and this argues for the presence of two species in the formation. A. galaktion and A. nexuosus are the most likely candidates, because the collection includes the distinctive holotype premaxilla of the former species and dentaries that cannot be differentiated from the figured holotype (Estes, 1964:fig. 44c) of the latter. Associating elements of the two species is complicated by three factors. First, the holotypes of A. nexuosus and A. galaktion are not directly comparable because the respective specimens are a dentary and a premaxilla. Second, most of the topotypic specimens for A. nexuosus, including the holotype and all figured specimens, are missing and presumed lost (P. Holroyd, pers. comm. 1996). Consequently, any consideration of this important reference collection relies on Estes' (1964, 1981) published descriptions and figures and on examination of the surviving topotypic dentaries. Third, compared to the situation in the Milk River Formation, albanerpetontids are less well represented in collections from younger Cretaceous horizons in the Western Interior. The sparse Edmontonian and Lancian records consist almost exclusively of incomplete jaws. Evidence for identifying and associating jaws and frontals of Albanerpeton nexuosus and A. galaktion is presented below.

Dentaries (Fig. 6-2)—Estes' figure (1964:fig. 44c; redrawn here in Fig. 2-4P) of the now lost Lancian holotype dentary (UCMP 49547) of Albanerpeton nexuosus shows that teeth about one-third of the distance from the anterior end of the tooth row are markedly larger relative to nearby teeth and that the dorsal edge of the dental parapet is sinuous in lingual outline, with the apex highest adjacent to the longest teeth. These features are also evident in Estes' (1964:fig. 43e) figure of another lost topotypic dentary

(UCMP 49538) and can be seen firsthand in two of the surviving topotypic dentaries: UCMP 49540 (Fig. 6-2A, B) and 49535 (Fig. 6-2C). Both features are unique within the genus and, thus, are reliably diagnostic for A. nexuosus. A further 48 non-topotypic dentaries from another seven formations of Aquilan-Lancian age in the Western Interior exhibit these diagnostic character states (Fig. 6-2D-I) and can also be referred to A. nexuosus. These dentaries, particularly larger ones, are also relatively robust in construction. Among these newly referred dentaries are specimens from the Milk River Formation that conform to the second of the two dentary morphs originally described by Fox and Naylor (1982:125) for A. galaktion. Referred dentaries of A. nexuosus from the Milk River Formation (Fig. 6-2G-I) come from individuals of different body sizes, yet all specimens have similarly heterodont teeth and a dorsally convex dental parapet. This indicates that the diagnostic character states of the dentary for A. nexuosus are neither ontogenetic nor sexually dimorphic, because such characters tend to become more pronounced with growth.

Other dentaries from the Milk River Formation are less robust, relative to comparable sized dentaries of Albanerpeton nexuosus, and retain the inferred primitive albanerpetontid pattern of having the more anterior teeth at best only weakly heterodont in size and the dorsal edge of the dental parapet essentially horizontal or shallowly convex dorsally in labial outline (Fig. 6-2J-M). These conform to Fox and Naylor's (1982) first dentary morph for Albanerpeton galaktion and, by default, are best retained in this species. As dentaries of A. galaktion lack any apomorphies or distinctive combinations of features, I have not been able to confidently identify examples of these from other formations. In the collection from the Milk River Formation, dentaries of A. nexuosus are more than twice as abundant as those of A. galaktion (n = 30 and 12, respectively).

None of Estes' (1981) remaining four topotypic dentaries can be referred with confidence to Albanerpeton nexuosus. UCMP 49533 and 49539 (the latter number was also assigned by Estes [1964] to a topotypic maxilla) are lost and have neither been figured nor described, whereas an incomplete right dentary (UCMP 49534; unfigured here) lacks the diagnostically informative anterior part of the bone. UCMP 49536 (unfigured here) is the anterior one-half of a right dentary that cannot be referred to A. nexuosus because the teeth are weakly heterodont anteriorly and the dorsal edge of the dental parapet is essentially straight in labial outline. These four topotypic dentaries are thus best attributed to an indeterminate albanerpetontid genus and species. UCMP 49536 is important for showing that more than one albanerpetontid species is represented at the holotype locality of A. nexuosus, a point that is relevant below when considering the identities of the four topotypic upper jaws from the same locality.

Maxilla (Fig. 6-3)—Because the dentary and maxilla work in concert, the structure of one can be predicted with some confidence from the other. Based on the holotype and referred dentaries of Albanerpeton nexuosus, the maxilla in this species can be expected to exhibit three complementary features: teeth strongly heterodont anteriorly; ventral edge of pars dentalis sinuous in labial or lingual outline; and robust build. The two topotypic maxillae (UCMP 49539 and 55775) of A. nexuosus are lost. Judging by Estes' figure (1964:fig. 43d) of the former specimen and his descriptions (1964, 1981) of both, the maxilla lacks the expected strongly heterodont teeth and convex ventral edge of the pars dentalis, nor does it appear to have been particularly robust. I thus consider it unlikely that these maxillae pertain to A. nexuosus. As no other taxonomically informative features are evident from Estes' published accounts (1964, 1981), these maxillae are better regarded as pertaining to an indeterminate albanerpetontid genus and species.

Maxillae having the predicted structure for Albanerpeton nexuosus and, thus, referrable to the species are known from elsewhere in the Lance Formation and three Campanian formations (Fig. 6-3A–H), including the Milk River Formation. Other maxillae from the Milk River Formation lack the morphology predicted for A. nexuosus. These specimens instead are more gracile in build and primitively retain weakly heterodont teeth and a nearly horizontal ventral edge on the pars dentalis (Fig. 6-3I–N). These features complement those in dentaries that I here refer to A. galaktion and argue for assigning the second kind of maxilla in the formation to the same species. Referred maxillae of A. nexuosus and A. galaktion differ further in the proportions and outline of the premaxillary lateral process: relatively short, with length ≈ height at base, and obtuse in lingual or labial outline in A. nexuosus, versus relatively longer and more spatulate in outline in A. galaktion. In the collection from the Milk River Formation, maxillae of A. nexuosus ($n = 12$) are about twice as common as those of A. galaktion ($n = 7$). I have not identified maxillae of A. galaktion from outside of the Milk River Formation.

Premaxilla (Figs. 6-4, 6-5; Tables 6-2, 6-3)—Fox and Naylor (1982) named

Albanerpeton galaktion on a nearly complete left premaxilla (UALVP 16203; Fig. 6-4A, B) and referred ten catalogued premaxillae from the Milk River Formation to the species. Fox and Naylor (1982:124) noted that the collection included two distinctive kinds of premaxillae, but because they were unsure of the significance of this variation they conservatively attributed all specimens to A. galaktion. These authors' first premaxillary morph (Fig. 6-4) differs from the second (Fig. 6-5) as follows: build relatively gracile (versus more robust); consistently paired (versus variably fused medially); pars dorsalis relatively tall (versus shorter); dorsal edge of pars dorsalis at best weakly sutured with nasal (versus strongly sutured); boss covers about dorsal one-quarter to one-third of pars dorsalis and ornamented with anastomosing ridges and grooves (versus boss covers about dorsal one-half of process and ornamented with polygonal pits enclosed by ridges); suprapalatal pit relatively large and triangular in outline (versus relatively smaller and oval); internal strut present medial to suprapalatal pit (versus strut absent); internal strut lateral to suprapalatal pit lingually deep, mediolaterally narrow, and perforated laterally by numerous tiny foramina (versus lingually shallower, mediolaterally broader, and perforated by one or a few larger foramina); dorsal flange on lingual edge of maxillary process a shallow ridge separate from base of lateral internal strut (versus flange markedly taller and continuous labiomedially with ridge from base of lateral internal strut); and palatal foramen relatively large (versus relatively smaller). There is no substantial variation in these features within each morph nor overlap between the two morphs. With the benefit of having examined more comparative material than was available to Fox and Naylor (1982), it is evident to me that the two premaxillary morphs cannot readily be accommodated within one species. As the first morph includes the holotype of A. galaktion, I retain this and other premaxillae more similar to it in A. galaktion and refer premaxillae in the second morph to A. nexuosus. In the collection from the Milk River Formation, premaxillae of A. nexuosus are about twice as common as those of A. galaktion (n = 26 versus 12). Premaxillae of A. galaktion and A. nexuosus can be associated with their respective maxillae and dentaries based on relative frequencies in the collection from the Milk River Formation and build. Upper jaws in each species can further be associated by the proportions and outline of the premaxillary lateral process on the maxilla and the complementary facet on the premaxilla. Premaxillae of both species have also been identified from Judithian and Lancian horizons in the Western Interior.

The identities of the two topotypic premaxillae (UCMP 55779 and 55780) reported by Estes (1981) for Albanerpeton nexuosus are uncertain, as both are lost and the published accounts (Estes 1964, 1981) are not particularly informative. Estes' figures (1964:fig. 43a–c) of UCMP 55779 suggest that this specimen is relatively gracile, more so than I would expect based on his figures (1964:figs. 43e, 44c) of topotypic dentaries of A. nexuosus. Until these premaxillae are relocated they, like the topotypic maxillae, should be regarded as pertaining to an indeterminate genus and species of albanerpetontid.

Frontals (Fig. 6-6)—Frontals are uncommon in Upper Cretaceous deposits in the Western Interior and, until recently, none had been identified for Albanerpeton nexuosus. The UALVP collection from the Milk River Formation includes a modest number of frontals and two morphs can be recognized by differences in the form of the internasal process and ventrolateral crest. The first morph (Fig. 6-6A–E) differs from the second (Fig. 6-6F–K) in having the internasal process relatively narrow and acuminate or spike-like in dorsal outline (versus relatively broader and acute) and, more subtly, in having the ventrolateral crest relatively broad and shallow, with the ventral face more concave dorsally (versus relatively narrower and deeper, with the ventral face nearly flat). As I have not identified any reliable morphological criteria for associating frontals and jaws of albanerpetontids, I associate these elements based on relative frequencies. In the collection of the UALVP from the Milk River Formation, jaws of A. nexuosus (n = 68) are about twice as numerous as those of A. galaktion (n = 31). A similar pattern exists between the two kinds of frontals (15 as compared to nine) and on this basis I attribute the first and second frontal morphs to, respectively, A. nexuosus and A. galaktion. I have not identified frontals of either species outside of the Milk River Formation.

SYSTEMATIC PALEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order ALLOCAUDATA Fox and Naylor, 1982
Family ALBANERPETONTIDAE Fox and Naylor, 1982
Genus ALBANERPETON Estes and Hoffstetter, 1976

Remarks—The three species considered below are known by jaws and frontals. Each species can be assigned to Albanerpeton based on diagnostic frontal character states listed in Chapter 2—most notably frontals relatively short, triangular in dorsal or ventral outline, with internasal process pointed anteriorly and having lateral groove for contact with nasal. Elsewhere (Fig. 2-2) I presented reconstructions of the frontals for each congener. Membership within Albanerpeton is further supported by character states that are synapomorphic for less inclusive clades in the genus. Each species has two premaxillary character states—suprapalatal pit low on pars dorsalis and occupying four percent or more of lingual area of pars dorsalis—that are unique among albanerpetontids to a clade within Albanerpeton consisting of all congeners, except the basal species A. arthridion Fox and Naylor (chapters 2, 4, and 7). Additional synapomorphies, listed in the relevant accounts below, further nest each species in either the less inclusive robust- or gracile-snouted sister-clades.

ALBANERPETON NEXUOSUS Estes, 1981

(Figs. 6-2A–I, 6-3A–H, 6-5, 6-6A–E; Tables 6-2, 6-3)

Prodesmodon copei Estes, 1964:88–96, figs. 43, 44 [in part: referred jaws and femur subsequently assigned by Estes (1981) to Albanerpeton nexuosus].

"Albanerpeton n.sp. A Estes" Fox and Naylor, 1982:120.

"Albanerpeton sp. A" Fox and Naylor, 1982:table 1.

Albanerpeton galaktion Fox and Naylor, 1982:121–127, figs. 2d, e, 3d, e [in part: nine referred, catalogued jaws here transferred to A. nexuosus].

Albanerpeton ?nexuosus (Estes) McGowan, 1998a:191.

?Albanerpeton nexuosus (Estes) Rage and Hossini, 2000.

Holotype—UCMP 49547, nearly complete left dentary lacking posterior end and having about 24 teeth and four empty tooth slots (Estes, 1964:fig. 44a, c). The holotype is missing and presumed lost (P. Holroyd, pers. comm. 1996).

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Lance Formation; UCMP V-5620, Niobrara County, Wyoming, USA.

Referred Specimens—Deadhorse Coulee Member, Milk River Formation, seven localities, Alberta: UALVP MR-2: UALVP 40007, dentary; UALVP MR-4: UALVP 39953, 39954, premaxillae; UALVP 40000, 40001, 40008, dentaries; UALVP 39994, frontals; UALVP MR-6: UALVP 39955–39959, premaxillae; UALVP 16209, 39971, fused premaxillae; UALVP 16239, 39973-39975, maxillae; UALVP 16220, 39998, 39999, 40003–40006, 40009–40011, 40015–40021, 40032, dentaries; UALVP 39984, 39987, 39989–39993, 39996, frontals; UALVP MR-8: UALVP 16253, premaxillae; UALVP MR-9: UALVP 16254, 39960, premaxillae; UALVP 39997, dentaries; UALVP MR-12: UALVP 16207, 16208, premaxillae; UALVP 39961, fused premaxillae; UALVP 39976, 39977, maxillae; UALVP 39983, 39988, 43812, frontals; UALVP MR-20: UALVP 39962–39970, premaxillae; UALVP 16206, 39972, fused premaxillae; UALVP 16242, 39978–39982, maxillae; UALVP 16237, 16238, 40002, 40012–40014, 40022, dentaries; UALVP 39985, 39986, 39995, frontals. Oldman Formation, two localities, Alberta: TMP L0406: TMP 95.177.15, dentary; TMP L1127: TMP 96.78.152, dentary. Kaiparowits Formation, two localities, Utah: OMNH V6: OMNH 60245, maxilla; OMNH V61: OMNH 23964, dentary. Aguja Formation, OMNH V58/TMM 43057, Texas: OMNH 25345, 60238, premaxillae; OMNH 60239, maxilla; OMNH 25235, 25238, 60240, 60241, 60243, 60244, dentaries. Upper Fruitland Formation or lower Kirtland Formation, KUVP NM-37, New Mexico: KUVP 129739, dentary. Hell Creek Formation, Bug Creek Anthills, Montana: UALVP 40035, dentary. Lance Formation, three localities, Wyoming: UCMP V-5620 (holotype locality): UCMP 49535, 49538 (now lost), 49540 dentaries; UCMP V-5711: AMNH 15259, 22950, 22951, 22955, 22959, 27177, dentaries; UW V-79032: UW 14587, maxilla; UW 14584, 15019, dentary. Laramie Formation, UCM locality 77062, Colorado: UCM 38713, premaxilla; UCM 38714, dentary.

Distribution (Table 6-1)—Campanian and Maastrichtian, North American Western Interior: early Campanian (Aquilan): Deadhorse Coulee Member, Milk River Formation, Alberta; middle Campanian (Judithian): Oldman Formation, Alberta; Kaiparowits Formation, Utah; and Aguja Formation, Texas; late Campanian–early Maastrichtian (Edmontonian): upper Fruitland Formation or lower Kirtland Formation, New Mexico; late Maastrichtian (Lancian): Hell Creek Formation, Montana; Lance Formation, Wyoming, and Laramie Formation, Colorado.

Revised Diagnosis—Large-bodied species of Albanerpeton differing from congeners in the following autapomorphies: boss on premaxilla covers about dorsal one-half of pars dorsalis; premaxillary ornament consists of polygonal pits enclosed by a ridges arranged in a reticulate pattern; dorsal flange on lingual edge of maxillary process on premaxilla prominently expanded dorsally and continuous labially with base of lateral internal strut; teeth on maxilla and dentary strongly heterodont in size anteriorly; and occlusal margins of pars dentalis on maxilla and dental parapet on dentary sinuous in labial outline, with apex adjacent to longest teeth. Most closely resembles A. inexpectatum and unnamed Paleocene species, but differs from other congeners, in the following synapomorphies: premaxilla robustly constructed, variably fused medially, with pars dorsalis short and strongly sutured dorsally with nasal; maxilla with relatively short premaxillary lateral process; and frontals with internasal process relatively narrow and acuminate or spike-like in dorsal or ventral outline. Primitively differs from A. inexpectatum in having maxilla and dentary unornamented labially, dentary lacking dorsal process behind tooth row, and fused frontals relatively narrower in dorsal outline, with ventrolateral crest relatively narrower and ventral face less concave dorsally; from unnamed Paleocene species in having premaxilla with prominent vomerine process and inferred larger body size; and from both species in having premaxilla with boss present and ornament limited dorsally on pars dorsalis and in having maxilla with anterior end of tooth row in front of leading edge of nasal process.

Description

Of the 13 topotypic specimens attributed by Estes (1981) to Albanerpeton nexuosus, only the holotype (UCMP 49547) and three referred dentaries (UCMP 49535, 49538, and 49540) can be assigned with any confidence to the species. The remaining topotypic jaws (four dentaries, two maxillae, and two premaxillae) are not identifiable below the familial level, as noted above, whereas the topotypic femur belongs to an indeterminate salamander (see "Remarks," below). Jaws and frontals from elsewhere in the Western Interior can be referred to the species. Many of these non-topotypic specimens come from the Milk River Formation and include nine jaws (UALVP 16206–16209, premaxillae; UALVP 16239, 16242, maxillae; 16220, 16237, 16238, dentaries) previously listed by Fox and Naylor (1982:121) for A. galaktion. Unless stated otherwise, descriptions below are composites.

Premaxilla (Fig. 6-5; Tables 6-2, 6-3)—Twenty-six specimens are available from the Milk River Formation and these adequately document the structure of the premaxilla. The bone is robustly constructed and the largest specimen, an isolated premaxilla (UALVP 16207; not figured), is about 3.5 mm high. Five pairs of premaxillae, including UALVP 16206 (Fig. 6-5A–C), are solidly fused along the midline. Each fused pair retains a faint median line of fusion lingually and UALVP 16209 (Fox and Naylor, 1982:fig. 2e) also preserves an incomplete line of fusion labially. Other premaxillae are isolated, but because the medial flange is broken on many of these specimens it is uncertain, as Fox and Naylor (1982) noted, whether the premaxillae in life were sutured medially (i.e., paired) or lightly fused and fell apart after death. UALVP 39955 (Fig. 6-5D, E) preserves a nearly complete medial flange that is medially narrow and extends down the medial edge of the bone along the lower two-thirds of the pars dorsalis onto the upper one-half of the pars dentalis. Sizes of fused and unfused premaxillae overlap considerably, more so than in Albanerpeton inexpectatum (Chapter 3). This implies that if premaxillae also fused ontogenetically in A. nexuosus, the timing of fusion was more variable. The pars dorsalis is moderately low and broad (Tables 6-2, 6-3). The dorsal edge of the process bears prominent ridges and grooves, indicating it was strongly sutured with the nasal. The lacrimal notch is typically deep and wide, but these dimensions vary considerably (cf., Fig. 6-5B, D) in both absolute and relative terms (Tables 6-2, 6-3), independent of size. The notch is narrowest in the two pairs of fused premaxillae (UALVP 16206 and 16209) that preserve an intact pars dorsalis. Labially, the pars dentalis and the lower one-half of the pars dorsalis are perforated by small, scattered, external nutritive foramina. The dorsal one-half of the pars dorsalis is covered by a prominent, raised boss set off from the rest of the process by a thick ventral rim. The boss is best developed on UALVP 16206 (Fig. 6-5A). On this specimen, the boss is continuous across the two halves of the fused premaxillae. The external face of the boss is flattened and prominently ornamented with narrow ridges that are arranged in a reticulate pattern and enclose broad, flat-bottomed, polygonal pits. Given that essentially identical pits on the dorsal surface of albanerpetontid frontals and parietals each housed a dermal ossicle (McGowan and Evans, 1995), it is probable that each of the pits on the premaxillary boss in A. nexuosus also contained an ossicle.

In lingual view, the suprapalatal pit opens about midway across the pars dorsalis and is located low on the pars dorsalis (Fig. 6-5B, D), with the ventral edge of the lingual opening of the pit continuous with, or slightly dorsal to, the dorsal face of the pars palatinum. Specimens broken across the pars dorsalis (Fig. 6-5H) show that the floor of the pit is formed by the pars palatinum. The suprapalatal pit is ovoid to elliptical in lingual outline and moderate in size (Table 6-2), accounting for 0.09–0.13 (n = 8) of the lingual surface area of the pars dorsalis. Only one internal strut is present, lateral to the suprapalatal pit. This strut is perforated laterally by one large and, often, one or two smaller foramina (Fig. 6-5E), all opening medially inside the suprapalatal pit. The strut is mediolaterally broad and expands lingually as it descends down the lingual face of the pars dorsalis. The base of the strut continues linguolaterally across the dorsal surface of the pars palatinum as a low, rounded ridge that grades into the unnamed dorsal process (see below) on the posterior edge of the maxillary process.

The pars palatinum is expanded lingually (Fig. 6-5C, F, G) and bears prominent vomerine and maxillary processes with shallow, lingual facets for contact with one or more palatal bones. Medial edges of the vomerine processes are solidly fused in the five fused pairs of premaxillae (Fig. 6-5C, F); by contrast, these processes are at best only weakly fused in azygous premaxillae of Albanerpeton inexpectatum. The unnamed dorsal process, mentioned above, on the lingual edge of the maxillary process is prominently developed into a raised, labiolingually-compressed flange that is dorsally convex in lingual outline. The unnamed process on the ventral surface of the maxillary process is low, ventrally convex, and varies from a drumlin-shaped knob (e.g., UALVP 16206; Fig. 6-5C) to a short ridge (e.g., UALVP 39971; Fig. 6-5F). The palatal foramen (Fig. 6-5F, H:arrow 1) is small, with a diameter no more than three-quarters the diameter of the medial teeth and usually considerably less. The canal connecting the dorsal and ventral openings of the palatal foramen extends dorsoventrally through the pars palatinum. The foramen opens ventrally in the pars palatinum in line with the third to fourth tooth positions, just lingual to the junction with the pars dentalis, and dorsally in the pars palatinum at, or slightly inside, the opening of the suprapalatal pit. One or two smaller unnamed foramina (Fig. 6-5G, H:arrow 2) penetrate the bone well labial to the palatal foramen, ventrally in the junction between the pars palatinum and pars dentalis and dorsally in the floor of the suprapalatal pit. Differentiating foramina in the ventral surface of the pars palatinum can be difficult in specimens in which the ventral opening of the palatal foramen is unusually small and close to the labial limit of the pars palatinum. This is especially true for UALVP 16206 (Fig. 6-5C), a specimen for which I have not been able to reliably identify the ventral opening of the palatal foramen on either the left or right side. Tiny foramina may perforate the lingual face of the pars dentalis above the tooth bases.

Three incomplete left premaxillae, two (OMNH 25345 and 60238; Fig. 6-5I, J, respectively) from the Aguja Formation and one (UCM 38713; Fig. 6-5K) from the Laramie Formation can be referred to Albanerpeton nexuosus based on resemblances to specimens from the Milk River Formation. These geologically younger specimens provide no further details about premaxillary structure in the species.

Maxilla (Fig. 6-3A–H)—None of the 12 specimens from the Milk River Formation and one specimen each from the Aguja, Kaiparowits, and Lance formations are complete, but collectively they document most of the structure of the maxilla except for the posterior end. The most nearly complete specimen is UALVP 16242 (Fig. 6-3A, B), a right maxilla broken posteriorly behind the sixteenth tooth position and anteriorly across the premaxillary lateral process and anterior edge of the premaxillary dorsal process. The largest specimen, UALVP 39973 (Fig. 6-3C), is about 5.3 mm long and would have been slightly longer than 6 mm when complete. The bone is unornamented labially, except for small external nutritive foramina scattered across the anterior one-third (Fig. 6-3A, D, E). As in other albanerpetontids, the nasal process is triangular in labial outline and the pars facialis is low, becoming shallower posterior from the nasal process. The ventral edge of the pars dentalis is sinuous in labial outline, being ventrally convex and deepest labial to the longest teeth (Fig. 6-3A, D). Damage to the ventral edge of the pars dentalis in some specimens (e.g., UALVP 39973; Fig. 6-3C) creates the impression that this edge is more nearly straight. The anterior end of the tooth row lies several loci anterior to the point of maximum indentation along the leading edge of the nasal process.

The premaxillary process is anteriorly short (length subequal to height at base) and obtuse in lingual outline, with a nearly truncate to slightly rounded anterior margin (cf., Fig. 6-3E versus F, G). The lingual surface of the process on larger specimens is roughened for contact with the complementary facet on the premaxilla. The premaxillary dorsal process is broad (Fig. 6-3H) and ventrally bears a transverse ridge, best developed on larger maxillae (Fig. 6-3F), that in life abutted against the posterior edge of the maxillary process on the premaxilla. The pars palatinum is broad lingually, tapers towards its posterior end, and dorsally bears a raised, saddle-like bony patch for contact with the base of the lacrimal and a trough more lingually for contact with one or more unknown palatal bones. The internal narial margin spans four or five tooth positions.

Dentary (Fig. 6-2A–I)—Fifty-two dentaries are available from seven formations, but none of these are as nearly complete as the two figured and now lost topotypic dentaries (UCMP 49547 and 49538). Published figures show that the holotype (UCMP 49547; Estes, 1964:fig. 44a, c) was a nearly complete left dentary that lacked only the posteriormost part of the area for attachment of the postdentary bones, whereas UCMP 49538 (Estes, 1964:figs. 43e, 44b) was a less nearly complete right dentary broken immediately behind the posterior end of the tooth row. One of the surviving topotypic jaws, a right mandible (UCMP 49540; Fig. 6-2A, B), consists of the anterior tip of the angular in articulation with an incomplete dentary. Although the latter bone in UCMP 49540 lacks the distal end of the symphyseal prong, much of the area for attachment of the postdentary bones, and the posteriormost end of the tooth row, it remains the most nearly complete dentary currently available for Albanerpeton nexuosus. Several dentaries, including UCM 38714 (Fig. 6-2D, E) are from slightly larger individuals and I estimate a maximum dentary length of about 10 mm for the species. The dentary is robustly constructed, even in small specimens. The dentary is unornamented labially and a row of rarely more than six external nutritive foramina extends along the anterior one- to two-thirds of the bone. The ventral scar and ridge for attachment of the intermandibularis muscles are prominently developed, particularly on larger dentaries. In contrast to the typical albanerpetontid condition, the dorsal edge of the dental parapet is sinuous in labial or lingual outline: the parapet is highest about one-third of the distance along the tooth row from the anterior end, lingual to the tallest teeth, and descends anteriorward and posteriorward from this region. Adjacent to the highest teeth, the dorsal edge of the parapet varies from dorsally convex to angular in labial or lingual outline. Smaller dentaries also exhibit this sinuous pattern (Fig. 6-2C, F, G). Dentaries from the Milk River Formation suggest that the profile of the dorsal edge of the parapet changed from convex to angular with growth (cf., Fig. 6-2G, H). This pattern may not hold true for geologically younger individuals, because the dorsal edge of the dental parapet is already angular in outline on the two smallest dentaries (UCMP 49535 and TMP 96.78.152; Fig. 6-2C, F, respectively) from elsewhere. No dorsal process is present behind the tooth row (Fig. 6-2I). The symphyseal eminence is prominently developed and one or two symphyseal prongs occur on either the left or right dentary. The remainder of the lingual structure is typical for albanerpetontids in having the subdental shelf shallow and gutter-like anteriorly, becoming deeper anteriorly, the Meckelian canal closed posteriorly, and a broad area of attachment posteriorly for the postdentary bones.

Dentition (Figs. 6-2A–I, 6-3A–G, 6-5A–G, I–K)—As in all albanerpetontids, the marginal teeth are straight, highly pleurodont, non-pedicellate, and have labiolingually compressed, chisel-like, and faintly tricuspid crowns. Teeth on different jaws range from short, robust, and widely spaced to more elongate, gracile, and closely spaced (cf., Fig. 6-5B, D). This variation occurs independent of the size or geological age of jaws. Premaxillae with a complete tooth row have eight (n = 4) or nine (n = 5) loci. No maxilla available to me has an intact tooth row: UALVP 39973 (Fig. 6-3C) and 39977 (Fig. 6-3E) preserve the anterior 17 and 18 tooth positions, respectively, and I estimate that each bone probably held about 25 loci when complete. Figures of UCMP 49538 (Estes, 1964:fig. 43e) and 49547 (Estes, 1964:fig. 44c) indicate that these now lost topotypic dentaries had complete tooth rows with, respectively, about 24 and 28 tooth positions. Of the dentaries at hand, UCMP 49540 has the most nearly complete tooth row, with the anterior 23 loci preserved. Unlike other congeners, teeth are markedly heterodont in size anteriorly on the maxilla and dentary. Teeth are longest about one-third of the distance along the tooth row, typically at the fourth to sixth loci on the maxilla and the sixth to ninth loci on the dentary. As this markedly heterodont pattern occurs in small dentaries (Fig. 6-2C, F) it can be expected in small maxillae as well, although no examples of the latter are known. Ample evidence for tooth replacement occurs in the form of tooth slots for replacement teeth, a lingual resorption pit in the base of the occasional tooth, and, in rare specimens, a replacement crown in situ within a tooth slot.

Frontals (Fig. 6-6A–E)—Frontals have not previously been described for Albanerpeton nexuosus. Here I refer to the species 15 incomplete specimens from the Milk River Formation. The two most nearly complete of these are UALVP 39996 and

39983. UALVP 39996 (Fig. 6-6A, B) is a crushed pair of frontals that is missing the distal ends of the internasal and anterolateral processes, the posterior end of the ventrolateral crest on both sides, and much of the posterior edge of the frontal roof. The specimen is about 5 mm in preserved midline length and was probably nearly 6 mm long when the bone was complete. UALVP 39983 (Fig. 6-6C) is the anterior three-fifths of an uncrushed pair of frontals from an individual of about the same size. Several specimens (e.g., UALVP 39989 and 39987; Fig. 6-6D, E, respectively) were from larger individuals and I estimate that when complete these frontals approached 7 mm in midline length. Frontals are solidly fused along the midline, triangular in dorsal or ventral outline, and longer than wide. The ratio of midline length to width across the posterior edge between the lateral edges of the ventrolateral crests is about 1.25 in UALVP 39996, as preserved, but would have been less when the bone was complete. The internasal process, preserved on four specimens and complete on two of these (UALVP 39983 and 43812), is slightly longer than wide and acuminate or spike-like in dorsal outline. The groove along the lateral face of the process for contact with the nasal, the two pairs of slots for receipt of the nasal and prefrontal, and the anterolateral processes are all well developed. The dorsal and ventral edges of the more posterior slot for receipt of the prefrontal are moderately excavated medially. Posterior from the base of the anterolateral process, the lateral wall of the frontal diverges at about 20° from the midline and the orbital margin is shallowly concave in dorsal or ventral outline. UALVP 39989 (Fig. 6-6D) shows that the posterior edge of the frontal roof is nearly transverse and was sutured posteriorly in life with the paired parietals.

Frontals dorsally bear the typical albanerpetontid ornament of broad polygonal pits enclosed by low, narrow ridges. The pits are moderately deep on most specimens, but on several frontals the pits are so shallow they are difficult to see except under low-angled light (Fig. 6-6C). This variation occurs independent of frontal size, indicating it is not ontogenetic in origin. The well-preserved processes on UALVP 39983 argue against the indistinct dorsal ornament on this specimen being an artifact of weathering or abrasion.

In ventral view, the ventrolateral crest is broad—i.e., width of crest immediately behind slot for receipt of prefrontal is about 1.2 mm in UALVP 39987 (Fig. 6-6E)—but the crest is absolutely and relatively narrower than on comparable-sized frontals of Albanerpeton inexpectatum (Fig. 3-2L). The crest is low and triangular in transverse view, being deepest medially and becoming shallower towards the lateral margin. The ventral surface faces ventrolaterally and is shallowly concave in the orbital region, again less so than in frontals of A. inexpectatum. As in other albanerpetontids, the posterior end of the ventrolateral crest extends past the posterior end of the frontals and would have underlapped the parietal in life.

Remarks

Diagnostic Features and Affinities of Albanerpeton nexuosus—Estes (1981) and Rage and Hossini (2000) relied on four features to differentiate Albanerpeton nexuosus from other albanerpetontids. A closed notochordal pit in the atlas (Estes, 1981) can be dismissed as a diagnostic character state because atlantes are not available for A. nexuosus. Among albanerpetontids as a whole, a closed notochordal pit is probably derived, but this condition is widespread and occurs in all known atlantal specimens (e.g., Estes and Hoffstetter, 1976; Estes and Sanchíz, 1982; Fox and Naylor, 1982; McGowan, 1996; McGowan and Ensom, 1997; Gardner, 1999a, b, c, in press, this study), save for an indeterminate atlas (Seiffert, 1969:fig. 1D) from the early Bathonian of France. The claim that A. nexuosus differs from A. inexpectatum "in lacking a large palatal shelf [= pars palatinum, here] of the premaxilla and maxilla" (Estes, 1981:24; see also Rage and Hossini, 2000) is difficult to evaluate because the four topotypic upper jaws Estes (1981) attributed to A. nexuosus are unavailable and his figures (Estes, 1964:fig. 43a–d) do not depict these bones in an informative view. Estes (1981) may have misinterpreted the structure of these jaws, as he (Estes, 1981:20) did when he identified a similarly weak pars palatinum on an Albian premaxilla then referred to the salamander Prosiren elinorae Goin and Auffenberg, but now designated as the holotype of A. arthridion (Fox and Naylor, 1982). In fact, the pars palatinum on the Albian specimen is broken and largely missing (Fox and Naylor, 1982; Gardner, 1999b; here:Chapter 4). Regardless, as I argued above, Estes' (1981) four topotypic upper jaws cannot reliably be assigned to A. nexuosus. Upper jaws that I refer to A. nexuosus have a pars palatinum that is as well developed (i.e., lingually broad; vomerine and maxillary process on premaxilla prominent) as in other albanerpetontid species. The third feature, lack of a dorsal process behind the dentary tooth row (Estes, 1981; Rage and Hossini, 2000), is not particularly diagnostic for A. nexuosus because the process is primitively absent in all albanerpetontids, except A. inexpectatum. The final feature, maxillary and dentary teeth strongly heterodont in size (Estes, 1981; Rage and Hossini, 2000), is indeed diagnostic for A. nexuosus and is discussed below.

Albanerpeton nexuosus is readily diagnosed by five autapomorphies of the jaws. The first three of these are unique among albanerpetontids to A. nexuosus, whereas the last two are unique within the genus: (1) boss on labial face of premaxilla covers about dorsal one-half of pars dorsalis (if present, boss primitively covers dorsal one-quarter to one-third of pars dorsalis); (2) premaxillary ornament consists of a regular arrangement of polygonal pits and ridges (ornament primitively consists of irregular pits, grooves, and ridges); (3) dorsal process on lingual edge of maxillary process on premaxilla a tall flange, continuous labiomedially with ridge that extends across dorsal face of pars palatinum to base of lateral internal strut (dorsal process primitively a low ridge and isolated from base of internal strut); (4) occlusal edge of pars dentalis on maxilla and dental parapet on dentary sinuous in labial outline, with apex strongly convex or angular and adjacent to longest teeth (margin primitively straight or shallowly convex); and (5) teeth on maxilla and dentary strongly heterodont in size, with longest teeth located about one-third of the distance from anterior end of tooth row and up to one-quarter again as long as nearby teeth (teeth primitively weakly heterodont in size).

Albanerpeton nexuosus is allied with A. inexpectatum and the unnamed Paskapoo species in the robust-snouted clade by the following synapomorphies: premaxillae robust, variably fused, with pars dorsalis short and strongly sutured dorsally with nasal; premaxillary lateral process on maxilla short; and internasal process on frontals narrow and spike-like. In diagnosing a clade within Albanerpeton, these synapomorphies further support assigning A. nexuosus to the type genus. Elsewhere, I (Gardner, 1999a; here:Chapters 2, 7) suggested that many of the synapomorphies of the robust-snouted clade strengthened the snout for burrowing, feeding, or some combination of these. Premaxillary autapomorphies of A. nexuosus probably further strengthened the snout for these activities. The most obvious explanation for the enlarged maxillary and dentary teeth in A. nexuosus is for subduing larger or more resilient prey. These enlarged teeth may also have been used to bite and injure opponents during intra- and interspecific fights, as has been documented for some extant salamanders (see review by Mathis et al., 1997), particularly plethodontids (e.g., Jaeger and Forester, 1993; Staub, 1993). The sinuous labial profiles of the occlusal edges of the maxilla and dentary in A. nexuosus are a direct consequence of the pars dentalis and dental parapet being deepest adjacent to the longest teeth, in order to adequately buttress these teeth labially.

Problematic Reports of Albanerpeton nexuosus and Mis-identified Specimens—Estes (1981) assigned a topotypic femur (UCMP 55782) to Albanerpeton nexuosus largely because he could not attribute the specimen to any known Lancian caudate. Although UCMP 55782 is lost, Estes' descriptions (1964, 1981) and figures (1964:fig. 44d, e) show that the specimen differs substantially from unequivocal albanerpetontid femora (cf., Estes and Hoffstetter, 1976:pl. 9, fig. 5; McGowan and Evans, 1995:fig. 1a, c) in being relatively shorter and more stout and in having the trochanter shorter and positioned more proximally. UCMP 55782 compares more favorably in these features with salamander femora (e.g., see Francis, 1934:pl. 5, figs. 31–33) and should be regarded as such.

The identities of most of the non-topotypic jaws from the Lance, Hell Creek, Oldman, and Judith River formations that Estes (1981:24) referred to Albanerpeton nexuosus cannot be confirmed because he provided no figures, descriptions, or catalogue numbers for voucher specimens. Estes' (1981:24) references to specimens from Montana reported by Estes et al. (1969) and Sahni (1972) refer to, respectively, trunk vertebrae (MCZ 3652) of Prodesmodon from the Hell Creek Formation and indeterminate albanerpetontid dentaries (AMNH 8479 and 8480) from the type area of the Judith River Formation. Specimens available to me and listed here confirm that A. nexuosus occurs in the Lance, Hell Creek, and Oldman formations. Although I have not been able to establish the presence of A. nexuosus in the Judith River Formation, considering the widespread distribution of the species and that indeterminate albanerpetontid dentaries have already been collected from the formation, I predict the species will eventually be identified in the unit.

Breithaupt (1982:133) referred a dozen jaws (UW 14582–14588, 14591, 14592 [incorrectly listed as UW 14542], 14593, 15030, 15031) from the Lance Formation (UW V-79032, Wyoming) to Albanerpeton nexuosus. Just two of these can be referred to the species: an incomplete dentary (UW 14584) and maxilla (UW 14582; misidentified as a dentary by Breithaupt [1982]). Of the remaining specimens, UW 14593 is a fragmentary premaxilla of A. galaktion, UW 15031 is the anterior end of a lizard dentary, and the other eight are fragmentary, indeterminate albanerpetontid jaws.

Standhardt (1986) reported Albanerpeton nexuosus in the Aguja Formation of Texas on the strength of a fragmentary right maxilla (LSUMG V-1371) from LSUMG VL-113 and subsequently recorded the species in a faunal list (Langston et al., 1989:19) for the formation. Her figures (Standhardt, 1986:fig. 29) confirm that LSUMG V-1371 is an albanerpetontid maxilla, but the specimen cannot be identified to genus or species.

Bryant (1989:31) recorded Albanerpeton nexuosus in the Hell Creek Formation based on two dentaries (UCMP 130683) from UCMP V-75162, in McCone County, Montana. Neither of the specimens in question is from an albanerpetontid: the first is an incomplete frog maxilla, whereas the second is an incomplete salamander dentary.

Most recently, Eaton et al. (1999:table 5) reported Albanerpeton sp., cf. A. nexuosus in a faunal list for the Kaiparowits Formation, Utah. I cannot comment on this identification because no description or illustrations were provided and no voucher specimens were listed. Nevertheless, jaws reported here verify that albanerpetontids are abundant in the Kaiparowits Formation and that A. nexuosus, A. galaktion, and the new Judithian species are all represented.

ALBANERPETON GALAKTION Fox and Naylor, 1982
(Figs. 6-2J–M, 6-3I–N, 6-4, 6-6F–K; Tables 6-2, 6-3)

Albanerpeton nexuosus Estes, 1981:24 [in part: referred jaws from the Milk River Formation].

Holotype—UALVP 16203, nearly complete left premaxilla missing maxillary process and dorsomedial end of pars dorsalis, and having five complete and three broken teeth (Fox and Naylor, 1982:figs. 1a, b, 2a–c; here:Fig. 6-4A, B).

Holotype Horizon and Locality—Early Campanian (Aquilan); Deadhorse Coulee Member, Milk River Formation; UALVP MR-6, Verdigris Coulee, Alberta, Canada.

Referred Specimens—Deadhorse Coulee Member, Milk River Formation, eight localities, Alberta: UALVP MR-2: UALVP 16218, dentary; UALVP MR-4: UALVP 16255, maxilla; UALVP 39940, 39941, dentaries; UALVP 39950, frontals; UALVP MR-

6: UALVP 16210–16212, 39930, 39934, premaxillae; UALVP 16240, 39935, 39936, maxillae; UALVP 16219, 16236, 39939, 39942, dentaries; UALVP 16216, 39946, 39948, 39949, 39951, 39952, frontals; UALVP MR-8: UALVP 39931, premaxilla; UALVP MR-9A: UALVP 39932, premaxilla; UALVP MR-9B: UALVP 16217, dentary; UALVP MR-12: UALVP 16221, dentary; UALVP 39945, frontals; UALVP MR-20: UALVP 16204, 16205, 16213, 39933, premaxillae; UALVP 16241, 39937, 39938, maxillae; UALVP 16222, 39943, 39944, dentaries; UALVP 39947, frontals. Oldman Formation, five localities, Alberta: TMP L0406: TMP 95.177.81, premaxilla; TMP L1127: TMP 96.78.186, premaxilla; TMP L1128: TMP 96.78.118, 96.78.184, premaxillae; TMP L1131: TMP 96.78.122, premaxilla; TMP L1137: TMP 96.78.124, premaxilla. Kaiparowits Formation, OMNH V6, Utah: OMNH 60326, premaxilla. Lance Formation, UW V-79032, Wyoming: UW 14593, premaxilla.

Distribution (Table 6-1)—Campanian and Maastrichtian, North American Western Interior: early Campanian (Aquilan): Deadhorse Coulee Member, Milk River Formation, Alberta; middle Campanian (Judithian): Oldman Formation, Alberta, and Kaiparowits Formation, Utah; late Maastrichtian (Lancian): Lance Formation, Wyoming.

Revised Diagnosis—Large-bodied species of Albanerpeton differing from all other albanerpetontid species in two premaxillary autapomorphies: lingual opening of suprapalatal pit occupying about one-fifth to one-quarter lingual surface area of pars dorsalis and palatal foramen diameter greater than one and one-third diameter of medial teeth. Differs further from most congeners, but resembles A. cifellii and the new Judithian species in one premaxillary synapomorphy: suprapalatal pit triangular to slit-shaped in lingual outline. Primitively differs from A. cifellii in having premaxilla with lingual face of pars dorsalis lacking facet and dorsally expanded lateral internal strut for contact with nasal and from the new Judithian species in having maxilla with anterior end of tooth row lying well anterior to leading edge of nasal process.

Description

Albanerpeton galaktion is best known from the Milk River Formation and my descriptions below rely largely on specimens from this unit in the collection of the UALVP. Of the 39 catalogued specimens listed by Fox and Naylor (1982:121) for A.

galaktion, I retain the holotype premaxilla and 15 referred specimens (UALVP 16204, 16205, 16210–16213, premaxillae; 16240, 16241, maxillae; UALVP 16217–16219, 16221, 16222, 16236, dentaries; UALVP 16216, frontals) in the species. Other catalogued jaws listed by Fox and Naylor (1982) belong to A. nexuosus (see previous account), whereas parietals and atlantes from the formation cannot reliably be assigned to either species and, accordingly, are considered under the account for "Genus and Species indeterminate." Other jaws and frontals from the Milk River Formation and eight premaxillae from Judithian and Lancian units are also referrable to A. galaktion. Descriptions below are composites, unless stated otherwise.

Premaxilla (Fig. 6-4; Tables 6-2, 6-3)—Twenty premaxillae are available. The two most nearly complete specimens are the holotype UALVP 16203 (Fig. 6-4A, B) and UALVP 16204 (Fig. 6-4C, D). The latter is also the largest specimen, with a height of nearly 3.4 mm. Although the largest available premaxillae of Albanerpeton galaktion and A. nexuosus are comparable in size, in the former species the bone is more gracile in build, the pars dorsalis is relatively taller and narrower (Table 6-3), and the dorsal end of the pars dorsalis is smoother, indicating that the process was less strongly sutured in life with the nasal. All premaxillae at hand for A. galaktion are isolated and none shows evidence of having been fused medially in life with its opposite. The medial flange on the holotype is medially broad and dorsoventrally short, being restricted along the medial edge of the bone to the upper one-half of the pars dentalis and basalmost part of the pars dorsalis; however, on many referred premaxillae the flange is narrower and extends further dorsally up the medial edge of the pars dorsalis. The lacrimal notch typically is deep, but varies considerably in width (Tables 6-2, 6-3). Labially, the upper one-quarter to one-third of the pars dorsalis bears an indistinct boss, best developed on UALVP 16204 (Fig. 6-4C) and TMP 95.177.81 (Fig. 6-4E), that is weakly ornamented with low, anastomosing ridges and shallow, irregular pits. The remainder of the labial surface is smooth, except for scattered, small external nutritive foramina. Although not visible in Figure 6-4E, specimens such as TMP 95.177.81 show that some of the foramina perforate the pars dorsalis to open medially inside the suprapalatal pit.

The lingual face of the pars dorsalis is dominated by a cavernous suprapalatal pit that approaches the shape of a right-angled triangle in lingual outline (Fig. 6-4B, D, G).

The suprapalatal pit is large in both absolute (Table 6-2) and relative terms, occupying slightly more than one-fifth (0.21–0.23; n = 4) of the lingual surface area of the pars dorsalis. This enlarged pit extends across the medial two-thirds to three-quarters of the pars dorsalis and is located low on the process, with the ventral floor of the pit formed by the dorsal surface of the pars palatinum. Specimens broken across the pars dorsalis reveal that the tooth pulp cavities open dorsally into the floor of the pit. The medial and lateral walls of the suprapalatal pit are each formed by a mediolaterally narrow, but lingually deep and prominent internal strut. Each strut arises adjacent to the dorsal margin of the suprapalatal pit and expands lingually as it extends down the inner face of the pars dorsalis. The base of each strut extends about one-half of the distance lingually across the dorsal face of the pars palatinum. The lateral face of the more lateral strut is perforated by up to ten tiny foramina (Fig. 6-4F) that open inside the suprapalatal pit.

Preserved intact on UALVP 16212 (Fig. 6-4G, H) and TMP 96.78.124 (Fig. 6-4I), the pars palatinum is lingually broad and bears prominent vomerine and maxillary processes, both of which are indented lingually by shallow facets for contact with one or more palatal bones. The unnamed dorsal and ventral processes adjacent to the lingual edge of the maxillary process are each weakly developed—the former is a low ridge, isolated from the lateral internal strut, and the latter is a low, drumlin-shaped knob. The palatal foramen is remarkably large in absolute and relative terms, with a diameter about one and one-third to two times greater than the diameter of the bases of the medial teeth. The palatal foramen opens dorsally into the floor of the suprapalatal pit and ventrally about one-half the distance lingually across the pars palatinum, in line with the second to fourth loci. The canal connecting the dorsal and ventral openings of the foramen extends dorsoventrally through the pars palatinum. A tiny, unnamed foramen typically penetrates the bone ventrally at the junction between the pars palatinum and pars dentalis to open dorsally in the floor of the suprapalatal pit. In most premaxillae, this unnamed foramen is lateral to the palatal foramen, but in two specimens (UALVP 16210 and 39932, both unfigured) the unnamed foramen is medial to the palatal foramen.

Maxilla (Fig. 6-3I–N)—The two most nearly complete of the seven specimens at hand from the Milk River Formation are UALVP 16240 (Fig. 6-3I–K) and 16241 (Fig. 6-3L–N). These overlap in the region of about the second to fifteenth tooth positions, document essentially all of the structure of the element, and are from comparable-sized individuals. The former specimen is about 4 mm long as preserved and the bone was probably about 5 mm long when complete. A less nearly complete specimen, UALVP 39935 (not figured), was from an individual about one-fifth again as large as those represented by UALVP 16240 and 16241. The labial surface is unsculpted, except for several small external nutritive foramina scattered across the anterior one-third of the bone. In labial view, the nasal process is triangular in outline and the pars facialis becomes shallower posteriorly. UALVP 16241 preserves most of the posterior end of the bone, which labially bears a shallow, anteroposteriorly elongate facet for articulation with the jugal. The ventral edge of the pars dentalis is straight to shallowly convex ventrally. The anterior end of the tooth row extends several loci anterior to the point of maximum emargination along the leading edge of the nasal process.

The premaxillary lateral process is longer than its height at the base and somewhat spatulate in labial or lingual outline, with the ventral edge strongly convex ventrally. The premaxillary dorsal process is a broad flange, with a low ventral ridge extending transversely across the posterior limit of the process. The pars palatinum is broad lingually, narrows towards the posterior end of the bone, and bears a raised patch dorsally for contact with the base of the lacrimal and a shallow trough dorsolingually for articulation with one or more unknown palatal bones. The internal narial margin spans seven or eight tooth positions.

Dentary (Fig. 6-2J–M)—Twelve incomplete dentaries from the Milk River Formation can be referred to the species. The two most nearly complete specimens, UALVP 16221 (Fig. 6-2J) and 16217 (Fig. 6-2K–M), are each broken posteriorly between the anterior edge of the opening for the Meckelian canal and the posterior end of the tooth row. UALVP 16221 is from a small individual and exhibits features typical of dentaries from smaller individuals, such as a more gracile build, a poorly developed ventral scar for attachment of the intermandibularis muscles, and a relatively low dental parapet that extends only up the ventral one-half of the tooth pedicels. UALVP 16217 is from a larger individual and the bone would have been nearly 10 mm long when complete. Although comparable in size to the largest available dentaries of *Albanerpeton nexuosus*, UALVP 16217 is less robust in build. Each of the referred dentaries of *A. galaktion* is unornamented and bears a short row of external nutritive foramina along about the anterior one-third of the bone. The dorsal edge of the dental parapet is straight in labial outline. The presence or absence of a dorsal process behind the tooth row cannot be determined, because no specimen at hand preserves this part of the bone. The symphyseal eminence is prominently developed, particularly on large dentaries. Nine specimens preserve intact symphyseal prongs and show that one or two prongs occur with about equal frequencies on either the left or right dentary. The remainder of the lingual structure of the dentary is unremarkable.

Dentition (Figs. 6-2J–M, 6-3I, J, L, M, 6-4)—Marginal teeth exhibit the characteristic albanerpetontid pattern of attachment and construction: highly pleurodont, non-pedicellate, with labiolingually compressed, chisel-like, and faintly tricuspid crowns. Of the eight premaxillae with a complete tooth row, six have eight tooth positions and one each has seven and ten positions. The maxilla with the most nearly complete tooth row, UALVP 16241 (Fig. 6-3M), preserves the posterior 21 loci and likely had no more than 25 tooth positions when complete. The two figured dentaries each have a nearly complete tooth row: UALVP 16217 preserves the first 26 tooth positions and probably had a further four to six teeth when complete, whereas UALVP 16221 retains 17 intact teeth and spaces for about 12–14 more teeth. Maxillary and dentary teeth are weakly heterodont in size anteriorly, with the longest teeth only slightly longer than nearby teeth. The longest teeth occupy about the fifth position on the maxilla and the sixth to tenth positions on the dentary. The relative sizes of teeth at the eighth and ninth positions on UALVP 16217 (Fig. 6-2L) are exaggerated by the presence of shorter replacement teeth at adjacent tooth positions. Most jaws have at least one empty tooth slot and one premaxilla (TMP 96.78.124; Fig. 6-4I) has a nearly functional replacement tooth at the fourth locus from the medial edge.

Frontals (Fig. 6-6F-K)—Nine azygous pairs of frontals are available from the Milk River Formation. UALVP 16216 (Fig. 6-6F, G), the most nearly complete specimen, is missing most of the anterior end (contra McGowan, 1998a), including the internasal and anterolateral processes, and the posterior end of both ventrolateral crests. This specimen is about 3.8 mm long as preserved and the bone was probably about 4.4 mm long in midline length when complete. UALVP 39946 (Fig. 6-6H) consists of the anterior part of a pair of fused frontals, broken obliquely between the slots for receipt of the prefrontals, and was from an individual about 1.5 times larger than that represented by UALVP 16216. Frontals are solidly fused along the midline, regardless of size.

UALVP 16216 shows that the fused frontals are triangular in outline and moderately elongate, with ratio of midline length to width across posterior edge between lateral edges of ventrolateral crests about 1.12, as preserved, and probably no more than about 1.2 when the bone was complete. UALVP 39946 demonstrates that the internasal and anterolateral processes and the more anterior slot for receipt of the nasal are well developed. The internasal process is acute and relatively broad (i.e., length subequal to width across the base) in dorsal outline and laterally has the groove for contact with the nasal. UALVP 16216, 39945 (Fig. 6-6I, J), and 39951 (Fig. 6-6K) collectively show that the lateral edge of the bone behind the anterolateral process diverges at about 20-25° from the midline, the dorsal and ventral margins of the more posterior slot for receipt of the prefrontal are emarginated medially, the orbital margin is shallowly concave, and the posterior edge of the frontal roof is shallowly concave to either side of the midline.

Frontals dorsally bear the usual albanerpetontid ornament of broad, polygonal pits enclosed by low ridges. As in Albanerpeton nexuosus, this ornament varies independent of overall frontal size and is more prominent on some specimens than others (cf., Fig. 6-6F, H, I).

The ventrolateral crest is moderately wide and triangular in transverse view. The crest widens with growth: width of crest behind slot for receipt of prefrontal increases from 0.65-0.71 mm and ratio of crest width to width across posterior edge of frontals between medial face of crests increases from 0.25-0.40 (n = 3). The transverse profile of the crest also changes with growth as the bevelled ventral face broadens, assumes a more ventrolateral orientation, and becomes flatter or, at most, shallowly concave on the largest specimens (cf., Fig. 6-6G, J, K, respectively). The remainder of the ventral structure of the frontals is unremarkable, with one notable exception. UALVP 16216 is unique among albanerpetontid frontals in having one large foramen opening at the midline between the anterior ends of the ventrolateral crests. This anomalous condition differs from the typical albanerpetontid pattern (see Fig. 6-8C), in which a smaller foramen opens to either side of the midline in the ventral face of the anterior part of the ventrolateral crest.

Remarks

In addition to the diagnostic frontal characters, assignment of Albanerpeton galaktion to Albanerpeton is further supported by the triangular lingual outline of the suprapalatal pit. A triangular to slit-shaped suprapalatal pit is unique among albanerpetontids to A. galaktion, A. cifellii, and the new Judithian species, and allies these species in the less inclusive gracile-snouted clade (Gardner, 1999c; here:Chapter 7).

Fox and Naylor (1982:121) diagnosed Albanerpeton galaktion using five features of the jaws. Their first feature—"deep, large pit behind pars facialis"—refers to the enlarged suprapalatal pit; this feature occurs in all premaxillae that I attribute to A. galaktion and is reliably diagnostic for the species (see below). None of the other four features are as diagnostically useful. Lack of labial ornament on the more ventral part of the premaxillae is a symplesiomorphy of albanerpetontids that differentiates A. galaktion only from the two Tertiary congeners, both of which have ornament covering the labial face of the pars dorsalis in large individuals. Fox and Naylor's (1982:121) statement that Albanerpeton galaktion is diagnosed by "enlarged teeth in anterior part of dentary and maxillary" is based on specimens from the Milk River Formation that I attribute to A. nexuosus. Maxillae and dentaries that I refer to A. galaktion have teeth that are weakly heterodont in size anteriorly. The latter pattern is not particularly diagnostic, because it is primitive for the genus and differentiates A. galaktion only from A. nexuosus. Neither a short medial flange nor a prominent lacrimal notch (= "medial ridge" and "indentation for prefrontal," respectively, of Fox and Naylor, 1982) are diagnostically useful for albanerpetontids, because the proportions of both structures vary more within and overlap more among species than Fox and Naylor (1982) suspected (see also Gardner, 1999b; here:Chapters 2, 4).

McGowan (1998a) recently presented a revised diagnosis for Albanerpeton galaktion based on four frontal characters. In formulating his diagnosis, McGowan (1998a) relied entirely on photographs (Fox and Naylor, 1982:fig. 1d, e) of the referred frontals UALVP 16216 (Fig. 6-6F, G). McGowan (1998a) believed UALVP 16216 was relatively complete, at least anteriorly. In fact, the specimen is broken between the slots for receipt of the prefrontals (= "lacrimal facets" of McGowan, 1998a) and lacks about the anterior one-quarter of the bone. UALVP 16216 thus provides no information about the form of the internasal process (= "anterior process" of McGowan, 1998a). The surface that McGowan (1998a) regarded as the outline of the internasal process is actually the broken leading edge of the specimen (Gardner, in press; here:Chapter 2). UALVP 39946 (Fig. 6-6H) shows that the internasal process is acute in outline, with the length and width subequal—not short, broad, and wedge-shaped as depicted in McGowan's (1998a:fig. 1B) reconstruction. In lacking the anterior part of the bone, UALVP 16216 also underestimates the relative length of the orbital margin. When the bone was complete, the anterior end of the orbital margin would have been about in line with the anteroposterior midpoint of the bone, not anterior to this point as McGowan (1998a) claimed; the former condition occurs in all species of Albanerpeton and is diagnostic for the genus (Gardner, 2000; here:Chapters 2, 7). Contrary to McGowan (1998a), emargination of the slot for receipt of the prefrontal is not useful for differentiating species of Albanerpeton because there is no substantial interspecific variation in the degree of emargination among large individuals (Gardner, 2000; here:Chapter 2). Emargination of the slot increases with growth (Fig. 3-2G–L) and this alone accounts for the shallowly excavated slots in UALVP 16216. McGowan (1998a) correctly observed that the orbital margins in UALVP 16216 are less divergent than in frontals of A. inexpectatum. The former condition is a function of the azygous frontals being relatively more elongate and resembling an isosceles triangle in outline. This condition is primitive for the genus and differentiates A. galaktion only from A. inexpectatum, a species in which the frontals are relatively broader and more nearly resemble an equilateral triangle.

Albanerpeton galaktion is diagnosed by two premaxillary apomorphies that are unique among albanerpetontids: (1) suprapalatal pit occupies about one-fifth to one-quarter of lingual surface area of pars dorsalis (suprapalatal pit smaller in other albanerpetontids: accounts for about one percent of surface area of pars dorsalis in non-Albanerpeton albanerpetontids and A. arthridion, and four to fifteen percent of pars dorsalis in other species of Albanerpeton) and (2) palatal foramen large, with diameter about one and one-third to two times greater than bases of medial teeth on premaxilla (diameter of foramen primitively subequal to and generally smaller than that of medial teeth). Given that the suprapalatal pit and palatal foramen are intimately associated in albanerpetontids, enlargement of these bony openings in A. galaktion is probably linked. Soft structures associated with these openings probably were involved with feeding or olfaction (Chapter

2) and can be expected to have been enlarged in size and, presumably, enhanced in function in A. galaktion relative to other albanerpetontids.

ALBANERPETON GRACILIS, sp. nov.

(Figs. 6-7, 6-8A–E; Table 6-4)

"Albanerpeton species B" Gardner, 1999a:63.

"undescribed middle Campanian species" Gardner, 1999b:533.

Holotype—TMP 95.181.70, nearly complete left premaxilla missing vomerine process and lateral end of pars dentalis, and having three broken and three intact teeth (Fig. 6-7A, B).

Holotype Horizon and Locality—Middle Campanian (Judithian); Dinosaur Park Formation; TMP L0410, Dinosaur Provincial Park, Alberta, Canada.

Etymology—Specific name refers to the gracile build of the premaxilla.

Referred Specimens—Oldman Formation, seven localities, Alberta: TMP L0406: TMP 95.177.82, 95.177.83, premaxillae; TMP 95.177.80, maxilla; TMP L0411: TMP 96.1.57, frontals; TMP L0413: TMP 95.180.64, premaxilla; TMP L1127: TMP 96.78.187–96.78.197, premaxillae; TMP 96.78.103, dentary; TMP L1128: TMP 96.78.135, frontals and incomplete right prefrontal; TMP L1137: TMP 96.78.185, premaxilla; TMP L1141: TMP 96.78.126, premaxillae. Dinosaur Park Formation, eight localities, Alberta: TMP L0051: TMP 95.145.67, premaxilla; TMP L0054: TMP 86.60.110, frontals; TMP L0086: TMP 95.182.22, premaxilla; TMP L0410 (holotype locality): TMP 95.181.72, 95.181.73, premaxillae; TMP 95.181.69, 95.181.71, maxillae; TMP 95.181.68, dentary; TMP 86.194.8, 95.181.67, frontals; TMP L1108: TMP 95.157.73, maxilla; TMP L1118: TMP 95.174.59, maxilla; TMP L1119: TMP 95.163.50, premaxilla; TMP L1120: TMP 95.171.20, premaxilla. Kaiparowits Formation, OMNH V6, Utah: OMNH 60321–60323, premaxillae; OMNH 60237, 60324, maxillae. Aguja Formation, OMNH V58/TMM 43057, Texas: OMNH 60242, premaxilla; OMNH 25349, 60325, maxilla.

Distribution (Table 6-1)—Middle Campanian (Judithian), North American Western Interior: Dinosaur Park and Oldman formations, Alberta; Kaiparowits Formation, Utah; and Aguja Formation, Texas.

Diagnosis—Moderate-sized species of Albanerpeton having no recognizable autapomorphies, but differing from all congeners in a unique combination of primitive and derived character states. Differs from A. arthridion and shares with all Late Cretaceous and Tertiary congeners two premaxillary synapomorphies: suprapalatal pit low on pars dorsalis and larger, ranging from about four to 25 percent of lingual area of pars dorsalis depending on the species. Primitively resembles A. galaktion and A. cifellii and differs from A. nexuosus, A. inexpectatum, and unnamed Paleocene species in having premaxilla more gracile in build, paired, and with pars dorsalis relatively taller and less strongly sutured dorsally with nasal, in having maxilla (unknown for A. cifellii) with relatively longer premaxillary lateral process, and in having frontals (unknown for A. cifellii) with internasal process relatively broader and acute in dorsal or ventral outline; convergently resembles Tertiary congeners in having anterior end of tooth row on maxilla approximately in line with leading edge of nasal process. Most closely resembles A. galaktion and A. cifellii in one premaxillary synapomorphy, suprapalatal pit triangular to slit-like in lingual outline, but primitively differs from former species in retaining moderate-sized suprapalatal pit and smaller palatal foramen and from latter species in lacking facet and dorsally expanded lateral internal strut on lingual face of premaxillary pars dorsalis for contact with nasal.

Description

Descriptions below are composites, unless noted otherwise, and rely primarily on specimens from the Dinosaur Park and Oldman formations.

Premaxilla (Fig. 6-7A–I; Table 6-4)—With a height of just over 2.8 mm, the holotype (TMP 95.181.70; Fig. 6-7A, B) is the largest of the 27 premaxillae at hand. The most nearly complete specimen, TMP 96.78.91 (Fig. 6-7C–E), lacks only the lateral end of the pars dentalis and the teeth in this region. The premaxilla is gracile in construction. No specimen shows evidence of having been fused medially in life to its opposite. The medial flange is medially narrow and extends up the medial edge of the bone along the dorsal one-half of the pars dentalis onto the lower one-half to two-thirds of the pars dorsalis. The pars dorsalis is relatively tall and narrow (Table 6-4). In the holotype, the dorsal end of the pars dorsalis is swollen labiolingually and indented dorsolingually by a shallow concavity for receipt of the anterior end of the nasal. On smaller premaxillae, the dorsal end of the pars dorsalis is unswollen and lacks a concave depression, indicating that the pars dorsalis would have simply abutted against the nasal. The lacrimal notch is deep and markedly narrow, both in absolute and relative terms (Table 6-4). The external surface of the bone is perforated by small, scattered external nutritive foramina. On large premaxillae, including the holotype, the dorsal one-third of the pars dorsalis bears a low, indistinct boss that is weakly ornamented with irregular ridges and shallow pits.

In lingual view, the suprapalatal pit lies about one-half to two-thirds of the distance across the pars dorsalis from the medial edge and is located low on the process, with the ventral edge of the pit confluent with the dorsal face of the pars palatinum. The suprapalatal pit is moderate in size (Table 6-4) and occupies about four to ten percent (n = 4) of the lingual surface area of the pars dorsalis. In lingual outline, the suprapalatal pit is taller than wide and varies from triangular to slit-like (cf., Fig. 6-7B, D, F–H). TMP 95.171.20 (not figured) is unusual in having the opening of the suprapalatal pit subdivided into two smaller, ovoid openings. An internal strut is typically absent medial to the suprapalatal pit; where present, this strut is little more than a lingually shallow ridge that extends down the inner face of the pars dorsalis. The lateral edge of the suprapalatal pit is consistently bordered by a more prominent, but relatively narrow internal strut that is perforated laterally by one or a few tiny foramina. The strut expands lingually as it extends down the inner face of the pars dorsalis. The base of the strut rarely extends more than about one-third of the distance lingually across the dorsal face of the pars palatinum.

The pars palatinum is lingually broad and bears prominent vomerine and maxillary processes (Fig. 6-7E), both of which are indented lingually by a shallow facet for contact with one or more palatal bones. The unnamed dorsal process on the lingual edge of the maxillary process is a low, labiolingually compressed ridge that is not continuous labially with the base of the more lateral internal strut. In eight of the ten premaxillae preserving the maxillary process, the ventral face of the process bears a low, drumlin-shaped knob all but identical to that on other albanerpetontid premaxillae. However, in TMP

95.181.70 and 95.180.64 (Fig. 6-7B, I, respectively), this knob is prominently developed into a ventrally directed, procurved, and bulbous process. Elaboration of this ventral process does not appear to be size-related, because TMP 95.180.64 is about two-thirds the size of TMP 95.181.70. The significance, if any, of this unusual process is unclear. The palatal foramen is relatively small, with a diameter not greater than one-half the diameter of the bases of the medial teeth on the bone. The canal connecting the dorsal and ventral openings of the palatal foramen extends vertically through the pars palatinum. The palatal foramen opens dorsally in the pars palatinum, in or just lingual to the opening of the suprapalatal pit, and ventrally in the pars palatinum, just lingual to the pars dentalis and in line with the second to fourth tooth positions. Up to three smaller, unnamed foramina perforate the bone ventrally at the junction between the pars palatinum and pars dentalis. In TMP 96.78.196 (Fig. 6-7H), two such foramina are evident, one each above the second and fourth loci. I generally have not been able to determine the paths of these unnamed foramina, but in occasional premaxillae (e.g., OMNH 60242; Fig. 6-7G), a canal can be traced from the medialmost foramen vertically through the pars palatinum and opening dorsally in the junction between the pars palatinum and pars dorsalis, well medial to the suprapalatal pit.

Maxilla (Fig. 6-7J–N)—The largest of the nine available specimens, TMP 95.174.59 (unfigured), is about 4 mm long and would have been slightly longer when the bone was complete. The remaining specimens are from smaller individuals. The two figured specimens, TMP 95.157.73 (Fig. 6-7J–L) and 95.177.80 (Fig. 6-7M, N), overlap in the region of the anterior one-half of the tooth row and adequately document the structure of the element. The labial surface is unornamented, with up to ten external nutritive foramina scattered across the anterior part of the pars facialis. The nasal process is low and triangular in labial outline. The pars facialis is low and becomes shallower posteriorly. At its posterior end the pars facialis labially bears a shallow facet for contact with the jugal. The ventral edge of the pars dentalis is straight to shallowly convex ventrally in labial or lingual outline. The anterior end of the tooth row is approximately in line with the point of maximum indentation along the leading edge of the nasal process.

The premaxillary lateral process is anteriorly elongate, with its length greater than the height at the base, and tapers anteriorly to terminate in a blunt end. The premaxillary dorsal process is lingually broad and ventrally bears a low horizontal ridge for contact with the posterior edge of the maxillary process on the premaxilla. The pars palatinum is lingually broad, tapers towards its posterior end, and dorsolingually has the short trough for contact with one or more unknown palatal bones. The raised bony patch on the dorsal surface of the pars palatinum for contact with the base of the lacrimal is weakly developed. The internal narial margin spans four or five loci.

Dentary (Fig. 6-7O–Q)—Two incomplete dentaries are available: TMP 96.78.103 (Fig. 6-7O) preserves about the anterior two-thirds of the bone, whereas TMP 95.181.68 (Fig. 6-7P, Q) lacks about the anterior one-third of the ramus and much of the area for attachment of the postdentary bones. The two specimens overlap for about ten tooth positions anterior to the opening for the Meckelian canal. Both dentaries are from moderate-sized individuals, comparable in size to those represented by upper jaws. Each dentary is relatively gracile in construction. Neither specimen is ornamented labially. A row of external nutritive foramina is present labially, as is the scar ventrally for attachment of the intermandibularis musculature. The dorsal edge of the dental parapet is straight in labial or lingual outline. TMP 95.181.68 preserves enough of the dorsal edge immediately behind the tooth row to show that no dorsal process was present in this region. TMP 96.78.103 preserves a moderately prominent symphyseal eminence and two intact symphyseal prongs. The remainder of the lingual structure is unremarkable.

Dentition (Fig. 6-7A–J, L, M, O–Q)—As in other albanerpetontids, marginal teeth are highly pleurodont, non-pedicellate, and tipped with labiolingually compressed, chisel-like, and faintly tricuspid crowns. Minor differences are apparent among jaws in the relative length, build, and spacing of teeth; this variation does not appear to correlate with overall jaw size. On jaws having more robust teeth, the pedicels tend to be slightly expanded mesiodistally midway up the shaft, giving these teeth the appearance of being somewhat swollen or barrel-shaped in lingual view (Fig. 6-7D, J, O, P). Teeth are weakly heterodont in size along the maxillary tooth row, with the longest teeth occupying the third to fifth positions. Judging by intact and broken teeth on the two dentaries, a similarly weakly heterodont pattern occurred on this element. Six to ten loci are present in the 12 premaxillae having a complete tooth row. One maxilla (TMP 95.181.71; not figured) preserves a complete tooth row of 19 loci; other maxillary specimens appear to have a similarly low tooth count when complete. For example, TMP 95.174.59 (not figured) and 95.157.73 (Fig. 6-7J) preserve the anteriormost 17 and 14 tooth positions, respectively, and each specimen is probably missing only the posteriormost one or two loci. The dentaries TMP 95.181.86 and 96.78.103 preserve, respectively, the posterior 19 and anterior 18 tooth positions; I estimate that each held about 27 loci when the bone was complete. Most jaws preserve one or more empty tooth slots for replacement teeth. More advanced stages of tooth replacement are seen in a maxilla (TMP 95.177.80; Fig. 6-7M) with an in situ replacement crown in the tooth slot at the second locus and in a dentary (TMP 95.181.68; Fig. 6-7P) with replacement teeth at the fourth–sixth and fifteenth loci from the broken anterior end of the tooth row.

Frontals (Fig. 6-8A–E)—Two of the five pairs of fused frontals are nearly complete. TMP 86.194.8 (Fig. 6-8A, B), the smaller of the two pairs, lacks the distal ends of the anterolateral processes and the distalmost end and left edge of the internasal process. TMP 96.78.135 (Fig. 6-8C) consists of a more nearly complete pair of frontals, about 3.7 mm in midline length, that lacks the posterior end of the ventrolateral crest and adjacent part of the orbital margin on the right side, but has the medial end of the right prefrontal articulated in the more posterior slot on the right side (left in figure). The third figured specimen, TMP 95.181.67 (Fig. 6-8D, E), is broken transversely between the slots for receipt of the prefrontal and lacks the anterior part of the bone. Although the largest frontal specimens at hand suggest a midline length of about 4 mm, several jaws evidently are from slightly larger individuals. Frontals are solidly fused medially. In dorsal or ventral view, the fused frontals are triangular in outline and slightly longer than wide. Based on TMP 86.194.8 and 96.78.135, I estimate the ratio of midline length to width across the posterior edge between the lateral edges of the ventrolateral crests at between 1.1 and 1.2. The anterior processes and slots for receipt of the nasal and prefrontal are well developed. The internasal process is acute in dorsal view, with the length subequal to the width across the base, and laterally bears the groove for contact with the nasal. The dorsal and ventral edges of the slot for receipt of the prefrontal are shallowly excavated medially in most specimens. TMP 86.194.8 is unusual in having the slot completely open dorsally (Fig. 6-8A). This condition is not an artifact of preservation, as the dorsal margin of the slot on both sides of the specimen is smooth and exhibits no evidence of breakage. Posterior to the anterolateral process, the lateral edge of the bone diverges at about 25° from the midline and the orbital margin is shallowly concave medially in dorsal or ventral view. In TMP 86.194.8, the posterior edge of the frontal roof is shallowly concave to either side of the midline and clearly abutted in life against the paired parietals. In larger frontals, such as TMP 96.78.135 and 95.181.67, the posterior edge is more nearly transverse in dorsal view and was sutured with the parietals.

Frontals are consistently ornamented dorsally with the usual albanerpetontid pattern of broad, polygonal pits bordered by narrow ridges. Pits vary in relative depth, being shallow on some specimens and deeper on others (cf., Fig. 6-8A versus D).

The ventrolateral crest is relatively thick dorsoventrally. With increased frontal size, the crest becomes absolutely and relatively wider, with width of crest behind slot for receipt of prefrontal increasing from 0.40–0.65 mm (n = 4) and ratio of width of crest to width across posterior edge of bone between medial edge of crests increasing from 0.25–0.40 (n = 3). The transverse profile of the crest also changes with growth. On the two smallest frontals, TMP 86.194.8 (Fig. 6-8B) and 96.1.57 (not figured), the crest resembles that on frontals of Albanerpeton arthridion (Chapter 4) in being convex ventrally in transverse view. On TMP 96.78.135 and 95.181.67 (Fig. 6-8C, D, respectively), the ventral face of the crest is slightly bevelled, with the flattened surface facing ventrolaterally. The crest does not, however, approach the triangular transverse profile seen in frontals of A. inexpectatum, A. nexuosus, and A. galaktion.

Remarks

I recognize Albanerpeton gracilis as a new albanerpetontid species on the strength of distinctive jaws and frontals that are associated by structure, size, and provenance. Although I have not been able to identify any autapomorphies for A. gracilis, the species differs from its congeners, including the sympatric species A. nexuosus and A. galaktion, in the unique combination of primitive and derived character states given in the diagnosis above. The holotype premaxilla exhibits two unusual features: (1) distal end of pars dorsalis swollen and concave dorsolingually for contact with nasal and (2) unnamed ventral process on maxillary process is a bulbous, procurved projection. As both features vary among specimens, neither should be used to diagnose the species until this variation is better understood. Maxillae of A. gracilis differ from those of A. nexuosus and A. galaktion in having fewer teeth (~20 versus ~25) and a less prominent bony patch, for contact with the lacrimal, on the dorsal surface of the pars palatinum. It is unclear to me whether these maxillary features are taxonomically significant or simply associated with the smaller body size of A. gracilis.

Assignment of the new species to Albanerpeton is appropriate because referred frontals possess the diagnostic suite of character states for the genus, whereas the holotype and referred premaxillae exhibit synapomorphies of the suprapalatal pit that are diagnostic for less inclusive clades within the genus. The moderate-sized suprapalatal pit located low on the pars dorsalis places A. gracilis in the unnamed subgeneric clade containing all congeners, except A. arthridion, whereas the triangular to slit-shaped suprapalatal pit further nests A. gracilis in the less inclusive gracile-snouted clade. In lacking the respective autapomorphies of A. cifellii and A. galaktion, A. gracilis is the most generalized member of the gracile-snouted clade.

Genus and Species Indeterminate
(Fig. 6-8F–H)

Horizons, Localities, and Voucher Specimens—Early Campanian (Aquilan) horizons: Deadhorse Coulee Member, Milk River Formation; seven localities, Alberta: UALVP MR-4: UALVP 40033, parietal; UALVP 16224–16232, 40034, atlantes; UALVP MR-20: UALVP 16214, 16215, parietals; UALVP 16233–16235, atlantes; plus uncatalogued, fragmentary jaws and frontals from MR-2, -4, -6, -8, -9, -12, and -20; Wahweap Formation, three localities, Utah: OMNH V2: OMNH 24267, dentary; OMNH V11: OMNH 24007, dentaries; OMNH V16: OMNH 23658, premaxillae; OMNH 23625, maxilla; OMNH 23638, dentaries. Middle Campanian (Judithian) horizons: Foremost Formation, TMP L1124, Alberta: TMP 96.78.100, lot of four dentaries; Dinosaur Park Formation, TMP L0410, Alberta: TMP 86.242.74, frontals; Dinosaur Park or Oldman formations, Woodpile Creek locality, Saskatchewan: RSMNH P2155.79, dentaries; Judith River Formation, Clambank Hollow, Montana: AMNH 8479, 8480, dentaries; Kaiparowits Formation, three localities, Utah: OMNH V5: OMNH 23841, jaw fragments; OMNH V6: OMNH 23581, 34177, 34181, premaxillae; OMNH 34182, dentary; OMNH 34173, jaw fragments; OMNH V61: OMNH 23963, premaxilla; Aguja Formation, four localities, Texas: LSUMG VL-113: LSUMG V-1371, maxilla; LSUMG VL-140: LSUMG

140:5606, maxilla; LSUMG VL-491: LSUMG 491:5958, jaw fragment; OMNH V58/TMM 43057: TMM 43057-257, premaxilla; TMM 43057-249, -250, -251, -253, -254, -255, -258, dentaries. Late Campanian–early Maastrichtian (Edmontonian) horizons: St. Mary River Formation, Scabby Butte, Alberta: UALVP 40044, dentary; upper Fruitland Formation or lower Kirtland Formation, KUVP NM-37, New Mexico: KUVP 129740, 129741, dentaries; lower Kirtland Formation, KUVP NM-18, New Mexico: KUVP 129742, 129743, dentaries. Late Maastrichtian (Lancian) horizons: Scollard Formation, KUA-1 locality, Alberta: UALVP 40043, dentary; UALVP 40042, fragmentary frontal; Frenchman Formation two localities, Saskatchewan: Wounded Knee: UALVP 40039–40041, dentaries; Gryde: RSMNH P1927.945, .958, .959, .1016, dentaries; Hell Creek Formation, Bug Creek Anthills, Montana: UALVP 43841–43843, dentaries; Lance Formation, three localities, Wyoming: UCMP V-5620: UCMP 49534, 49536, dentaries; UCMP V-5711: AMNH 22952–22954, dentaries; UW V-79032: UW 14585, premaxilla; UW 14588, maxilla; UW 14583, 14586, 14587, 14591, 15030, dentaries; UW 14592 (listed as UW 14542 by Breithaupt [1982:133]), jaw fragment.

Remarks

Voucher Specimens—Specimens listed above are incomplete skull bones and rare atlantes that are too fragmentary, insufficiently diagnostic, or both to be identified below the familial level. Nevertheless, these specimens are further evidence that albanerpetontids were widespread in the Western Interior during the Campanian and Maastrichtian. Specimens from the Wahweap Formation of Utah, Kirtland Formation of New Mexico, and St. Mary River and Scollard formations of Alberta are the first records for albanerpetontids in these units. Other voucher specimens substantiate previous reports in faunal lists of albanerpetontids in the Frenchman Formation of Saskatchewan (Fox, 1989:16) and Foremost Formation of Alberta (Peng, 1997:appendix 2), while specimens from the Woodpile Creek locality extend the range of albanerpetontids in Saskatchewan back into the Judithian.

Most of the listed voucher specimens are fragmentary jaws that are easily identified by their characteristic structure and teeth. These include 11 jaws (collections of LSUMG and TMM) previously referred to Albanerpeton nexuosus (Standhardt, 1986:109), "Albanerpeton cf. A. nexuosus" (Rowe et al., 1992:appendix 1), and Albanerpeton sp. (Rowe et al., 1992:table 1; Sankey, 1998:110) from the Aguja Formation and eight jaws (collection of UW) previously referred to A. nexuosus (Breithaupt, 1982:133) from the Lance Formation. Frontals are less commonly recovered and, outside of the Milk River Formation, are represented by one incomplete specimen each from the Dinosaur Park and Scollard formations. The only other albanerpetontid skull bones are fragmentary, indeterminate parietals (unfigured here) from the Milk River Formation, including two (UALVP 16214 and 16215) referred by Fox and Naylor (1982) to A. galaktion. These specimens are indistinguishable in structure and dorsal ornament from isolated albanerpetontid parietals from the European Middle Jurassic (McGowan, 1996:fig. 5) and Miocene (Estes and Hoffstetter, 1976:pl. 8, figs. 2, 3) and cannot reliably be referred to either of the species known from the Milk River Formation.

Unequivocal albanerpetontid postcranial remains identified to date from Campanian and Maastrichtian deposits in the Western Interior are limited to a nearly complete atlas (UALVP 16234; Fox and Naylor, 1982:fig. 1f–h; here:Fig. 6-8F–H) and 12 atlantal centra (UALVP 16224–16233, 16235, 40034), all from the Milk River Formation. These resemble other albanerpetontid atlantes (see Seiffert, 1969; Estes and Hoffstetter, 1976; Estes, 1981; Estes and Sanchíz, 1982; McGowan, 1996, 1998b; McGowan and Ensom, 1997; here:Chapters 3–5) in having a broad and dorsally concave odontoid process, kidney-shaped anterior cotyles, and a posterior cotyle with the dorsal edge deeply excavated, the ventral edge excavated to either side of the midline, and the inner face indented by three, faint articular facets for contact with the axis. Each of the 13 specimens has a closed notochordal canal in the posterior cotyle and a spinal foramen on either side immediately behind the anterior cotyle. UALVP 16234 lacks only part of the left wall of the neural arch, making it one of the most nearly complete albanerpetontid atlantes yet reported. Further preparation of the specimen reveals that the neural arch is complete dorsally, not unfused along the midline as reported by Fox and Naylor (1982). UALVP 16234 differs from referred atlantes of Albanerpeton inexpectatum (see Estes and Hoffstetter, 1976:pl. 6, fig. 14) in being larger, in having the neural arch roof more expanded anteroposteriorly, and in having a notch in the base of the leading edge of the neural arch wall. The taxonomic significance, if any, of these differences is uncertain. None of the atlantes from the Milk River Formation can be identified to genus or species, nor have I been able to recognize two atlantal morphs that could be interpreted as belonging to either A. nexuosus or A. galaktion.

Other albanerpetontid elements (e.g., lacrimal, quadrate, post-atlantal vertebrae, limb and girdle bones) reported from European localities (Estes and Hoffstetter, 1976; Estes and Sanchíz, 1982; McGowan, 1996; McGowan and Ensom, 1997) remain unaccounted for in North American Upper Cretaceous deposits.

Problematic and Mis-identified Specimens—Although Armstrong-Ziegler (1978, 1980) did not identify albanerpetontids from the Fruitland Formation in the San Juan Basin of New Mexico, at least seven jaws reported in her 1980 paper can be attributed to albanerpetontids. The first six jaws (UALP 75137-Y, -Z, -cc, -dd, -ee, -ff) are incomplete and were described as belonging to Prodesmodon based on resemblances with jaws then referred by Estes (1964) to the genus. Although Armstrong-Ziegler (1980) did not figure any of the six specimens, her descriptions on page 13 of "prominent interdigitating lobes" on the dentary symphysis and the characteristic structure of the teeth leave no doubt that these jaws are instead from albanerpetontids. Gao and Fox (1996:37) noted that one and, possibly, more of another six jaws (UALP 75137-D, -E, -K to -N) described by Armstrong-Ziegler (1980:18–20) for the lizard Leptochamops denticulatus (Gilmore) are also from albanerpetontids. Armstrong-Ziegler's photograph (1980:pl. 2d) of one specimen, a purported dentary fragment (UALP 75137-D) of Leptochamops, convincingly shows an incomplete albanerpetontid premaxilla (Gao and Fox, 1996), oriented upside down with the teeth directed towards the top of the page. Armstrong-Ziegler's (1980) descriptions of teeth on a second supposed dentary (UALP 75137-K) and on two supposed fragmentary maxillae (UALP 75137-M, -N) imply that these jaws are also from albanerpetontids (Gao and Fox, 1996).

Carpenter (1979:43) questionably identified UCM 38762 from the Laramie Formation (UCM locality 77062, Colorado) as the "anterior part of a small pterygopalatine" and suggested the specimen may pertain to Albanerpeton. If correctly identified, this specimen would be of considerable interest because palatal bones have not been formally described for albanerpetontids. Unfortunately, UCM 38762 is lost (P. C. Murphey, pers. comm. 1997). Carpenter's figure (1979:fig. 15) suggests that UCM 38762 was probably an amphibian palatal element, but his figure provides no further information about the structure or identity of the specimen.

The identities of trunk vertebrae from the Oldman Formation of Alberta that Peng (1997:82–83) referred to Albanerpeton sp. are uncertain, as these were only briefly described and none are complete. The sole figured specimen (TMP 96.78.144; Peng, 1997:pl. 8a, b) resembles albanerpetontid trunk vertebrae in having an amphicoelous centrum and, evidently, unicipital transverse processes but the specimen is too large and otherwise incomplete to be assigned with confidence to the Albanerpetontidae.

BIOGEOGRAPHY AND SYMPATRY OF NORTH AMERICAN CAMPANIAN AND MAASTRICHTIAN ALBANERPETONTIDS

As interpreted here, Albanerpeton nexuosus and A. galaktion range from the Aquilan to Lancian (Table 6-1). The apparent absence of A. galaktion during the Edmontonian is a sampling artifact. Microvertebrate assemblages of this age are poorly documented in the Western Interior, to the extent that the Edmontonian record for A. nexuosus is founded on a single dentary from the San Juan Basin of New Mexico. The range of these two species is nearly 20 million years, according to the time scale of Gradstein et al. (1995). This temporal range is extensive and raises the possibility that more than two species may be involved. At present, there is no morphological basis for this—jaws that I attribute to A. galaktion and A. nexuosus are essentially identical within each species, regardless of the horizon or locality from which they were collected, and show no obvious temporal or geographic variation. While current evidence is admittedly incomplete, specimens at hand nonetheless favor the interpretation that A. nexuosus and A. galaktion were long lived and contemporaneous species. By contrast, A. gracilis is currently known only from Judithian horizons.

Except for indeterminate, incomplete dentaries and humeri from the late Campanian or early Maastrichtian Laño site in Spain (Duffaud and Rage, 1999) and jaws, vertebrae, and other isolated elements from the late Maastrichtian of Romania (Grigorescu et al., 1999), the Campanian and Maastrichtian record of albanerpetontids is restricted to the North American Western Interior. Campanian lissamphibian assemblages are known elsewhere on the continent from the Marshalltown Formation of New Jersey (Denton and O'Neill, 1998) and the "El Gallo formation" of Baja California (Lillegraven, 1972, 1976), but albanerpetontids have not been identified from either unit. Through much of the Late

Cretaceous, beginning at about the Early–Late Cretaceous boundary, western North America was isolated to the east from the remainder of the continent by the Western Interior Seaway and connected to the northwest across the Bering Land Bridge with Asia (e.g., Kauffman and Caldwell, 1993; Smith et al., 1994). Although there is evidence for faunal exchanges between Asia and the North American western subcontinent during this time, especially among dinosaurs (e.g., Russell, 1993; Sereno, 1997), the situation for albanerpetontids is unclear. The Asian albanerpetontid record is limited to indeterminate dentaries from the Cenomanian and Coniacian of Uzbekistan (Gardner and Averianov, 1998) that show no obvious affinities with those of North American taxa, beyond primitive resemblances. Previously I (Gardner, 1999b; here:Chapter 4) suggested on paleogeographic grounds that albanerpetontids may have been in eastern North America prior to the establishment of the Western Interior Seaway. With retreat of the Western Interior Seaway beginning in the middle Maastrichtian (Kauffman and Caldwell, 1993), land connections were re-established between the western and eastern parts of the continent. It is reasonable to expect that faunal exchanges between the two regions occurred soon thereafter, but there is no evidence for this in the albanerpetontid record. The two species in western North America after the seaway began retreating were Albanerpeton nexuosus and A. galaktion, both of which had been there since at least the early Campanian (i.e., Aquilan).

Instead albanerpetontids appear to have evolved largely in isolation, although sympatrically, on the North American western subcontinent through at least the Late Cretaceous. The three species of Albanerpeton reported herein belong to a pair of less inclusive sister-clades: A. nexuosus in the robust-snouted clade and A. galaktion and A. gracilis in the gracile-snouted clade. Based on current fossil evidence, these sister-clades can be traced back to the early Late Cretaceous on the western subcontinent (Chapters 5, 7). The existence of all three species during the Judithian marks the time of maximum known taxonomic diversity for albanerpetontids on the western subcontinent. Judging by collections available to me, in terms of numerical abundance albanerpetontids appear to have been more plentiful during the Aquilan and Judithian than during the Lancian.

At least two of the albanerpetontid species reported herein have been identified in some of the same Aquilan, Judithian, and Lancian formations, while three Judithian microsites (TMP L0406 and L1127, Oldman Formation, Alberta; OMNH V6, Kaiparowits Formation, Utah) have yielded diagnostic elements of all three congeners. These records indicate that Albanerpeton galaktion, A. gracilis, and A. nexuosus were at least broadly sympatric across the coastal plain during their respective temporal ranges and invite speculation about the nature of albanerpetontid communities, especially during the Judithian. Plethodontid salamanders are a useful modern analogue for this exercise, in part, because many plethodontids resemble albanerpetontids in being small and terrestrial and, in part, because these salamanders have been the focus of numerous ecological studies. Field studies of plethodontid communities have documented food and microhabitat partitioning among closely related species (see reviews by Hairston, 1987; Jaeger and Forester, 1993) and it seems reasonable to expect a similar situation for albanerpetontids. Differences among the three Albanerpeton congeners in such features as size heterodonty of maxillary and dentary teeth, construction of the snout, and inferred body size are consistent with different lifestyles for each species. By comparisons with plethodontids, for which body size, head width, and tooth morphology may be important predictors of prey size (Lynch, 1985), A. galaktion and A. nexuosus can be expected to have taken larger prey than A. gracilis. Differences in relative tooth size and snout construction among the three species suggest further differences in feeding strategies, probably with A. nexuosus taking more active or resilient prey. The robustly built premaxilla of this species may also be associated with strengthening the skull for head-first burrowing. If correct, this implies a more fossorial lifestyle than A. galaktion and A. gracilis, both of which lack the osteological novelties of their robust-snouted congeners for strengthening the snout.

CONCLUSIONS

My survey documents the presence of albanerpetontids in 16 formations of Campanian and Maastrichtian age in the Western Interior. The main findings of my study are as follows:

(1) Skull and postcranial specimens previously described for Albanerpeton nexuosus and A. galaktion were incorrectly associated. The topotypic collection for A. nexuosus includes dentaries that can be retained in the species, dentaries and upper jaws from an indeterminate albanerpetontid, and a femur from an indeterminate caudate.

Albanerpetontid material from the Milk River Formation previously assigned to *A*. *galaktion* includes jaws and frontals of both species, along with parietals and atlantes from an indeterminate albanerpetontid. As interpreted here, *A*. *nexuosus* and *A*. *galaktion* are diagnosed by autapomorphies of the jaws and both species range from the Aquilan to Lancian. Membership of both species in *Albanerpeton* is supported by diagnostic character states of referred frontals and by derived premaxillary synapomorphies that diagnose less inclusive clades in the genus.

(2) The new Judithian species *A*. *gracilis* is described for jaws and frontals from Alberta, Utah, and Texas and differentiated from its congeners by a unique combination of symplesiomorphies and synapomorphies of the jaws and frontals. *A*. *gracilis* is allied with *A*. *galaktion* and the Turonian species *A*. *cifellii* in the gracile-snouted clade, but primitively lacks premaxillary autapomorphies characteristic for the last two species.

(3) Species of *Albanerpeton* evolved largely in isolation during the Late Cretaceous in North America. *A*. *nexuosus* is a member of the robust-snouted clade, whereas *A*. *galaktion* and *A*. *gracilis* belong in the gracile-snouted clade. Both sister-clades can be traced back to the early Late Cretaceous. There is no evidence of immigration into the Western Interior, either during the Late Cretaceous from Asia across the Bering Land Bridge or during the latest Cretaceous from eastern North America with retreat of the Western Interior Seaway.

(4) *Albanerpeton nexuosus*, *A*. *galaktion*, and *A*. *gracilis* were broadly sympatric during their respective temporal ranges across the Western Interior coastal plain. Differences in tooth and premaxillary structure and inferred body size suggest that these species favored different ecological niches and need not have competed directly with one another for resources.

TABLE 6-1. Occurrences of Albanerpeton nexuosus Estes, A. galaktion Fox and Naylor, and A. gracilis, sp. nov. in the North American Western Interior. Abbreviations: den, dentary; fm, formation; fr, frontals, mx, maxilla; pmx, premaxilla. An asterisk denotes an element known by only one specimen. Absolute dates are from Gradstein et al. (1995) and durations of stages and NALMAs are not proportional.

Ma	STAGE	NALMA	FORMATIONS AND OCCURRENCES			
65.0	MAASTRICHTIAN	Lancian	LANCE FM, WYOMING *A. nexuosus* den, mx* *A. galaktion* pmx*	LARAMIE FM, COLORADO *A. nexuosus* den*, pmx*	HELL CREEK FM, MONTANA *A. nexuosus* den*	
		Edmontonian	FRUITLAND or KIRTLAND FM, NEW MEXICO *A. nexuosus* den*			
71.3	CAMPANIAN	Judithian	AGUJA FM, TEXAS *A. nexuosus* den, mx*, pmx *A. gracilis* mx, pmx*	KAIPAROWITS FM, UTAH *A. nexuosus* den*, mx* *A. galaktion* pmx* *A. gracilis* mx, pmx	OLDMAN FM, ALBERTA *A. nexuosus* den *A. galaktion* pmx *A. gracilis* den*, mx*, pmx, fr	DINOSAUR PARK FM, ALBERTA *A. gracilis* den*, mx, pmx, fr
83.5		Aquilan	MILK RIVER FM, ALBERTA *A. nexuosus* den, mx, pmx, fr *A. galaktion* den, mx, pmx, fr			

TABLE 6-2. Straight line measurements for premaxillae of *Albanerpeton nexuosus* Estes and *A. galaktion* Fox and Naylor; Campanian and Maastrichtian (Aquilan-Lancian), North American Western Interior. Measurements follow Figure 1-2. For each entry, first row is number of specimens (left and right sides in fused premaxillae measured separately), second row is measurement (one specimen) or range (two or more specimens); and third line is mean and standard deviation (three or more specimens).

Species and Formations	PmH (mm)	PDH (mm)	PDW^1 (mm)	PDW^2 (mm)	LaND (mm)	LaNW (mm)	SPH (mm)	SPW (mm)
A. nexuosus								
All specimens	9	11	12	18	11	12	13	19
	2.95-3.50	1.70-2.24	1.03-1.48	1.20-1.77	0.65-1.12	0.06-0.40	0.40 - 0.72	0.26 - 0.69
	3.22±0.18	1.97±0.18	1.30±0.13	1.52±0.17	0.91±0.17	0.25±0.09	0.58±0.11	0.49±0.09
Milk River Formation	7	9	9	15	9	9	10	16
(Aquilan)	2.95-3.50	1.70-2.24	1.03-1.48	1.27-1.77	0.65-1.12	0.06-0.40	0.40-0.72	0.26-0.59
	3.22±0.20	2.01±0.17	1.29±0.13	1.55±0.16	0.87±0.16	0.26±0.10	0.58±0.11	0.49±0.09
Aguja Formation	2	2	2	2	2	2	2	2
(Judithian)	3.18-3.24	1.73-1.80	1.22-1.45	1.38-1.54	1.04-1.15	0.14-0.23	0.58-0.62	0.46-0.69
	—	—	—	—	—	—	—	—
Laramie Formation	1	1	1	1	1	1	1	1
(Lancian)	>2.69	>1.24	0.84	1.20	>0.48	0.23	0.53	0.44
	—	—	—	—	—	—	—	—
A. galaktion								
All specimens	5	5	10	14	5	10	6	15
	2.82-3.39	1.61-2.30	0.96-1.30	0.78-1.40	0.77-1.15	0.09-0.33	0.47-0.77	0.24-0.84
	3.08±0.21	1.99±0.24	1.05±0.15	1.14±0.15	0.99±0.13	0.21±0.07	0.64±0.11	0.61±0.20
Milk River Formation	3	3	7	8	3	7	4	10
(Aquilan)	3.01-3.39	1.95-2.30	1.00-1.30	1.00-1.30	0.77-1.15	0.18-0.33	0.68-0.77	0.24-0.77
	3.22±0.16	2.14±0.26	1.10±0.12	1.18±0.09	0.95±0.16	0.25±0.06	0.72±0.03	0.55±0.21
Oldman and Dinosaur	2	2	3	6	2	3	2	5
Park formations	2.82-2.94	1.61-1.89	0.74-1.09	0.78-1.40	1.05-1.05	0.09-0.16	0.47-0.50	0.53-0.84
(Judithian)	—	—	0.93±0.14	1.19±0.20	—	0.13±0.03	—	0.72±0.12

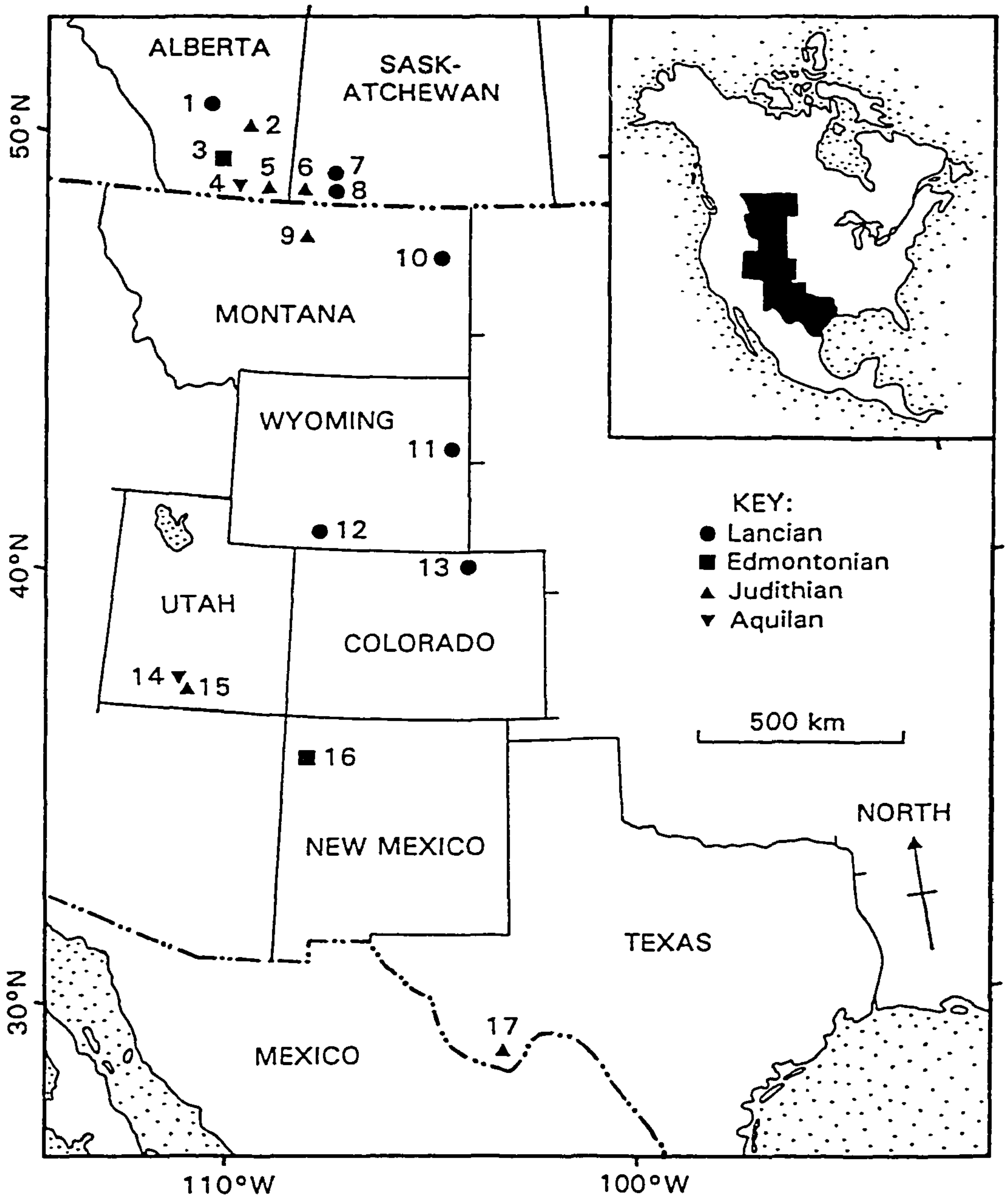
TABLE 6-3. Ratios for premaxillae of Albanerpeton nexuosus Estes and A. galaktion Fox and Naylor; Campanian and Maastrichtian (Aquilan-Lancian), North American Western Interior. Ratios defined in caption for Table 6-4. For each entry, first row is number of specimens (values for left and right sides in fused premaxillae calculated separately), second row is value (one specimen) or range (two or more specimens); and third line is mean and standard deviation (three or more specimens).

Species and Formations	PDH:PDW^2	LaND:PDH	LaNW:PDW^1	SPH:PDH	SPW:PDW^2
A. nexuosus					
All specimens	11	11	11	11	18
	1.17-1.65	0.33-0.66	0.05-0.35	0.20-0.36	0.20-0.45
	1.37±0.14	0.47±0.10	0.19±0.08	0.31±0.05	0.33±0.06
Milk River Formation	9	9	9	9	15
(Aquilan)	1.20-1.65	0.33-0.53	0.05-0.35	0.20-0.36	0.20-0.45
	1.41±0.13	0.43±0.07	0.20±0.08	0.30±0.05	0.32±0.06
Aguja Formation	2	2	2	2	2
(Judithian)	1.17-1.25	0.58-0.66	0.11-0.16	0.34-0.34	0.35-0.45
	—	—	—	—	—
Laramie Formation	1	0	1	1	1
(Lancian)	>1.03	—	>0.27	<0.43	0.37
	—	—	—	—	—
A. galaktion					
All specimens	5	5	10	5	12
	1.40-2.10	0.39-0.65	0.13-0.30	0.26-0.36	0.44-0.87
	1.86±0.24	0.51±0.10	0.20±0.05	0.31±0.04	0.62±0.10
Milk River Formation	3	3	7	3	7
(Aquilan)	1.90-1.95	0.39-0.53	0.16-0.30	0.30-0.36	0.51-0.65
	1.93±0.02	0.44±0.06	0.22±0.04	0.33±0.02	0.58±0.04
Oldman and Dinosaur	2	2	3	2	5
Park formations	1.40-2.10	0.56-0.65	0.13-0.16	0.26-0.29	0.44-0.87
(Judithian)	—	—	0.15±0.01	—	0.67±0.14

TABLE 6-4. Straight line measurements and ratios for premaxillae of Albanerpeton gracilis, sp. nov.; middle Campanian (Judithian), Oldman and Dinosaur Park formations, Alberta. Columns are: "Measurement or Ratio;" "n," number of specimens; "R," range; and "$\bar{x}$" and "SD," mean and standard deviation, respectively. Measurements follow Figure 1-2.

Measurement or Ratio	n	R	$\bar{x}$ and SD
PmH (height of premaxilla; mm)	11	2.17–2.82	2.50±0.18
PDH (height of pars dorsalis; mm)	11	1.30–1.86	1.50±0.16
PDW^1 (width of pars dorsalis across base of lacrimal notch; mm)	11	0.50–1.02	0.72±0.17
PDW^2 (width of pars dorsalis across suprapalatal pit; mm)	18	0.65–1.71	0.86±0.15
LaND (depth of lacrimal notch; mm)	10	0.34–1.12	0.77±0.22
LaNW (width of lacrimal notch; mm)	11	0.03–0.18	0.08±0.05
SPH (height of suprapalatal pit; mm)	18	0.25–0.56	0.35±0.07
SPW (maximum width of suprapalatal pit; mm)	18	0.16–0.37	0.27±0.06
PDH:PDW^2 (relative height of pars dorsalis)	11	1.48–2.25	1.75±0.21
LaND:PDH (relative depth of lacrimal notch)	10	0.26–0.70	0.51±0.11
LaNW:PDW^1 (relative width of lacrimal notch)	11	0.05–0.19	0.10±0.05
SPH:PDH (relative height of suprapalatal pit)	11	0.19–0.30	0.24±0.04
SPW:PDW^2 (relative width of suprapalatal pit)	17	0.21–0.45	0.33±0.07

FIGURE 6-1. Map showing locations of important Upper Cretaceous (Campanian and Maastrichtian) albanerpetontid-bearing sites in the North American Western Interior. Inset map in upper right shows areas (shaded) of provinces in Canada and states in the United States depicted in larger map. Localities and formations: **1**, KUA-1, Red Deer River Valley, Scollard Formation; **2**, TMP L0406, L0411, and L0413, Oldman Formation, and TMP L0051, L0054, L0086, L0410 (holotype locality of Albanerpeton gracilis, sp. nov.), L1108, L1118–L1120, Dinosaur Park Formation, all in Dinosaur Provincial Park; **3**, Scabby Butte, near Lethbridge, St. Mary River Formation; **4**, UALVP MR-2, -4, -6 (holotype locality of A. galaktion Fox and Naylor, 1982), -8, -9, -12, -20, Verdigris Coulee, Deadhorse Coulee Member, Milk River Formation; **5**, TMP L1124, Foremost Formation, and TMP L1127, L1128, L1131, L1137, and L1141, Oldman Formation, all near Manyberries; **6**, Woodpile Creek, near Willow Creek, Oldman or Dinosaur Park formations; **7**, Wounded Knee, Frenchman River Valley, Frenchman Formation; **8**, Gryde, Frenchman River Valley, Frenchman Formation; **9**, Clambank Hollow, Chouteau County, Judith River Formation; **10**, Bug Creek Anthills, McCone County, Hell Creek Formation; **11**, UCMP V-5620 (holotype locality of A. nexuosus Estes, 1981) and -5711, Niobrara County, Lance Formation; **12**, UW V-79032, Sweetwater County, Lance Formation; **13**, UCM locality 77062, Weld County, Laramie Formation; **14**, OMNH V5, V6, and V61, Garfield and Kane counties, Kaiparowits Formation; **15**, OMNH V2, V11, and V16, Kane County, Wahweap Formation; **16**, KUVP NM-37, upper Fruitland Formation or lower Kirtland Formation, KUVP NM-18, lower Kirtland Formation, and localities in Fruitland Formation listed by Armstrong-Ziegler (1980), all San Juan Basin; **17**, OMNH V58/TMM 43057, Brewster County, Aguja Formation. Locality information from Clemens et al. (1979), Carpenter (1979), Breithaupt (1982), Cifelli (1990), Rowe et al. (1990), Storer (1993), and D. Miao (personal communication 1999).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30°N
110°W
100°W
KEY:
● Lancian
■ Edmontonian
▲ Judithian
▼ Aquilan
500 km
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FIGURE 6-2. Dentaries of Albanerpeton nexuosus Estes and A. galaktion Fox and Naylor; Campanian (Aquilan and Judithian) and late Maastrichtian (Lancian), North American Western Interior. A. nexuosus (A–I): **A**, **B**, UCMP 49540, topotypic right mandible consisting of incomplete dentary and anterior tip of angular, in (**A**) lingual and (**B**) occlusal views; **C**, UCMP 49535, incomplete topotypic right dentary, in lingual view; **D**, **E**, UCM 38714, incomplete left dentary, in (**D**) labial and (**E**) lingual views; **F**, TMP 96.78.152, anterior part of left dentary, in lingual view; **G**, UALVP 16238, anterior part of right dentary, in labial view; **H**, UALVP 40014, anterior part of right dentary, in labial view; **I**, UALVP 40032, posterior part of left dentary missing posteriormost end of area for attachment of postdentary bones, in lingual view. Provenances: UCMP 49535 and 49540, Lance Formation, Wyoming, and UCM 38714, Laramie Formation, Colorado, all Lancian; TMP 96.78.152, Oldman Formation (Judithian), Alberta; and UALVP 16238, 40014, 40032, Deadhorse Coulee Member, Milk River Formation (Aquilan), Alberta. A. galaktion (J–M): **J**, UALVP 16221, incomplete small, left dentary, in lingual view; **K–M**, UALVP 16217, incomplete large, right dentary, in (**K**) labial, (**L**) lingual, and (**M**) occlusal views. Provenances: both specimens from Deadhorse Coulee Member, Milk River Formation (Aquilan), Alberta. Specimens at different scales: middle top (A–I), left (J), and bottom right (K–M) scale bars = 1 mm.

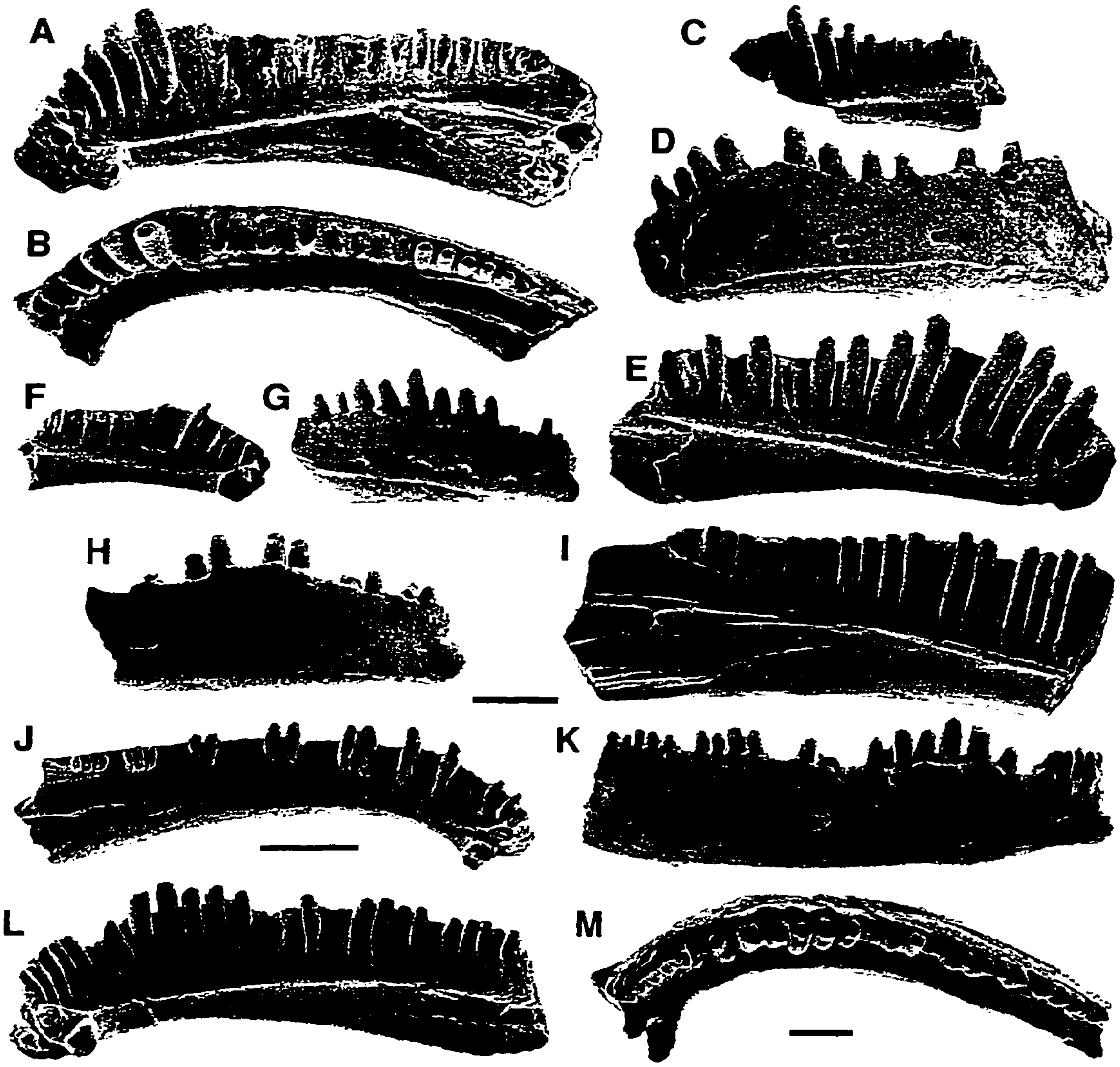
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FIGURE 6-3. Maxillae of Albanerpeton nexuosus Estes and A. galaktion Fox and Naylor; early and middle Campanian (Aquilan and Judithian), North American Western Interior. A. nexuosus (A–H): **A**, **B**, UALVP 16242, incomplete right maxilla, in (**A**) labial and (**B**) lingual views; **C**, UALVP 39973, incomplete right maxilla, in lingual view; **D**, OMNH 60245, incomplete right maxilla, in labial view; **E**, UALVP 39977, incomplete right maxilla, in labial view; **F**, OMNH 60239, anterior part of left maxilla, in lingual view; **G**, **H**, UALVP 16239, anterior part of right maxilla, in (**G**) lingual and (**H**) dorsal views. Provenances: OMNH 60239, Aguja Formation (Judithian), Utah; OMNH 60245, Kaiparowits Formation (Judithian), Utah; UALVP 16239, 16242, 39973, 39977, Deadhorse Coulee Member, Milk River Formation (Aquilan), Alberta. A. galaktion (I–N): **I–K**, UALVP 16240, incomplete right maxilla, in (**I**) labial, (**J**) lingual, and (**K**) dorsal views; **L–N**, UALVP 16241, incomplete right maxilla, in (**L**) labial, (**M**) lingual, and (**N**) dorsal views. Provenances: all from Deadhorse Coulee Member, Milk River Formation (Aquilan), Alberta. Specimens at different scales: middle (A–H) and bottom (I–N) scale bars = 1 mm.

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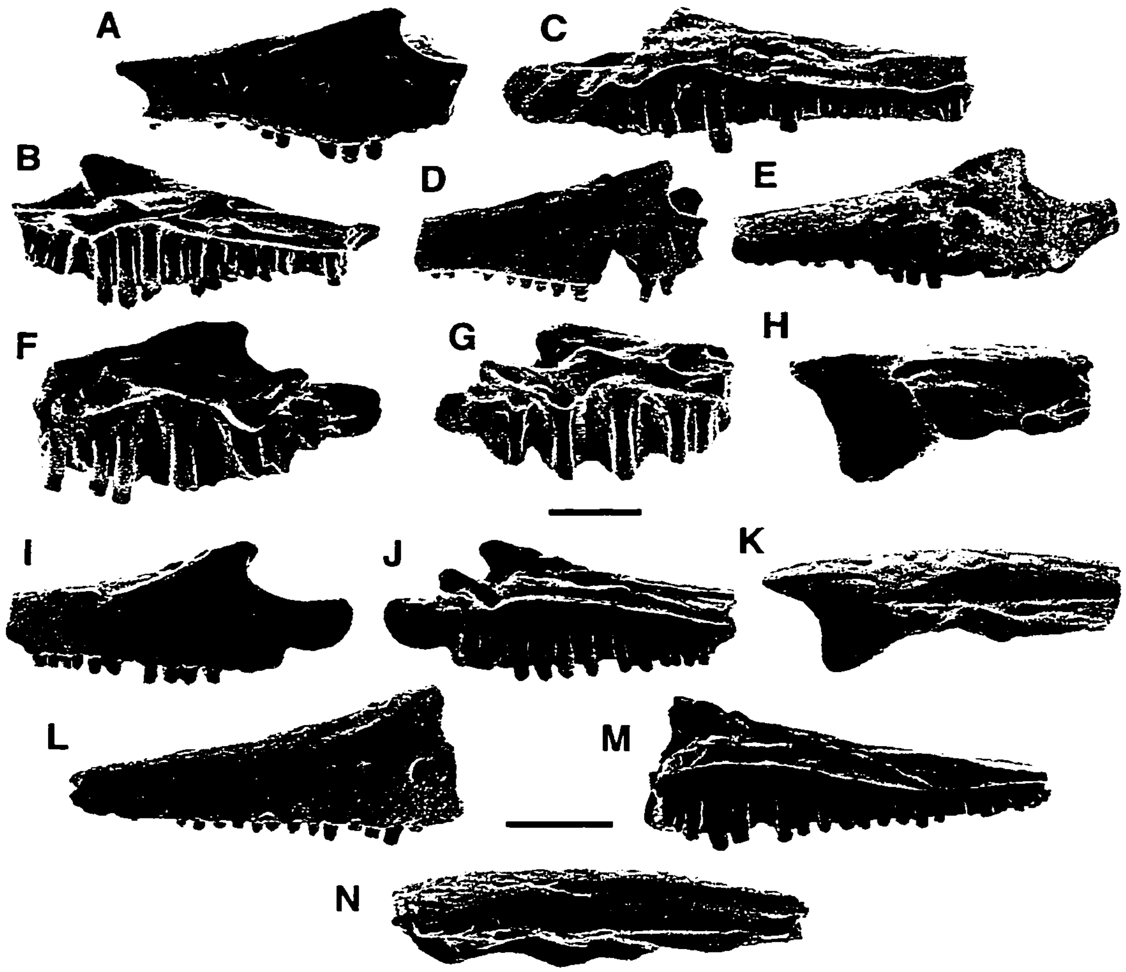

FIGURE 6-4. Premaxillae of Albanerpeton galaktion Fox and Naylor; early and middle Campanian (Aquilan and Judithian), Alberta. **A**, **B**, UALVP 16203, holotype, nearly complete left premaxilla, in (**A**) labial and (**B**) lingual views; **C**, **D**, UALVP 16204, nearly complete right premaxilla, in (**C**) labial and (**D**) lingual views; **E**, **F**, TMP 95.177.81, nearly complete right premaxilla, in (**E**) labial and (**F**) lateral and slightly dorsal views; **G**, **H**, UALVP 16212, left premaxilla missing dorsal part of pars dorsalis, in (**G**) lingual and (**H**) occlusal views; **I**, TMP 96.78.124, left premaxilla, in occlusal view. Provenances: UALVP 16203, 16204, 16212, Deadhorse Coulee, Milk River Formation (Aquilan) and TMP 95.177.81 and 96.78.124 Oldman Formation (Judithian). Arrows: 1, palatal foramen; 2, unnamed foramen in junction between pars palatinum and pars dentalis. Specimens at same scale: scale bar = 1 mm.

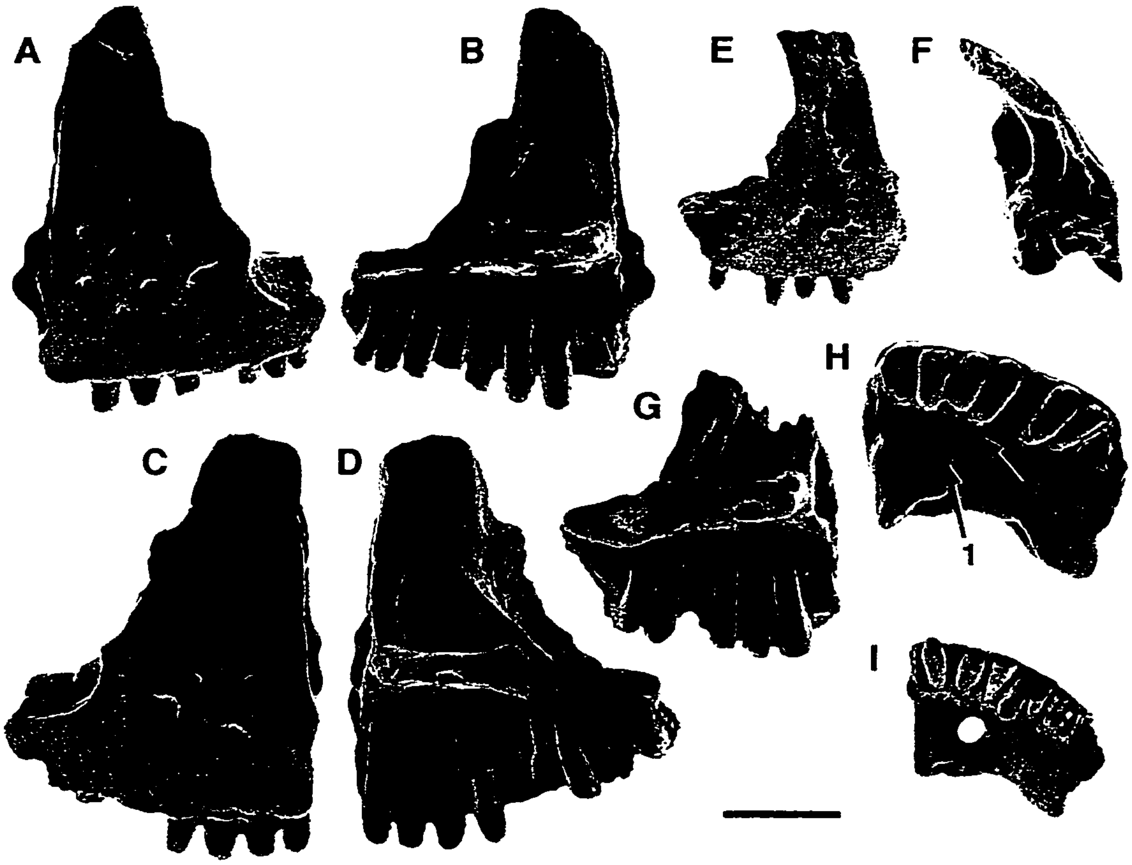
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FIGURE 6-5. Premaxillae of Albanerpeton nexuosus Estes; Campanian and Maastrichtian (Aquilan, Judithian, and Lancian), North American Western Interior. **A-C**, UALVP 16206, fused and nearly complete premaxillae, in (**A**) labial, (**B**) lingual, and (**C**) occlusal views; **D**, **E**, UALVP 39955, nearly complete left premaxilla, in (**D**) lingual and (**E**) lateral and slightly dorsal views; **F**, UALVP 39971, fused premaxillae missing most of right side, in occlusal view; **G**, UALVP 39960, left premaxilla, in occlusal view; **H**, UALVP 39969, left premaxilla broken transversely across pars dorsalis, in dorsal view showing dorsal openings of palatal and unnamed foramina in floor of suprapalatal pit; **I**, OMNH 25345, incomplete left premaxilla, in labial view; **J**, OMNH 60238, incomplete left premaxilla, in lingual and slightly ventral view; **K**, UCM 38713, incomplete left premaxilla, in lingual view. Provenances: UALVP 16206, 39955, 39960, 39969, 39971, Deadhorse Coulee Member, Milk River Formation (Aquilan), Alberta; OMNH 25345, 60238, Aguja Formation (Judithian); UCM 38713, Laramie Formation (Lancian), Colorado. Arrows: 1, palatal foramen; 2, unnamed foramen in junction between pars palatinum and pars dentalis. Specimens at same scale: scale bar = 1 mm.

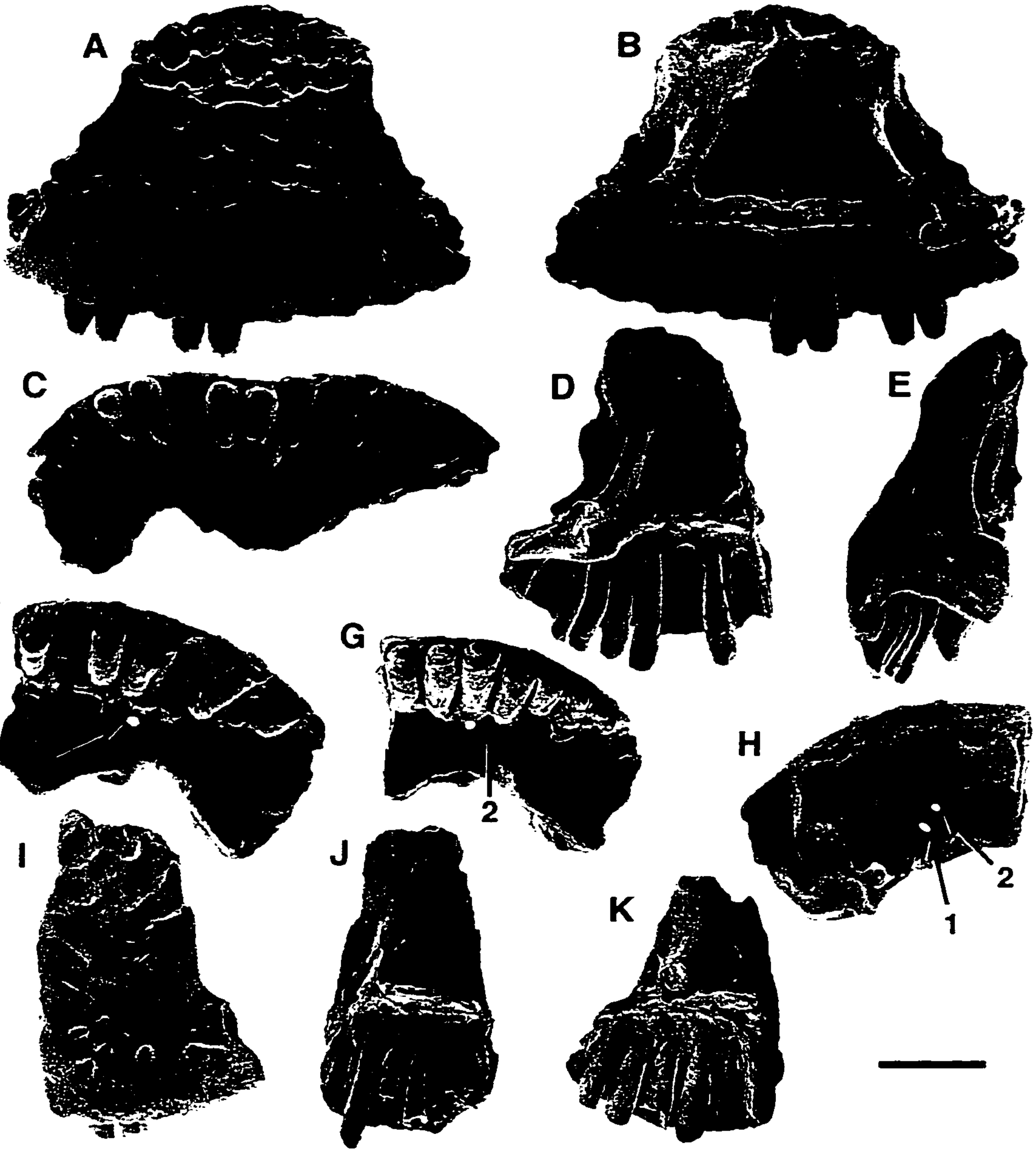
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FIGURE 6-6. Frontals of Albanerpeton nexuosus Estes and A. galaktion Fox and Naylor; early Campanian (Aquilan), Deadhorse Coulee Member, Milk River Formation, Alberta. A. nexuosus (A–E): **A**, **B**, UALVP 39996, fused frontals lacking anterior and posterior ends, in (**A**) dorsal and (**B**) ventral views; **C**, UALVP 39983, anterior part of fused frontals, in dorsal view; **D**, UALVP 39989, posterior part of left frontal, in ventral view; **E**, UALVP 39987, fragmentary fused frontals, in ventral view. A. galaktion (F–K): **F**, **G**, UALVP 16216, fused and incomplete frontals missing anterior end of bone and posterior end of both ventrolateral crests, in (**F**) dorsal and (**G**) ventral views; **H**, UALVP 39946, anterior part of fused frontals, in dorsal view; **I**, **J**, UALVP 39945, posterior one-half of fused frontals missing posterior end of both ventrolateral crests, in (**I**) dorsal and (**J**) ventral views; **K**, UALVP 39951, right posterior part of fused frontals, in ventral view. Specimens at different scales: top (A–E) and bottom (F–K) scale bars = 1 mm.

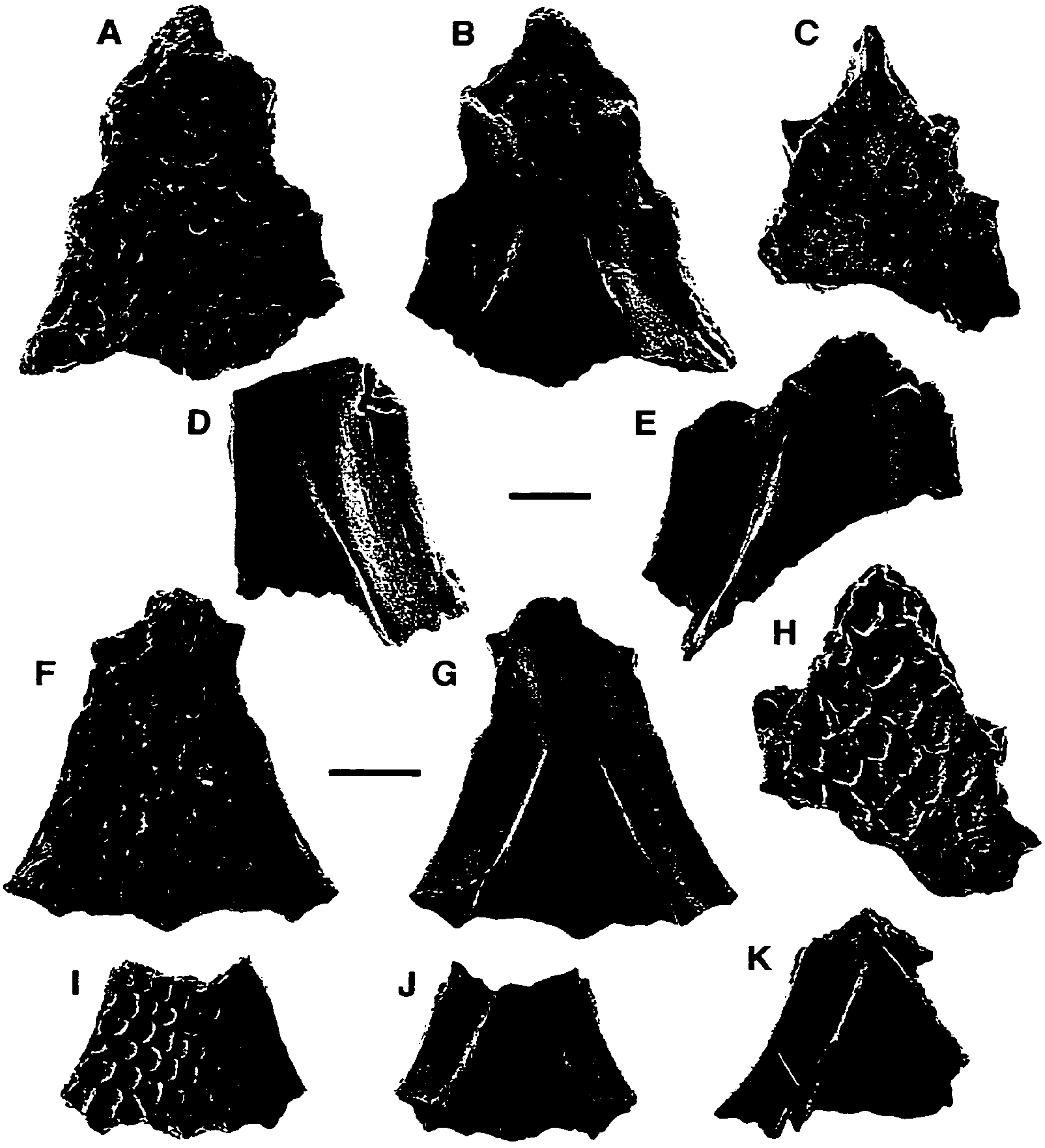
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FIGURE 6-7. Jaws of Albanerpeton gracilis, sp. nov.; middle Campanian (Judithian), North American Western Interior. Premaxillae: (**A–I**): **A**, **B**, TMP 95.181.70, holotype, incomplete left premaxilla, in (**A**) labial and (**B**) lingual views; **C–E**, TMP 96.78.191, nearly complete right premaxilla, in (**C**) labial, (**D**) lingual, and (**E**) occlusal views; **F**, OMNH 60321, incomplete right premaxilla, in lingual view; **G**, OMNH 60242, incomplete left premaxilla, in lingual view; **H**, TMP 96.78.196, incomplete right premaxilla, in lingual and slightly occlusal view; **I**, TMP 95.180.64, incomplete left premaxilla, in lateral view. Maxillae (**J–N**): **J–L**, TMP 95.157.73, nearly complete left maxilla, in (**J**) lingual, (**K**) dorsal, and (**L**) occlusal views; **M**, **N**, TMP 95.177.80, incomplete left maxilla, in (**M**) lingual and (**N**) dorsal views. Dentaries (**O–Q**): **O**, TMP 96.78.103, anterior part of left dentary, in lingual view; **P**, **Q**, TMP 95.181.68, medial part of left dentary, in (**P**) labial and (**Q**) lingual views. Provenances: TMP 95.181.70, 95.157.73, 95.181.68, Dinosaur Park Formation and TMP 95.177.80, 95.180.64, 96.78.103, 96.78.191, 96.78.196, Oldman Formation, Alberta; OMNH 60321, Kaiparowits Formation, Utah; OMNH 60242, Aguja Formation, Texas. Specimens at same scale: scale bar = 1 mm.

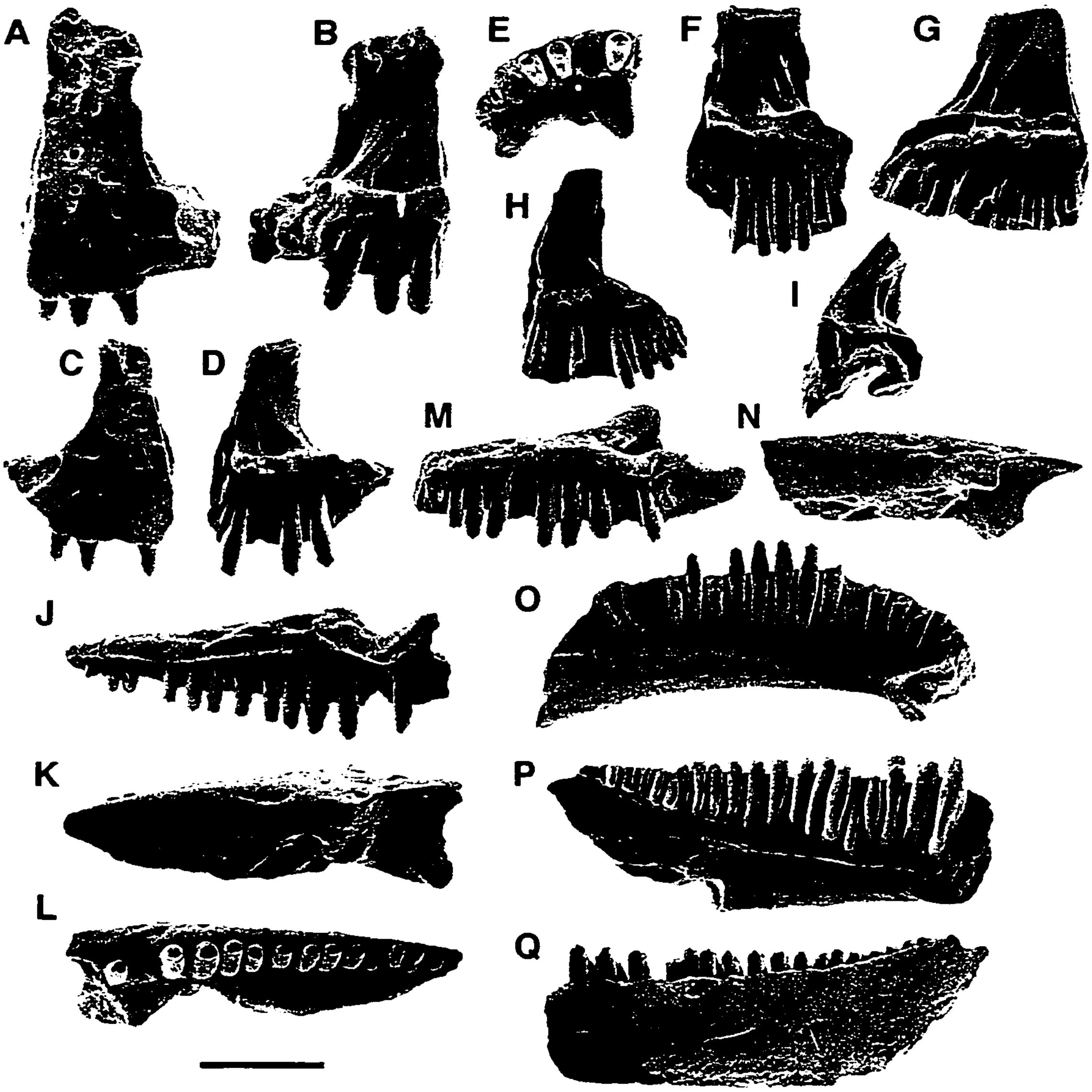
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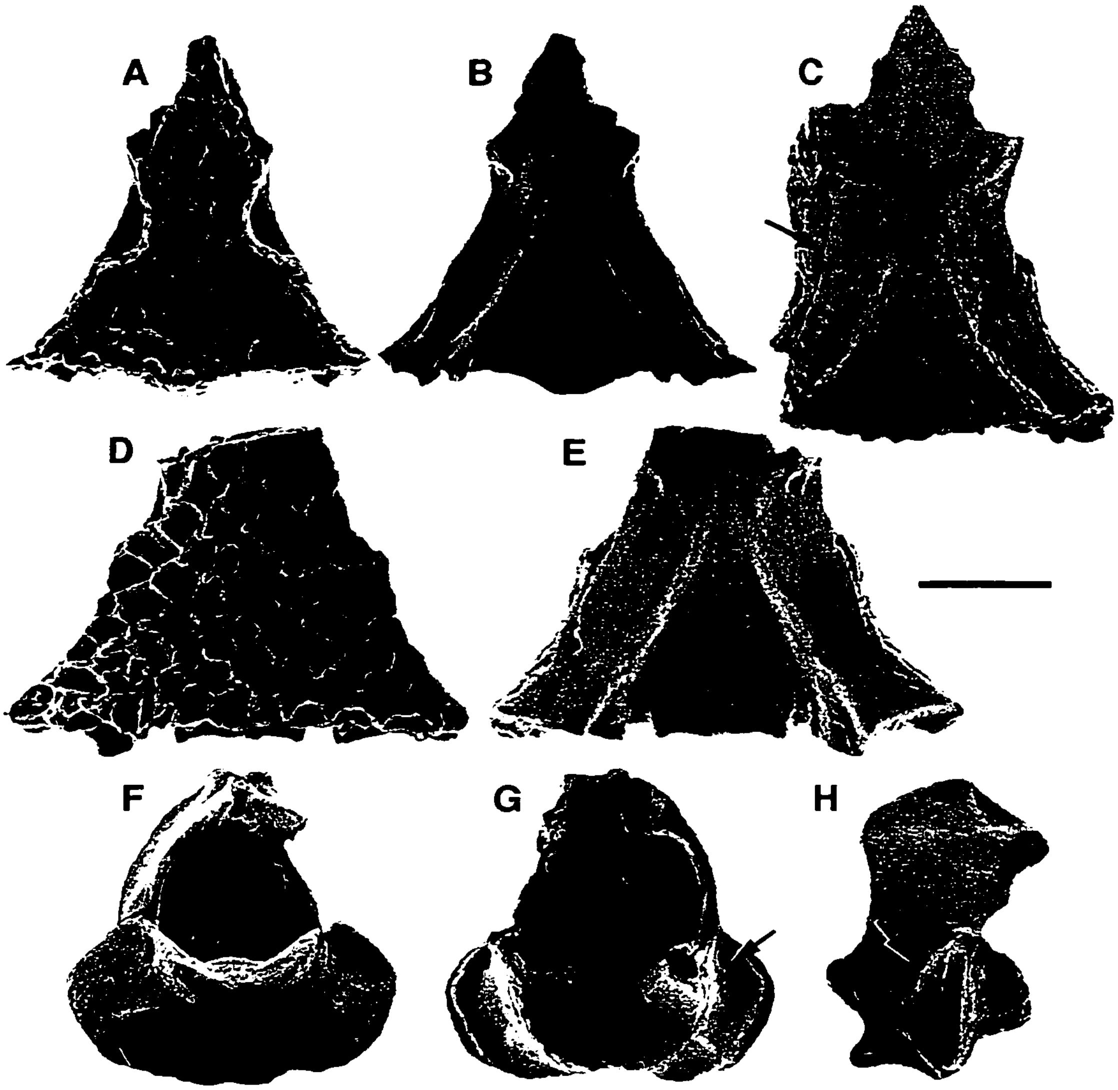
FIGURE 6-8. Frontals of Albanerpeton gracilis, sp. nov. and atlas of albanerpetontid genus and species indeterminate; early and middle Campanian (Judithian and Aquilan), Alberta. A. gracilis, sp. nov., frontals (**A–E**): **A**, **B**, TMP 86.194.8, fused and nearly complete frontals, in (**A**) dorsal and (**B**) ventral views; **C**, TMP 96.78.135, fused and nearly complete frontals with medial end of right prefrontal (arrow) preserved in articulation, in ventral view; **D**, **E**, TMP 95.181.67, fused frontals missing anterior part, in (**D**) dorsal and (**E**) ventral views. Provenances: TMP 86.194.8, 95.181.67, Dinosaur Park Formation (Judithian); TMP 96.78.135, Oldman Formation (Judithian). Genus and species indeterminate (**F–H**): UALVP 16234, nearly complete atlas missing part of left wall of neural arch, in (**F**) anterior, (**G**) posterior, and (**H**) right lateral views, with arrows indicating foramen on right side for exit of first spinal nerve. Provenance: Deadhorse Coulee Member, Milk River Formation (Aquilan). Specimens at same scale: scale bar = 1 mm.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CHAPTER 7 — MONOPHYLY AND INTRA-GENERIC RELATIONSHIPS OF ALBANERPETON ESTES AND HOFFSTETTER[1]

INTRODUCTION

Albanerpeton Estes and Hoffstetter is the type genus of the Albanerpetontidae Fox and Naylor and the better known of the two named genera currently included in the family. The genus includes seven species with a biogeographically interesting distribution: the type species is from the middle and, possibly, early Miocene of France (Estes and Hoffstetter, 1976; Estes, 1981; Gardner, 1999a; Rage and Hossini, 2000; here:Chapter 2), whereas the other six species range from the Aptian/Albian to late Paleocene of the North American Western Interior (Estes, 1981; Fox and Naylor, 1982; Gardner, 1999a, b, c, in press a; here:chapters 2–6). Relationships within Albanerpeton have not previously been considered in any detail, largely because until recently only four species were recognized, none of these were particularly well known, and few systematically informative characters had been identified. The phylogeny of Albanerpeton can now be examined thanks to recent redescriptions and reinterpretations of the four named congeners, the identification of additional characters and three new congeners (Gardner, 1999a, b, c, 2000, in press a; here:chapters 2–6), and new information on other albanerpetontid fossils and taxa (McGowan and Evans, 1995; McGowan and Ensom, 1997; McGowan, 1998; Gardner and Averianov, 1998; here:Chapter 2). My objectives here are to (1) assess the status and internal relationships of Albanerpeton and (2) use this phylogenetic framework to interpret the evolutionary history of the genus.

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[1] A version of this chapter has been submitted for publication. Gardner. Journal of Vertebrate Paleontology.

ANALYSIS

General Procedure and Searches for Trees

My analysis relies on 16 characters scored for the seven recognized species of Albanerpeton and three non-Albanerpeton albanerpetontids (Table 7-1). Another nine characters (6, 8, 12–14, and 16–19) are useful for diagnosing species, but are uninformative for assessing relationships within Albanerpeton; these were excluded from all searches. Taxa and characters are discussed further in separate sections below.

I used PAUP 3.1.1 (Swofford, 1993) for all searches and to compute consensus trees, generate tree statistics, perform bootstrap and decay analyses, and map the distribution of characters states. I employed the branch-and-bound search algorithm for all searches because this is an exact search method that finds all shortest trees (Swofford, 1993). I selected the "ladderize right" option for displaying trees (a personal preference that does not affect the topology of trees) and excluded the nine uninformative characters. In order to test for monophyly of Albanerpeton, I used the geologically oldest outgroup taxon, the Kirtlington species, to root the network and I did not constrain the ingroup (i.e., Albanerpeton) to be monophyletic. Using either of the other two non-Albanerpeton taxa to root the network did not alter topologies within Albanerpeton. I mapped the distribution of character states on the shortest trees using the accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) character state optimizations. These optimizations do not alter the topology of the tree, only the position at which a given character state is placed when alternative arrangements are equally parsimonious: ACCTRAN favours reversals over convergences when both interpretations are equally probable, whereas DELTRAN favours convergences over reversals (Swofford, 1993). Differences identified by these optimizations in the placement of character states may be important for formulating diagnoses for clades and tracing the evolution of characters. For all other operations, I used the default settings in PAUP 3.1.1.

Support for Clades

Of the various procedures available for assessing support for clades (see review by Olmstead and Palmer, 1994), here I use synapomorphy counts and bootstrap and decay analyses.

It is now widely accepted—although not always appreciated—that simply counting the number of synapomorphies supporting clades is a crude, and often, misleading way to assess support (e.g., Donoghue et al., 1992; Hillis and Bull, 1993; Olmstead and Palmer, 1994; Bremer, 1994; Wilkinson et al., 1998), except in rare cases where virtually no homoplasy exists (Olmstead and Palmer, 1994). I address this problem by differentiating between unambiguous synapomorphies and homoplasies. I also attempt to consider whether putative synapomorphies identified by one or the other of the character state optimizations are biologically reasonable.

Bootstrap analysis assesses support for clades by determining the number of times each clade appears in searches for shortest trees using resampled matrices. In brief, each bootstrap replicate or run begins by assembling a data matrix having the same taxa and number of characters that appear in the original matrix. Because the characters in the resampled matrix are chosen by random sampling with replacement (bootstrapping), some characters may appear more than once, whereas others may be absent. The shortest tree(s) are then constructed employing a user-specified search algorithm and compared with the original tree(s). This procedure is repeated numerous times ($\geq$ 100 replicates or runs). The frequency with which a given clade appears in all of the bootstrap runs is expressed as a percentage, called the bootstrap value. Felsenstein (1985), Sanderson (1989), Bryant et al. (1993), Hillis and Bull (1993), Bremer (1994), and Olmstead and Palmer (1994) provided useful overviews and discussed assumptions of the bootstrap analysis. Felsenstein (1985) proposed that bootstrap values can be used to place absolute confidence limits on phylogenies, but I follow Sanderson's (1989) and Hillis and Bull's (1993) more conservative interpretation in regarding bootstrap values as indicating relative support for clades in a given tree. As such, bootstrap values cannot be compared among different trees. For my bootstrap analysis, I ran 2000 replicates using the branch-and-bound search algorithm.

Decay analysis assesses the support for clades in a different manner, by using the original data matrix to search for trees successively longer than the shortest tree(s) until all clades collapse or dissolve (e.g., Bremer, 1988, 1994; Donoghue et al., 1992; Olmstead and Palmer, 1994). The number of extra steps longer than the minimum tree(s) needed to collapse a given clade is termed the decay index or Bremer value (Bremer, 1994). I ran a decay analysis for my matrix using the branch-and-bound search algorithm, beginning with a search for trees ≤ one step longer than the shortest trees and computing the strict consensus tree to determine if any clades were recovered in less than 100% of the saved trees. Each successive search saved and calculated the strict consensus for trees ≤ two steps longer than the shortest trees, ≤ three steps longer than the shortest tree, and so on, until all clades identified in the shortest tree were recovered in less than 100% of the saved trees.

TERMINAL TAXA

General Comments

Here I follow McGowan and Evans (1995) and my analysis in Chapter 8 (see also Gardner, in press b) in regarding (1) the Albanerpetontidae as a monophyletic clade nested within the Lissamphibia Haeckel, crownward of gymnophionans and as the sister-taxon to the salientians + caudates, and (2) lissamphibians as crown-clade temnospondyls. I also accept monophyly of Celtedens, the only supraspecific taxon included in my analysis, on the strength of the peculiar bulbous-shaped internasal process on the frontals (Gardner, 2000; here:Chapter 2). The remaining nine terminal taxa included in my analysis are diagnosable species, although not all have been formally named and described.

Outgroup Taxa

The most appropriate outgroups for assessing monophyly and intra-generic relationships of Albanerpeton are other albanerpetontids. Three Old World non-Albanerpeton albanerpetontids are known in sufficient detail to be included for this purpose and each character can be scored for at least one of the outgroups. Celtedens

McGowan and Evans includes two species known from skeletons—C. megacephalus (Costa) (early Albian, Italy) and C. ibericus McGowan and Evans (early Barremian, Spain) (Estes, 1981; McGowan and Evans, 1995). The genus is also represented by isolated elements, some of which may represent additional species from other Lower Cretaceous and Upper Jurassic sites in Europe (McGowan, 1998; Gardner, 2000; here:Chapter 2). The other two outgroup taxa are the unnamed Kirtlington species (late Bathonian, England) and the Anoual species (Berriasian, Morocco), both known by isolated jaws and frontals (Chapter 2). These unnamed taxa can justifiably be employed as separate outgroups because they differ in details of jaw and frontal construction, yet both exhibit a unique mixture of frontal and premaxillary character states that excludes them from Albanerpeton and Celtedens (Chapter 2).

Ingroup Taxa

Seven ingroup taxa are included in my analysis: the six named species of Albanerpeton described in the previous four chapters and the congeneric, unnamed Paskapoo species from the late Paleocene of Alberta. I did not include the A. nexuosus-like species from the latest Albian/earliest Cenomanian of Utah because the available, incomplete dentary and fused pair of premaxillae cannot be differentiated from those of A. nexuosus. This indeterminate species is informative, however, for establishing minimum times of origin for two of the less inclusive clades in the genus.

CHARACTER ANALYSIS AND DESCRIPTIONS

Character Analysis

My analysis uses 12 binary and four multistate informative characters, for a total of 20 derived states. Fifteen of these and the nine uninformative characters (eight binary and one multistate) describe attributes of the premaxilla, maxilla, dentary, and frontals. These elements are available for all but one of the terminal taxa. The exception is Albanerpeton cifellii, which is known only by its distinctive holotype premaxilla. The sole non-osteological character (25) describes body size. My scoring decisions for

Albanerpeton and the Kirtlington and Anoual species rely on firsthand study of specimens. Scoring decisions for *Celtedens* are composites based partly on McGowan and Evans' (1995) preliminary description and figures of skeletons of *C. ibericus* and my examination of the poorly preserved holotype skeleton of *C. megacephalus*, but largely on my examination of isolated skull elements (see McGowan and Ensom, 1997; Gardner, 2000; here:Chapter 2) of an indeterminate congener from the Early Cretaceous (Berriasian) of Purbeck, England. Specimens and literature examined are given in Appendix 7-1.

I polarized all but three characters against the three non-albanerpetontid outgroups using the outgroup comparison method (Watrous and Wheeler, 1981; Maddison et al., 1984; Bryant, 1991). Where polarities could not be decisively resolved (character 2) or were potentially misleading (characters 18 and 19) when assessed against non-*Albanerpeton* albanerpetontids, I instead relied on the condition in *A. arthridion*. The latter approach is one of two variations of the paleontological method for character state polarization (Bryant, 1991, 1997) and operates under the assumption that the geologically oldest member of the ingroup, in this case *A. arthridion*, exhibits the plesiomorphic condition for characters. Of the other 13 characters that can be scored for all three outgroup taxa, polarity decisions are unequivocal for nine characters (1, 3, 7, 9–11, 21, 22, and 25) and rely on the consensus of two of three outgroup taxa for two characters (23 and 24). For the remainder, polarity decisions are founded on two outgroups for six characters (12, 14–17, 20) and one outgroup for five characters (4–6, 8, 13).

I ran all characters as unweighted and most as unordered. I ran two multistate characters (10 and 22) as ordered because I regard states in each character as forming a linear transformation series. Running these characters as unordered did not alter the topologies or lengths of the shortest trees.

Character Descriptions

As specimens, structures, and characters relevant to the analysis are adequately figured in previous chapters and in papers cited in Appendix 7-2, I do not figure additional examples of these here.

Premaxilla (characters 1–14)

1. Build: 0, gracile; 1, robust—Although admittedly subjective, these two states are useful for describing differences in the relative build or construction of the premaxilla. This and the next three characters may be linked among species of Albanerpeton.

2. Height of pars dorsalis relative to width of process across suprapalatal pit (ratio of PDH:PDW^2): 0, "high," ratio of height versus width greater than about 1.55; 1, "low," ratio of height versus width less than about 1.55—The pars dorsalis is an elongate, broad process that extends dorsoposteriorly from the premaxilla. Outgroup comparisons are equivocal for interpreting polarities because the pars dorsalis is low in the Anoual species and, judging by McGowan and Evans' photograph (1995:fig. 1b) of the holotype skeleton of C. ibericus, high in Celtedens. I regard the latter state as primitive for Albanerpeton because this is the condition in A. arthridion.

3. Pattern of inter-premaxillary contact: 0, sutured; 1, fused—Premaxillae are sutured medially (i.e., paired) in most albanerpetontids, but are solidly fused in at least some individuals of Albanerpeton inexpectatum, A. nexuosus, and the Paskapoo species. Premaxillae fuse ontogenetically in A. inexpectatum (Gardner, 1999a; here:Chapter 3) and this may be true for the other two species.

4. Pattern of premaxillary-nasal contact: 0, premaxillary pars dorsalis minimally overlaps and abuts against or weakly sutures with anterior end of nasal; 1, premaxillary pars dorsalis minimally overlaps and strongly sutures with anterior end of nasal; 2, anterior end of nasal fits into lingual facet on premaxillary pars dorsalis and is braced ventrolaterally by expanded dorsal end of lateral internal strut—Although nasals remain unknown for Albanerpeton, the three patterns of premaxillary-nasal contact described above can be inferred from the structure of the dorsal end of the premaxillary pars dorsalis. The premaxilla and nasal are strongly sutured in A. inexpectatum, A. nexuosus, and the Paskapoo species, while the more complex third pattern is unique to A. cifellii.

5. Presence of boss: 0, present; 1, absent—The premaxillary boss is a raised bony patch or swelling dorsally on the labial face of the pars dorsalis. The boss is present in all Cretaceous species of Albanerpeton and is absent from both Tertiary congeners. Premaxillae of A. gracilis show that the boss appears ontogenetically (Chapter 6) and this may have been true for other species.

6. Relative size of boss, if present: 0, covers about dorsal quarter to third of pars dorsalis; 1, covers about dorsal half of pars dorsalis—The premaxillary boss is relatively small in most albanerpetontids and *Albanerpeton* *nexuosus* is unique in having a markedly larger boss. This character is inapplicable to the Tertiary congeners, because both lack the premaxillary boss.

7. Distribution of labial ornament, in large specimens: 0, restricted to dorsal part of pars dorsalis; 1, covers entire face of pars dorsalis—Premaxillary ornament in albanerpetontids generally is limited dorsally to the boss. Ornament is more extensive and covers the entire labial surface of the pars dorsalis on large premaxillae in the two Tertiary species of *Albanerpeton*. This character and character 5 may be linked, but I consider it prudent to regard these as distinct until the status of the premaxillary boss can be scored for non-*Albanerpeton* taxa other than the Anoual species.

8. Pattern of labial ornament: 0, discontinuous, anastomosing ridges and irregular pits; 1, continuous ridges enclosing polygonal pits; 2, pustulate—Premaxillary ornament in albanerpetontids typically consists of irregular pits and ridges. The second and third states are unique to, respectively, *Albanerpeton* *nexuosus* and *A*. *inexpectatum*.

9. Vertical position of suprapalatal pit on pars dorsalis: 0, "high," with ventral edge of pit well above dorsal face of pars palatinum; 1, "low," with ventral edge of pit just above or, more typically, continuous with dorsal face of pars palatinum—The suprapalatal pit opens high on the pars dorsalis in all non-*Albanerpeton* albanerpetontids and *A*. *arthridion*, but low in geologically younger species of *Albanerpeton*. In some referred premaxillae of *A*. *inexpectatum* a foramen opens lingually in the ventromedial corner of the pars dorsalis (Chapter 3, thereby displacing the suprapalatal pit dorsally to mimic the primitive state.

10. Size of suprapalatal pit relative to lingual surface area of pars dorsalis: 0, "small," about 1%; 1, "moderate," about 4–15%; 2, "large," about 20–25%—The relative size of the suprapalatal pit is described by three states that form a linear transformation series leading to increased size of the pit. The strikingly enlarged suprapalatal pit in *A*. *galaktion* is unique among albanerpetontids and is probably linked with enlargement of the palatal foramen (character 14).

11. Lingual outline of suprapalatal pit: 0, oval; 1, triangular or slit shaped—The suprapalatal pit is oval in most albanerpetontids, but triangular or slit shaped in Albanerpeton cifellii, A. gracilis, and A. galaktion.

12. Form of dorsal process on lingual edge of maxillary process: 0, low, isolated ridge; 1, high flange, continuous labially with base of lateral internal strut—The lingual edge of the maxillary process in albanerpetontids bears an unnamed dorsal process that, in life, abutted against and prevented the lingual margin of the complementary process on the maxilla from displacing posteriorly. This process typically is a low, isolated ridge. Albanerpeton nexuosus is unique in having the process developed into a high, labiolingually compressed, and dorsally convex flange that is continuous with a low ridge extending labiomedially across the dorsal face of the pars palatinum to the base of the lateral internal strut.

13. Form of vomerine process: 0, prominent; 1, weak—In most albanerpetontids the medial part of the pars palatinum on the premaxilla bears a lingually elongate and distally pointed vomerine process. The Paskapoo species is unique in having the process relatively shorter and blunt.

14. Diameter of palatal foramen relative to diameter of base of any one of the more medial premaxillary teeth: 0, "small," diameter of palatal foramen subequal to or, typically, considerably less than basal diameter of tooth; 1, "large," diameter of foramen greater than about one and one-third basal diameter of tooth—The palatal foramen is relatively small in all albanerpetontids, but it is markedly enlarged in Albanerpeton galaktion.

Maxilla and Dentary (characters 15–20)

15. Length of premaxillary lateral process on maxilla relative to height of process at base: 0, "long," length greater than height; 1, "short," length subequal to or less than height—The premaxillary lateral process on the maxilla extends anteriorly from the pars dentalis to labially overlap and fit into a complementary facet on the pars dentalis of the premaxilla. The process is primitively long in albanerpetontids, but it is relatively shorter in Albanerpeton inexpectatum, A. nexuosus, and the Paskapoo species.

16. Presence of dorsal process behind tooth row on dentary: 0, absent; 1, present—In most albanerpetontids, the dorsal edge of the dentary above the area for attachment of the postdentary bones descends posteroventrally from the posterior end of the tooth row. In Albanerpeton inexpectatum a process projects dorsally from behind the tooth row to labially overlap the coronoid process on the prearticular (Chapter 3).

17. Presence of labial ornament on maxilla and dentary, in large specimens: 0, absent; 1, present—The labial surfaces of the maxilla and dentary are typically smooth in albanerpetontids. On large maxillae and dentaries of Albanerpeton inexpectatum the labial surface is sparsely ornamented with pustules and short, anastomosing ridges (Chapter 3).

18. Labial or lingual profile of occlusal margins of maxilla and dentary: 0, occlusal margins essentially straight; 1, occlusal margins strongly convex or angular, with pars dentalis on maxilla and dental parapet on dentary deepest adjacent to tallest teeth, becoming shallower anterior and posterior from this region—This character cannot be decisively polarized by outgroup comparisons with non-albanerpetontids because the first state occurs in Celtedens, whereas the second state occurs in the Anoual and Kirtlington species. I regard an essentially straight occlusal margin on the maxilla and dentary as primitive for Albanerpeton because this is the condition in A. arthridion. Within the genus a more convex or angular occlusal margin is unique to A. nexuosus.

19. Size heterodonty of teeth on maxilla and dentary: 0, weakly heterodont; 1, strongly heterodont—Teeth vary in relative size along the maxilla and dentary in albanerpetontids: teeth are longest about a third of the distance along the row from the anterior end, and become smaller anterior and posterior from this region. Maxillary and dentary teeth in albanerpetontids generally are weakly heterodont in size, with the largest teeth only slightly longer relative to nearby teeth in the row. The Anoual and Kirtlington species and Albanerpeton nexuosus differ in having the teeth more strongly heterodont in size, with the longest teeth about a fifth to quarter again as long as nearby teeth. As outgroup comparisons are equivocal for assessing the polarity of this character, I view the weakly heterodont teeth in A. arthridion as reflecting the primitive condition for the genus.

Characters 18 and 19 are probably linked—as teeth about a third of the distance along the tooth row lengthen, the pars dentalis on the maxilla and dental parapet on the dentary must deepen to ensure that the teeth remain adequately braced labially. Although these characters could be combined into one I have not done so here, in part, because neither character is informative for assessing relationships within Albanerpeton and, in part, because I have found it easier to use separate characters to describe the profile of the jaw margin and heterodonty of the teeth.

20. Position of anterior end of maxillary tooth row relative to point of maximum indentation along leading edge of nasal process: 0, anterior to; 1, approximately in line—In albanerpetontids the leading edge of the nasal process is anteriorly concave in lingual outline. The anterior end of the tooth row generally lies several loci forward of a line extending ventrally from the point of maximum indentation along the leading edge of the nasal process, but in Albanerpeton inexpectatum, A. gracilis, and the Paskapoo species the anterior end of the tooth row lies approximately in line with the point of maximum indentation along the leading edge of the process.

Frontals (characters 21–24)

21. Dorsal or ventral outline of fused frontals: 0, bell or hourglass shaped; 1, triangular—The fused frontals are approximately triangular in Albanerpeton and more nearly hourglass or bell shaped in other albanerpetontids. The former condition more closely resembles the pattern in gymnophionans and non-lissamphibian temnospondyls—making allowances for the fact that frontals are paired, rather than fused—and can be regarded as primitive for albanerpetontids.

22. Midline length of fused frontals relative to width across posterior edge of bone, between lateral edges of ventrolateral crests (ratio of FL:FW[1]), in large specimens: 0, "long," ratio of length versus width greater than about 1.2; "moderate," ratio of length versus width between about 1.2 and 1.1; 2, "short," ratio of length versus width equal to or less than 1.0—Variation in the relative proportions of frontals are described using three states that form a linear transformation series leading to relatively shorter frontals. The intermediate state characterizes most Albanerpeton, whereas the more derived state is restricted to A. inexpectatum. Specimens available for A. inexpectatum show that frontals become relatively shorter with growth (Chapter 3); hence, estimates of relative frontal length for a given species ideally should be made from the largest available frontals.

23. Proportions of internasal process: 0, "short," length subequal to width; 1, "long," length greater than width—The internasal process projects anteriorly from the midline of the fused frontals. I regard a short internasal process as primitive for Albanerpeton because this state occurs in A. arthridion and two of the three non-

Albanerpeton outgroups. The Kirtlington species, A. inexpectatum, A. nexuosus, and the Paskapoo species have a more elongate internasal process.

24. Form of ventrolateral crest, in large specimens: 0, narrow and convex ventrally to bevelled ventrolaterally in transverse profile; 1, narrow and triangular in transverse profile, with ventral face flat to shallowly concave; 2, wide and triangular in transverse view, with ventral face deeply concave—Considering that the ventrolateral crest becomes more bevelled and relatively wider with growth (Gardner, 1999a; here:chapters 3, 6), this character should ideally be scored from the largest available specimens. Despite these problems, differences in crest form remain useful for characterizing species of Albanerpeton. I describe the width of the crest in relative terms, using the ratio (VCW:FW^2) of the width of the crest immediately behind the slot for receipt of the prefrontal versus the width across the posterior edge of the bone between the medial edges of the ventrolateral crests. The crest is relatively narrow (ratio less than about 0.40) in large individuals of all albanerpetontids, except for A. inexpectatum in which the crest is wider (ratio greater than about 0.45).

Body Size

25. Estimated, maximum snout-pelvic length (SPL): 0, "large," greater than about 50 mm; 1, "small," less than about 40 mm—I describe body size in albanerpetontids using the snout-pelvic length (see Chapter 2). This value can be measured directly from skeletons, but more commonly it is estimated from the midline length of frontals assuming a ratio of about 10:1 (Gardner, 1999b). This character is admittedly problematic, in part, because snout-pelvic length can be measured directly from only a few skeletons and, in part, because any measure of absolute size requires a large sample in order to estimate the upper size limit with any confidence. Despite these problems, I believe that maximum body size varies in an informative manner within Albanerpeton and that such differences are potentially important for inferences about lifestyles (Gardner, 1999b). In absolute terms albanerpetontids were relatively small animals and most taxa appear to have maximum inferred snout-pelvic lengths of about 50 mm to, perhaps as much as, 70 mm. Inferred body sizes in this range form a continuum. Albanerpeton arthridion and the Paskapoo species evidently were smaller, with maximum estimated snout-pelvic lengths of no more than 40 mm.

RESULTS

The branch-and-bound search yielded six shortest trees of 26 steps. Figure 7-1 depicts the strict consensus of these trees. Each of the shortest trees recovers a monophyletic Albanerpeton and the same four subgeneric clades. There are two sources of topological variation among the shortest trees. The first involves the inferred relationship between Albanerpeton and Celtedens: three of the trees identify these as sister-taxa, whereas the other three trees identify only an unresolved polychotomy among the three outgroups and Albanerpeton. Although the relationship between Albanerpeton and Celtedens is interesting and worthy of future study, it is irrelevant for assessing monophyly and relationships in Albanerpeton. The only significant variation concerns the unresolved relationships among the three members (A. galaktion, A. gracilis, and A. cifellii) of the gracile-snouted clade.

Below I report on the synapomorphies and support for the five clades of interest. Figure 7-1A and Table 7-2 show that levels of support for the five clades range from moderate to strong, with bootstrap values of 63 to 97% and decay values of one to four steps. Figure 7-1B reports the distribution of apomorphies for and within Albanerpeton, while Figure 7-2 presents the same information for topological variants in the gracile-snouted clade.

Albanerpeton: A. arthridion (robust-snouted clade + gracile-snouted clade)—Albanerpeton is supported by two frontal synapomorphies: 21(1), frontals triangular in outline; and 22(1), frontals moderately elongate. Support for Albanerpeton is modest, with the clade having the second lowest bootstrap value (72%) and decay value (two steps; tied with the post-middle Albian clade).

Post-middle Albian clade: robust-snouted clade + gracile-snouted clade—A less inclusive clade containing all species of Albanerpeton except A. arthridion is diagnosed by having the suprapalatal pit low on the premaxillary pars dorsalis [9(1)] and occupying at least four percent of the area of the pars dorsalis [10(1)]. Support for this clade is also modest. The clade has the third lowest bootstrap value (73%) and collapses after two additional steps.

Robust-snouted clade: Albanerpeton nexuosus (A. inexpectatum + Paskapoo species)—The robust-snouted clade is diagnosed by a suite of four jaw synapomorphies that are unique within the Albanerpetontidae: 1(1), premaxillae robust; 3(1), premaxillae variably fused medially; 4(1), premaxilla strongly sutured dorsally with nasal; and 15(1), relatively short premaxillary lateral process on maxilla. Two homoplastic characters also support the clade. A short pars dorsalis on the premaxilla [2(1)] is convergent with the Anoual species, whereas an elongate internasal process on the frontal [23(1)] is convergent with the Kirtlington species. The robust-snouted clade is one of the two best supported clades in my analysis, with the second highest bootstrap value (95%) and the highest decay value (four steps). Even in the 589 trees of ≤ 30 steps (i.e., minimum plus four steps), the clade is still recovered in 585 or over 99% of the trees (Table 7-2).

Tertiary clade: Albanerpeton inexpectatum + Paskapoo species—Loss of the premaxillary boss [5(1)] and development of extensive ornament across the labial face of the premaxillary pars dorsalis [7(1)] are synapomorphic for the two Tertiary species of Albanerpeton. This sister-pair relationship is also supported by a homoplasy—anterior end of maxillary tooth row located more posteriorly [20(1)]—convergent with A. gracilis. The ACCTRAN optimization further postulates that a short frontal [22(2)] is synapomorphic for the two Tertiary congeners, but this is unreliable because the character cannot be scored from the one incomplete pair of frontals available for the Paskapoo species. The more conservative and preferred DELTRAN optimization regards a short frontal as autapomorphic for A. inexpectatum. The Tertiary clade is the second of the two best supported clades in my analysis, with the highest bootstrap (97%) and second highest decay (three steps) values.

Gracile-snouted clade: Albanerpeton galaktion + A. gracilis + A. cifellii—Members of the gracile-snouted clade are united by a unique triangular to slit shaped suprapalatal pit [11(1)]. This is the weakest supported clade in my analysis, with both the lowest bootstrap (63%) and decay (one step) values. Three topological variants, of two trees each, are recovered (Fig. 7-2). The first two variants postulate a sister-pair relationship between A. cifellii and either A. galaktion, based on the narrow and triangular ventrolateral crest [24(1)], or A. gracilis, based on the more posterior position of the anterior end of the maxillary tooth row [20(1)] (Fig. 7-2A and B, respectively). Neither arrangement is defensible, as each hinges upon a character state that cannot be scored for A. cifellii and is postulated to be synapomorphic for the sister-pair only by the ACCTRAN optimization. Within the gracile-snouted clade DELTRAN more conservatively restricts character 24(1) to A. galaktion and character 20(1) to A. gracilis. In the third topological variant (Fig. 7-2C) relationships among A. cifellii, A. galaktion, and A. gracilis are unresolved; this is the most conservative and my preferred arrangement.

DISCUSSION

Monophyly of Albanerpeton and Taxonomic Implications

My analysis corroborates monophyly of Albanerpeton. The strength of this corroboration is admittedly moderate, as evidenced by bootstrap and decay values of 72% and two steps, respectively. Nevertheless, alternative arrangements that recover a paraphyletic Albanerpeton are far less well supported. For example, the most common topologies of this sort identified by the decay analysis (Anoual species + Celtedens + A. arthridion) and bootstrap analysis (same clade + species in the gracile-snouted clade) are recovered in, respectively, just 11% of 81 trees two steps longer than the minimum and 17% of 2000 bootstrap replicates. Although indices for support of the genus are moderate, both of the synapomorphies for Albanerpeton are unique within the Albanerpetontidae to the genus and one, frontals triangular in outline, appears to be unique at a more inclusive level among temnospondyls as a whole. Six other frontal character states collectively differentiate Albanerpeton from other albanerpetontids (Gardner, 2000; here:Chapter 2), but were not included here because they are uninformative for assessing relationships within the genus: internasal process pointed in dorsal or ventral outline; lateral face of internasal process indented by anteroposteriorly elongate groove for tongue-in-groove contact with medial edge of nasal; anterolateral process prominent and pointed distally; dorsal and ventral edges of slot for receipt of prefrontal excavated medially; anterior end of orbital margin located approximately in line with, or posterior to, anteroposterior midpoint of frontals; and orbital margin uniformly shallowly concave to nearly straight along entire length in dorsal or ventral outline. A pointed internasal process is primitive for albanerpetontids (Gardner, 2000; here:Chapter 4), but further work is needed to clarify polarities and distributions of the other five character states within the family.

As recognized here, Albanerpeton extends from the latest Aptian/earliest Albian to late Miocene (MN 7+8) or about 100 million years according to recent time scales for the Mesozoic (Gradstein et al., 1995), Cenozoic (Berggren et al., 1995), and European Neogene (Steininger et al., 1996) (Fig. 7-3). This range is admittedly extensive and the validity of the genus could be questioned on these grounds. Based on the phylogenetic framework proposed here, Albanerpeton could be partitioned and the generic name restricted to any of the four less inclusive monophyletic units that includes the type species—A. inexpectatum alone or the Tertiary, robust-snouted, or post-middle Albian clades. Compared to Albanerpeton, each of these four less inclusive groups is better supported (Fig. 7-1) and the stratigraphical ranges of the first two are also considerably shorter (Fig. 7-3), at about 40 and 4 million years, respectively. Depending on which less inclusive group is chosen to bear the name Albanerpeton, however, one to as many as four new genera would have to be erected to accommodate the excluded former congeners. The gracile-snouted clade and A. nexuosus may be distinctive enough to warrant separate generic rank, but this is more difficult to justify for A. arthridion and the Paskapoo species. Partitioning Albanerpeton into two or more less inclusive genera also does not better reflect the inferred phylogeny of taxa. In short, I see no compelling reason not to accept Albanerpeton as a long lived Euramerican genus.

Evolution of Albanerpeton

Over the first half of the known record for Albanerpeton, from the latest Aptian/earliest Albian to late Paleocene, and six of the seven congeners are restricted to the North American Western Interior. These occurrences, plus the apparent lack of pre-Miocene occurrences elsewhere and the phylogenetic framework proposed above, imply that much of the evolutionary history of the genus was centered in the Western Interior. Evolution of the genus in this region was undoubtedly tied to the fate of the lush, broad coastal plain that bordered the western margin of the Western Interior Seaway during the Late Cretaceous.

Three lines of evidence are consistent with a North American origin for Albanerpeton: (1) the geologically oldest record for the genus (A. arthridion) is in the latest Aptian or earliest Albian of Oklahoma (Gardner, 1999b; here:Chapter 4); (2) the phylogenetically most basal congener, also A. arthridion, is from the continent (Gardner, 1999b; here:Chapter 4); and (3) despite a modest record of paracontemporaneous and older albanerpetontids from elsewhere—Bathonian to Albian of Europe and Berriasian of North Africa (Fig. 7-3 and Appendix 7-2)—none of these pertain to Albanerpeton. The North American origin hypothesis will obviously be tested as additional Lower Cretaceous and older albanerpetontid fossils are discovered outside of North America. A minimum date of latest Aptian/earliest Aptian, or about 112 million years (Gradstein et al., 1995), for the origin of the genus is provided by A. arthridion in the middle Antlers Formation of Oklahoma (Gardner, 1999b; here:Chapter 4). Given that this occurrence is also the earliest, reliably dated record for albanerpetontids in North America and that putative Albanerpeton sister-taxa are even older, a basal Cretaceous or earlier origin for Albanerpeton is probable.

The phylogenetic hypothesis presented here provides a basis for tracing and interpreting character state evolution within Albanerpeton. Osteological modifications in the genus initially are limited to the frontals, then shift primarily to the jaws. The most obvious effects of these changes are in altering the relative dimensions of the head and strengthening the jaws and snout region. The functional significances of these modifications are largely speculative, but they probably acted in concert to enhance feeding and head-first burrowing. The triangular and moderately elongate frontals of Albanerpeton evidently are associated with increasing the width of the skull. Among extant lissamphibians a broad head has been implicated in increasing the size range of available prey, by virtue of increasing the gape of the mouth (e.g., Maglia, 1996).

The chronologically next series of modifications affect the suprapalatal pit in the premaxilla. These changes occur at two successively less inclusive nodes: the suprapalatal pit increases in size and shifts ventrally at the node for the post-middle Albian clade, then further changes from oval to slit or triangular shaped at the less inclusive node for the gracile-snouted clade. Assuming that the suprapalatal pit housed a gland involved in feeding, olfaction, or both (Fox and Naylor, 1982; Gardner, 1999c, 2000; here:Chapter 2), modifications to the pit presumably were reflected, in life, by changes to the form and function of the gland. An incomplete pair of Albanerpeton nexuosus-like premaxillae from the upper part of the Cedar Mountain Formation in Utah (Gardner, 1999c; here:Chapter 5) provides a minimum age of latest Albian/earliest Cenomanian for both the establishment of the post-middle Albian clade and the divergence of the gracile- and robust-snouted clades. The appearance of the A. nexuosus-like species coincides with the establishment of the Bering Land Bridge that linked Asia with the North American western subcontinent through the Late Cretaceous (Russell, 1993; Smith et al., 1994; Sereno, 1997). While this raises the possibility that the A. nexuosus-like taxon may be an Asian immigrant and, by implication, the post-middle Albian clade Asiatic in origin, further consideration of these ideas is hampered by the sparse record for albanerpetontids in Asia. The only Asian fossils identified to date are five indeterminate dentaries from the Cenomanian and Coniacian of Uzbekistan (Gardner and Averianov, 1998) that only primitively resemble dentaries of North American taxa.

The unique shape of the suprapalatal pit is the sole innovation identified for the gracile-snouted clade. Relationships within the gracile-snouted clade are unresolved and will probably continue to be so until additional elements are available for Albanerpeton cifellii. The middle Campanian species A. gracilis is a good structural ancestor for the gracile-snouted clade, although the species is too young to be ancestral to either A. cifellii (late Turonian) or A. galaktion (Campanian and Maastrichtian). The gracile-snouted clade is known only from the Late Cretaceous of the Western Interior and, thus, appears to be endemic to the region. Although the gracile- and robust-snouted clades presumably diverged around the Albian–Cenomanian boundary (see above), the earliest direct evidence for the gracile-snouted clade occurs some 10 million years later, in the form of the holotype premaxilla of A. cifellii from the late Turonian part of the Straight Cliffs Formation in Utah (Gardner, 1999c; here:Chapter 5). The last appearance of the clade is recorded by a referred premaxilla of A. galaktion from the late Maastrichtian Lance Formation in Wyoming (Chapter 6).

The robust-snouted clade is characterized by modifications to the premaxilla and maxilla that strengthened the snout, presumably for some combination of burrowing and feeding (Gardner, 1999a). The functional significance of the modified internasal process on the frontals is less certain, although this spike-like process may also have contributed in some way to strengthening the anterior part of the skull. Two divergent strategies are seen within the clade for further strengthening the premaxillary pars dorsalis. In Albanerpeton nexuosus, the boss expands ventrally to cover about the dorsal half of the process. The boss is absent in the two Tertiary congeners, but this loss evidently is compensated for by the labial ornament spreading across the entire face of the process. The robust-snouted clade includes the only albanerpetontids known to have survived the K/T extinction event. The last appearance of the genus in North America is marked by skull elements of the unnamed Paskapoo species in the late Paleocene of Alberta (Gardner, unpublished). In the absence of any earlier record for the genus in Europe and given the reconstructed phylogeny presented here, the best explanation for the presence of *A. inexpectatum* in the Miocene of France remains the Tertiary or, perhaps earlier, immigration of an unknown ancestral species from North America (Gardner, 1999a; here:Chapter 3).

CONCLUSIONS

My cladistic analysis of 16 characters scored for the seven species of *Albanerpeton* and three other albanerpetontid taxa yields the following results and observations:

(1) Monophyly of *Albanerpeton* is corroborated and the hypothesized pattern of relationships is as follows: *A. arthridion* ((*A. cifellii* + *A. galaktion* + *A. gracilis*) (*A. nexuosus* (Paskapoo species + *A. inexpectatum*))). The two frontal synapomorphies for *Albanerpeton* are associated with broadening the head. Synapomorphies for less inclusive clades and apomorphies of species largely involve character states related to strengthening the jaws and snout. In general, cranial modifications in the genus appear to be associated with feeding, burrowing, or some combination of these activities.

(2) Support for *Albanerpeton* is moderate, as evidenced by bootstrap and decay values of 72% and two steps, respectively, and the genus as recognized here has an extensive temporal range of some 100 million years. Nevertheless, the phylogenetic hypothesis I have presented remains the best arrangement for the seven species. A paraphyletic *Albanerpeton* that includes other albanerpetontids is far less well supported and there is no advantage to partitioning *Albanerpeton* into smaller monophyletic genera.

(3) Fossil occurrences and hypothesized relationships within the genus suggest that the history of *Albanerpeton* is centered in North America. *Albanerpeton* may have originated on the continent, but the earliest occurrence in the latest Aptian/earliest Albian of Oklahoma undoubtedly underestimates the time of origin for the genus. All four of the

less inclusive clades appear to have originated in North America. The final and only occurrence from elsewhere, that of the type species A. inexpectatum in the Miocene of France, is probably due to the immigration of an unknown ancestral species from North America.

(4) Despite advances in our understanding of relationships among species of Albanerpeton, the phylogenetic position of the genus is uncertain. No synapomorphies convincingly support a sister-pair relationship between Albanerpeton and any other albanerpetontid taxon. Studies now in progress by various workers on Old World albanerpetontid fossils and taxa should lead to a better understanding of generic level relationships in the family.

TABLE 7-1. Data matrix of the 25 characters scored for three non-*Albanerpeton* albanerpetontid outgroups and seven species of *Albanerpeton*. Nine characters (6, 8, 12–14, and 16–19) are uninformative for assessing relationships within *Albanerpeton* and were excluded from the analysis, but remain useful for diagnosing individual species. Conventions: 9, inapplicable character; ?, state unknown. Final column is percentage of missing records (i.e., unknown + inapplicable).

	00000	00001	11111	11112	22222	percent missing
	12345	67890	12345	67890	12345	
Kirtlington species	0?0??	?0?00	00000	00110	00110	20
Anoual species	01000	00000	00?00	??110	00000	12
Celtedens	000??	?0?00	0????	0000?	00000	36
Albanerpeton arthridion	00000	00000	0000?	00000	11001	4
Albanerpeton gracilis	00000	00011	10000	00001	11000	0
Albanerpeton galaktion	00000	00012	10010	?0000	11010	4
Albanerpeton cifellii	00020	00011	1000?	?????	?????	44
Albanerpeton nexuosus	11110	10111	01001	00110	11110	0
Albanerpeton inexpectatum	11111	91211	00001	11001	12120	4
Paskapoo species	11111	91011	00101	00001	1?101	8

TABLE 7-2. Bootstrap and decay values for Albanerpeton and less inclusive clades in searches for trees up to four steps longer than the minimum of 26 steps.

Clade	Bootstrap value (percent for 2000 runs)	Percentage of trees recovering clade				
		26 steps (6 trees)	≤ 27 steps (30 trees)	≤ 28 steps (81 trees)	≤ 29 steps (309 trees)	≤ 30 steps (589 trees)
Albanerpeton	72	100	100	56	49	46
post-middle Albian clade	73	100	100	78	54	34
robust-snouted clade	95	100	100	100	100	99
Tertiary clade	97	100	100	100	90	90
gracile-snouted clade	63	100	20	70	34	33

FIGURE 7-1. Strict consensus of six shortest trees based on 16 informative characters scored for three outgroup taxa and seven species of Albanerpeton. **A**, strict consensus tree showing names and indices of support for clades. Indices of support to left of node: upper values are number of unambiguous synapomorphies/total number of synapomorphies; lower values are bootstrap value (%) for 2000 replicates and, in brackets, decay index (steps). **B**, strict consensus tree, with outgroups deleted, showing distribution of apomorphies for all 25 characters within Albanerpeton as mapped by the DELTRAN character state optimization and the most conservative, preferred arrangement of apomorphies within the gracile-snouted clade. The ACCTRAN optimization differs only in shifting character state 22(2) stemward to the more inclusive node for the Tertiary clade. Figure 7-2 depicts alternative arrangements for apomorphies in the gracile-snouted clade. Symbols for apomorphies are: horizontal bar, unique apomorphy; solid circle, convergent within Albanerpeton; solid square, convergent with one or more non-Albanerpeton albanerpetontids; and open square, convergent within Albanerpeton and with a non-Albanerpeton albanerpetontid. Tree statistics (uninformative characters excluded): tree length = 26 steps; CI = 0.769, HI = 0.231, and RI = 0.818.

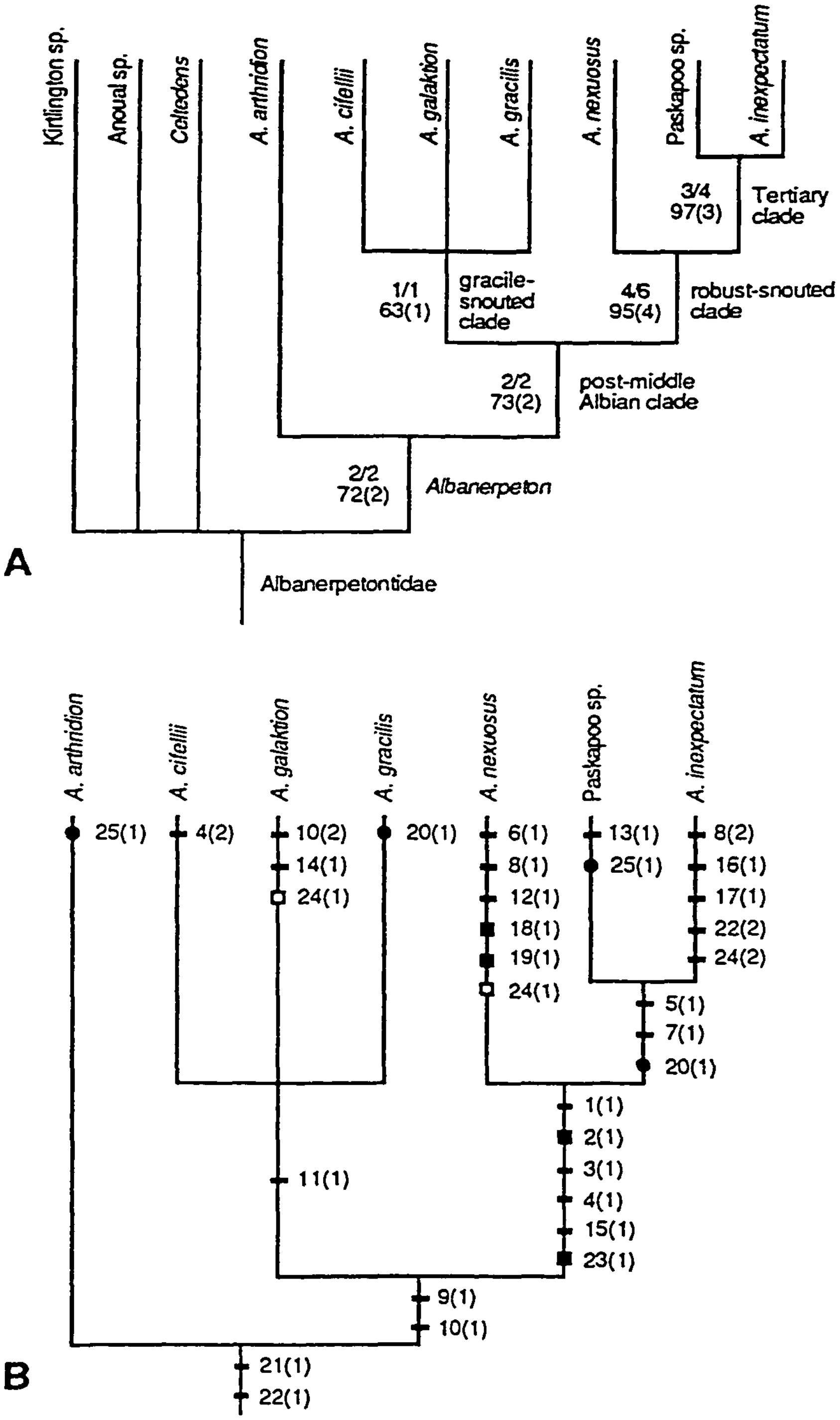

Kirtlington sp.
Anoual sp.
Celtedens
A. arthridion
A. cifellii
A. galaktion
A. gracilis
A. nexuosus
Paskapoo sp.
A. inexpectatum
3/4
97(3)
Tertiary clade
1/1
63(1)
gracile-snouted clade
4/6
95(4)
robust-snouted clade
2/2
73(2)
post-middle Albian clade
2/2
72(2)
Albanerpeton
A
Albanerpetontidae
A. arthridion
A. cifellii
A. galaktion
A. gracilis
A. nexuosus
Paskapoo sp.
A. inexpectatum
25(1)
4(2)
10(2)
14(1)
24(1)
20(1)
6(1)
8(1)
12(1)
18(1)
19(1)
24(1)
13(1)
25(1)
8(2)
16(1)
17(1)
22(2)
24(2)
5(1)
7(1)
20(1)
1(1)
2(1)
3(1)
4(1)
15(1)
23(1)
11(1)
9(1)
10(1)
21(1)
22(1)
B

FIGURE 7-2. The three topological variants recovered in the gracile-snouted clade and distribution of apomorphies as mapped by DELTRAN (left) and ACCTRAN (right) character state optimizations. A, topological variant I: Albanerpeton gracilis (A. galaktion + A. cifellii). B, topological variant II: A. galaktion (A. gracilis + A. cifellii). C, topological variant III: A. galaktion + A. gracilis + A. cifellii. Each topological variant is recovered in two trees. The hypothesized sister-pair relationships in the first two topological variants are each founded on one convergence identified only by ACCTRAN and involve a character that cannot be scored for A. cifellii. The unresolved trichotomy identified in the third topological variant is the most conservative and preferred arrangement.

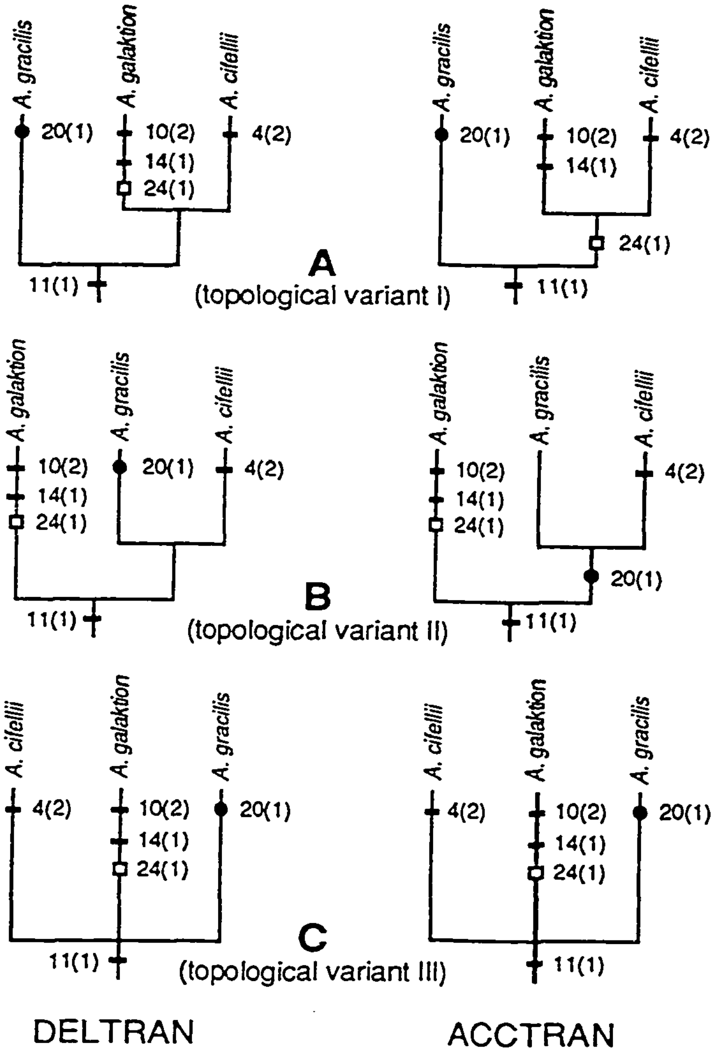
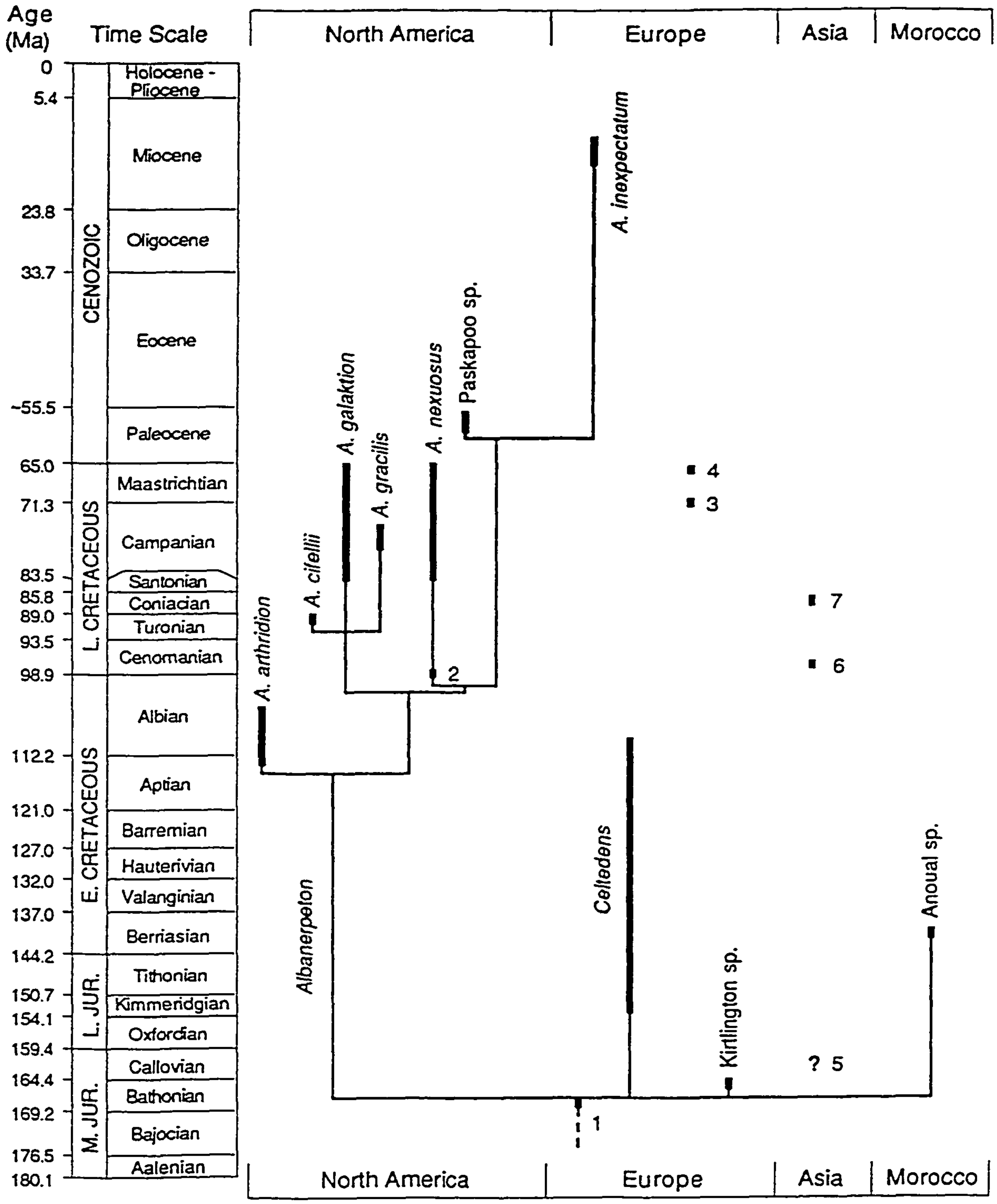


FIGURE 7-3. Strict consensus of the six shortest trees generated in my analysis, showing stratigraphical and geographical ranges of terminal taxa, estimated divergence times, and notable occurrences of other albanerpetontids (1–7; see Appendix 7-2). Absolute ages are from Gradstein et al. (1995) and Berggren et al. (1995).


Age (Ma)
Time Scale
North America
Europe
Asia
Morocco
0
5.4
23.8
33.7
~55.5
65.0
71.3
83.5
85.8
89.0
93.5
98.9
112.2
121.0
127.0
132.0
137.0
144.2
150.7
154.1
159.4
164.4
169.2
176.5
180.1
CENOZOIC
L. CRETACEOUS
E. CRETACEOUS
L. JUR.
M. JUR.
Holocene - Pliocene
Miocene
Oligocene
Eocene
Paleocene
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Tithonian
Kimmeridgian
Oxfordian
Callovian
Bathonian
Bajocian
Aalenian
A. arthridion
A. cifellii
A. galaktion
A. gracilis
A. nexuosus
Paskapoo sp.
A. inexpectatum
Albanerpeton
Celtedens
Kirtlington sp.
Anoual sp.
1
2
3
4
? 5
6
7
North America
Europe
Asia
Morocco

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APPENDIX 7-1. Taxa, specimens, and literature examined.

Albanerpeton: A. inexpectatum, jaws and frontals listed in Chapter 3; A. arthridion, jaws and frontals listed in Chapter 4; A. cifellii, holotype premaxilla described in Chapter 5; A. galaktion, A. gracilis, and A. nexuosus, jaws and frontals listed in Chapter 6; and Paskapoo species (unnamed Albanerpeton sp.), undescribed jaws and frontals in collections of the UALVP. **Celtedens**: specimens: C. megacephalus, holotype skeleton (MNP 542); and Celtedens sp., jaws and frontals from Purbeck (Berriasian), England, in collection of the DORCM, including specimens listed by McGowan and Ensom (1997) and in Chapter 2; literature: C. ibericus, holotype skeleton (LH 6020; McGowan and Evans, 1995). **Kirtlington species**: jaws and frontals listed by McGowan (1996) and in Chapter 2 in collections of the BMNH and UCL. **Anoual species**: undescribed jaws and frontals in collection of the MNHN.MCM.

APPENDIX 7-2. Stratigraphical and geographical information used to construct Figure 7-3.

Albanerpeton arthridion, first: middle clay unit (latest Aptian/earliest Albian) Antlers Formation, Oklahoma; last: upper sand unit (early-middle Albian) Antlers Formation, Texas; jaws, frontals, atlantes, and humeri (Fox and Naylor, 1982; Gardner, 1999b; here:Chapter 4). ***A. cifellii***, Smoky Hollow Member (late Turonian), Straight Cliffs Formation, Utah; holotype premaxilla (Gardner, 1999c; here:Chapter 5). ***A. galaktion***, first: Deadhorse Coulee Member (early Campanian), Milk River Formation, Alberta; last: Lance Formation (late Maastrichtian), Wyoming; jaws and frontals (Fox and Naylor, 1982; Gardner, in press a, here:Chapter 6). ***A. gracilis***, Dinosaur Park and Oldman formations, Alberta, Kaiparowits Formation, Utah, and Aguja Formation, Texas (all middle Campanian); jaws and frontals (Gardner, in press a, here:Chapter 6). ***A. nexuosus***, first: Deadhorse Coulee Member (early Campanian), Milk River Formation, Alberta; last: Lance Formation, Wyoming, Hell Creek Formation, Montana, and Laramie Formation, Colorado (all late Maastrichtian); jaws and frontals (Estes, 1981; Gardner, in press a, here:Chapter 6). **Paskapoo species** (unnamed *Albanerpeton* sp.), Paskapoo and Porcupine Hills formations (late Paleocene; Fox, 1990), Alberta (Fox and Naylor, 1982:table 1; Gardner, unpublished); undescribed jaws, frontals, and parietal. ***A. inexpectatum***, first: unnamed terrigenous unit (middle middle Miocene), Sansan, France; last: fissure fills (late middle Miocene) near La Grive-St. Alban, France; skull and postcranial bones (Estes and Hoffstetter, 1976; Estes, 1981; Gardner, 1999a; Rage and Hossini, 2000; here:Chapter 3). ***Celtedens***, first: *Celtedens* sp., unnamed unit (early Kimmeridgian; Zinke, 1998), Guimarota, Portugal; last: *C. megacephalus*, "Calcari ad Ittioliti," (early Albian; Bravi, 1994), Pietraroia, Italy; isolated bones and rare skeletons (Estes, 1981; McGowan and Evans, 1995; McGowan and Ensom, 1997; McGowan, 1998; Gardner, 2000; here:Chapter 2). **Kirtlington species**, Forest Marble Formation (late Bathonian), England; skull and postcranial bones (McGowan, 1996; Gardner, 2000; here:Chapter 2; Gardner, Evans, and Sigogneau-Russell, unpublished). **Anoual species**, unnamed limestone lens (Berriasian), "Couches-Rouges" sandstone, Morocco (Sigogneau-Russell et al., 1998); jaws and frontals (Gardner, Evans, and Sigogneau-Russell, unpublished). **1, Albanerpetontidae indet.**, unnamed unit, Gardies, France (Seiffert, 1969; Estes and Hoffstetter, 1976; Estes, 1981); atlantal centrum originally considered to be late Bajocian in age, but now regarded as early Bathonian (Kriwet et al., 1997). **2, *Albanerpeton* sp., cf. *A. nexuosus***, Mussentuchit Member (latest Albian/earliest Cenomanian) Cedar Mountain Formation, Utah; dentary and fused premaxillae (Gardner, 1999c; here:Chapter 5). **3, Albanerpetontidae indet.**, unnamed unit (late Campanian/early Maastrichtian; Le Loeuff and Buffetaut, 1995), Laño, Spain; dentaries and humeri (Duffaud and Rage, 1999). **4, Albanerpetontidae indet.**, Densuş-Ciula Formation (late Maastrichtian), Romania; incomplete jaws, frontals, and postcranial bones (Grigorescu et al., 1999). **5, ?Albanerpetontidae indet.**, upper part of Balabansay Formation (Callovian), Tashkumyr, Kirghizia; unproven record (Gardner and Averianov, 1998) based on an undescribed and unfigured frontal (Nessov, 1988). **6, Albanerpetontidae indet.**, upper part of Khodzhakul Formation (early Cenomanian), Chelpyk and Sheikdzheili localities, Uzbekistan (Nessov, 1981, 1988, 1997; Gardner and Averianov, 1998); dentaries, including holotype of *Nukusurus insuetus* Nessov *nomen dubium* (Gardner and Averianov, 1998). **7, Albanerpetontidae indet.**, upper part of Bissekty Formation (Coniacian) Dzhyrakuduk, Uzbekistan (Nessov, 1988, 1997); holotype dentary of *Nukusurus sodalis* Nessov *nomen dubium* (Gardner and Averianov, 1998).

CHAPTER 8 — MONOPHYLY AND AFFINITIES OF THE ALBANERPETONTIDAE FOX AND NAYLOR (TEMNOSPONDYLI; LISSAMPHIBIA)[1]

INTRODUCTION

While there is widespread agreement that the Albanerpetontidae Fox and Naylor are closely related to the lissamphibian clades Caudata Scopoli (sensu Milner, 1988), Salientia Laurenti, and Gymnophiona Rafinesque, the pattern of this relationship remains unclear. Species now recognized as albanerpetontids originally were interpreted as aberrant caudates and often have been allied with several undoubted caudate genera in the fossil family Prosirenidae Estes (Estes, 1969, 1981; Estes and Hoffstetter, 1976; Estes and Sanchíz, 1982; Nessov, 1981, 1988; Duellman and Trueb, 1986; Carroll, 1988; Trueb and Cloutier, 1991; Roček, 1994; McCord, 1999). Fox and Naylor (1982) argued that Albanerpeton, then the only recognized "albanerpetontid" genus, was not a caudate, but a member of a previously unrecognized lineage of possible lissamphibians, for which they erected the new family Albanerpetontidae and order Allocaudata. Fox and Naylor's proposal has been endorsed in many recent papers (McGowan and Evans, 1995; McGowan, 1996, 1998a; McGowan and Ensom, 1997; Nessov, 1997; Gardner and Averianov, 1998; Duffaud and Rage, 1999; Gardner, 1999a–c, 2000a, b, in press a, b), although the ordinal name Allocaudata has not been widely adopted. Milner (1988) considered evidence for or against an albanerpetontid–caudate relationship inconclusive, leading him (Milner, 1988, 1993a, 1994) and Rage and Hossini (2000) to regard the Albanerpetontidae as incertae sedis within the Lissamphibia Haeckel.

Attempts to elucidate the higher level relationships of albanerpetontids have, and continue to be, complicated by two major factors. First, albanerpetontids exhibit numerous autapomorphies, such as a peculiar interlocking joint between the mandibles, chisel-like marginal teeth, and highly modified cervical vertebrae. Although these unique

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[1] A version of this chapter has been accepted for publication. Gardner. Zoological Journal of the Linnean Society.

features are useful for characterizing albanerpetontids, they are uninformative for assessing the affinities of the group. Second, until recently albanerpetontids were represented largely by isolated and occasional articulated elements, particularly jaws, frontals, and vertebrae. Phylogenetically critical regions of the skeleton, such as the palate and girdles, were essentially unknown. Several years ago, McGowan and Evans (1995) announced the discovery of two well-preserved albanerpetontid skeletons from the Lower Cretaceous (Barremian) Las Hoyas locality of Spain. When described and interpreted in detail, these skeletons should prove useful for clarifying some aspects of albanerpetontid morphology and assessing the relationships of the clade.

In the meantime, however, the affinities of the Albanerpetontidae remain unresolved. Three published cladistic analyses have examined the position of albanerpetontids: Trueb and Cloutier (1991) and McCord (1999) hypothesized that albanerpetontids were caudates, whereas McGowan and Evans (1995) provisionally placed albanerpetontids as the sister-taxon of caudates plus salientians. During my studies on the group (Gardner and Averianov, 1998; Gardner, 1999a–c, 2000a, b, in press b), I have examined most of the important collections of albanerpetontid fossils. This has allowed me to evaluate characters used in past debates about the relationships of albanerpetontids and identify additional characters that bear on this issue. Here I present a cladistic analysis of higher level relationships among lissamphibians and select non-lissamphibian temnospondyls that (1) tests for monophyly of the Albanerpetontidae (i.e., Albanerpeton + Celtedens), (2) assesses whether albanerpetontids nest within the Lissamphibia, and (3) if so, examines whether albanerpetontids share a special relationship with caudates.

CRITIQUE OF PREVIOUSLY PUBLISHED CLADISTIC ANALYSES

Trueb and Cloutier's (1991) Analysis

Trueb and Cloutier (1991) used three different character sets to examine the higher level relationships of lissamphibians. Their third analysis relied on 58 osteological characters (51 informative and seven uninformative; their data set II) and loxommatids (= Baphetidae Cope; sensu Milner 1993a) and four basal and intermediate temnospondyl genera as outgroups to examine relationships among 12 dissorophoid-grade temnospondyl genera, five lissamphibian taxa, and Albanerpeton. Figure 8-1A depicts a simplified version of their published strict consensus tree (Trueb and Cloutier, 1991:fig. 4), showing Albanerpeton in an unresolved trichotomy with the Middle Jurassic stem-caudate Karaurus Ivachnenko and the crown-clade salamanders Urodela Dumèril (sensu Milner, 1988; = "Caudata" of Trueb and Cloutier, 1991). Trueb and Cloutier's (1991) consensus tree is founded on 12 equally shortest trees—six of these identified Albanerpeton as the sister-taxon of Karaurus and the other six identified Albanerpeton as the sister-taxon of the Urodela (cf., Trueb and Cloutier, 1991:figs. 6, 7).

Trueb and Cloutier's (1991) placement of Albanerpeton within the Caudata (= "Urodela" as used by these authors) needs to be reconsidered for three reasons. First, my re-analysis of their published data matrix (Trueb and Cloutier, 1991:appendix II), with their uninformative characters excluded, yielded a strict consensus tree (Fig. 8-1B) founded on 56 shortest trees at 113 steps (versus 12 trees at 104 steps). The topology of my strict consensus tree also differs in recognizing an unresolved polychotomy among the micromelerpetontid Micromelerpeton Bulman and Whittard, the branchiosaurids Leptorophus Bulman and Whittard, Schoenfelderpeton Boy, Branchiosaurus Fritsch, and Apateon Meyer, and the Lissamphibia. The 50% majority rule consensus tree (not shown) of my re-analysis differs from both strict consensus trees in placing Micromelerpeton as the sister-taxon to a now monophyletic Branchiosauridae Fritsch, with the latter being recovered in 57% of the shortest trees and just less than two-thirds (65%) of 200 bootstrap replicates. Failure to recover Trueb and Cloutier's (1991) strict consensus tree may be due, at least in part, to the fact that I was not able to include the Loxommatidae Lydekker as an outgroup, because these authors failed to provide the scores for the consensus of the three loxommatid genera they reportedly used (Trueb and Cloutier, 1991:241) to characterize the family. Second, my re-analysis indicates that the unresolved trichotomy of Albanerpeton, Karaurus, and Urodela reported by Trueb and Cloutier (1991) is not robust—the clade collapses after only one additional step and is recovered in only 67% of 200 bootstrap runs. Third, and most critically in my opinion, Trueb and Cloutier (1991) failed to examine any Albanerpeton specimens firsthand. This resulted in numerous coding errors for the genus. Of the 27 characters that these authors scored for Albanerpeton, 12 or nearly 45 percent were scored incorrectly. Trueb and Cloutier (1991) also misinterpreted certain character states for other taxa. With some modification and after correcting scoring errors, I consider 33 of Trueb and Cloutier's (1991) characters potentially useful for assessing the position of albanerpetontids. I have been able to score 26 of these characters for one or both albanerpetontid genera.

McGowan and Evans' (1995) Analysis

McGowan and Evans (1995) employed 30 osteological characters (25 informative and five uninformative) and two dissorophoid-grade temnospondyl genera as outgroups to examine relationships among the Gymnophiona, Salientia, Caudata, and Albanerpetontidae. Their published analysis is an abbreviated version of a more extensive, but as yet unpublished, study that incorporates additional characters and taxa (G. J. McGowan, letter dated 27 March 1995). Their shortest tree, reproduced here with modification as Figure 8-1C, placed the Albanerpetontidae within the Lissamphibia as the sister-group of the Batrachia (Brongniart). McGowan and Evans (1995:145) also stated, "a tree that reverses the positions of gymnophionans and albanerpetontids is only slightly longer." I re-analyzed their published matrix and found that such a tree requires two extra steps.

In using the Albanerpetontidae and Caudata as composite terminal taxa, McGowan and Evans' (1995) analysis tested neither for monophyly of the Albanerpetontidae, an important consideration given that two genera (Albanerpeton and Celtedens) are now included in the family, nor Trueb and Cloutier's (1991) claim that albanerpetontids (= Albanerpeton as used by the later authors) were caudates. Although the Albanerpetontidae are widely regarded as a monophyletic clade (e.g., Fox and Naylor, 1982; Milner, 1988, 1994; McGowan and Evans, 1995; Gardner, 2000a), this assumption has not been tested cladistically. The closest relationship that McGowan and Evans' (1995) study could have resolved between albanerpetontids and caudates was a sister-pair relationship. I address both of these issues in my analysis by including Albanerpeton and Celtedens as terminal albanerpetontid taxa and the stem-family Karauridae Ivachnenko and the crown-clade Urodela as terminal caudate taxa. With minor modifications, I regard 24 of McGowan and Evans' (1995) characters as potentially informative for assessing the position of albanerpetontids and I have been able to score all but one of these characters for one or both genera.

McCord's (1999) Analysis

McCord (1999) used 68 characters and two dissorophoid-grade temnospondyl genera as outgroups to assess relationships among seven lissamphibian terminal taxa: "albanerpetontines" (= albanerpetontids, here) and stem- and crown-clade caudates, gymnophionans, and salientians. McCord's (1999:table 2) matrix included no new characters; instead, he used three characters listed by Estes and Sanchíz (1982:28) to support their inclusion of Albanerpeton in the Caudata, 38 of the 58 characters in Trueb and Cloutier's (1991) data set II, and 27 of the 30 characters in McGowan and Evans' (1995) data set. McCord's (1999) shortest tree, shown here with modification as Figure 8-1D, nested "albanerpetontines" within the Caudata as the sister-taxon to the Urodela (= "extant Caudata" of McCord, 1999). I recovered a tree with the same topology when I analyzed McCord's (1999:table 2) published data matrix.

McCord's (1999) analysis is weakened by numerous problems, including the following: 1) in combining Albanerpeton and Celtedens into one terminal taxon, monophyly of "albanerpetontines" was assumed and not tested; 2) McCord (1999) accepted many characters without sufficient critical evaluation—e.g., three pairs of his characters (17 and 47; 22 and 35; 24 and 42) each consist of two essentially redundant characters and another 12 characters were uninformative for his analysis; 3) states for five characters (5, 14–17) were polarized incorrectly—e.g., supratemporal and postparietal (his characters 14 and 15, respectively) are primitively present in temnospondyls, not absent; 4) no information was provided about how characters were scored for "albanerpetontines"—hence, it is uncertain whether scoring decisions relied on specimens, literature, or both or which taxa were used to make these decisions; 5) not all relevant literature was consulted when scoring characters—e.g., six characters recorded as unknown for "albanerpetontines" could have been scored using literature published by 1995; and 6) there are numerous coding errors throughout his published matrix, to the extent that 12 of the 44 characters (27%) scored for "albanerpetontines" are incorrect. Finally, my analysis of McCord's (1999) published matrix reveals that support for his hypothesized arrangement of Karaurus ("albanerpetontines" + Urodela) is weak. This clade and the less inclusive sister-pair of "albanerpetontines" + Urodela collapse after just one additional step, with each clade recovered in less than half of the nine trees ≤

minimum plus one step, and both clades are supported by bootstrap values below 50% (2000 replicates).

McCord (1999) further suggested that "albanerpetontines" are best regarded as an informal subfamily within the urodele family Prosirenidae. This proposal is indefensible for two reasons. First, McCord's (1999) analysis demonstrates no such relationship because he failed to include as terminal taxa either of the monospecific prosirenid genera, namely the type genus Prosiren Goin and Auffenberg (sensu Fox and Naylor, 1982; Evans and Milner, 1996) and Ramonellus Nevo and Estes, which would have allowed him to test for a relationship between these genera and "albanerpetontines." Second, McCord (1999) did not identify any character states—derived or otherwise—that unite or potentially unite Prosiren, Ramonellus, and "albanerpetontines" to the exclusion of other lissamphibians.

ANALYSIS

My study relies on 59 informative characters scored for two outgroup and ten ingroup taxa (Table 8-1). Taxa and characters are discussed in more detail in separate sections below. As in the previous chapter, I used the branch-and-bound algorithm in PAUP 3.1.1 (Swofford, 1993) for all searches, including decay and bootstrap analyses. I also used PAUP 3.1.1 to generate tree statistics and both the accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) character state optimizations to map character state distributions on the shortest tree. I also selected the "ladderize right" option for displaying trees, designated Balanerpeton Milner and Sequeria and Dendrerpeton Owen as outgroups, and ran three multistate characters (18, 20, and 47) as ordered. Otherwise, I used the default settings in PAUP 3.1.1.

TERMINAL TAXA

General Comments

I follow Bolt (1977, 1979, 1991), Rage and Janvier (1982), Milner (1988, 1990, 1993b, 1997), Trueb and Cloutier (1991), and McGowan and Evans (1995) in regarding the Lissamphibia as a crown-clade nested within the more inclusive Temnospondyli Zittel (sensu Milner and Sequeira, 1994). I prefer this scheme because it results in a nested set of character states showing "progressive modification of the palate, the dentition, the ear, the pectoral girdle, and the humerus towards a lissamphibian condition, in a way that no other Palaeozoic group does" (Milner, 1988:89). In a recent series of large scale cladistic analyses, Laurin and Reisz (1997, 1999) and Laurin (1998a, b) proposed that lissamphibians (represented by select salientians, caudates, and gymnophionans only) instead nest within a more inclusive Lepospondyli Zittel. Proper evaluation of the latter hypothesis requires a comprehensive and critical assessment of the characters, specimens, and taxa used in Laurin and Reisz's (1997, 1999) and Laurin's (1998a, b) analyses. This would be a mammoth undertaking that is beyond the scope of my study here. At present I find a lepospondyl-lissamphibian relationship less convincing because it necessitates extensive convergence between lissamphibians and more crownward non-lissamphibian temnospondyls. Other aspects of Laurin and Reisz's (1997) initial study are discussed below where relevant.

Below I review the 12 terminal taxa and justify my use of each. Except for the Karauridae, monophyly of the terminal taxa is well established. Eight of the terminal taxa include more than one species. Bininda-Emonds et al. (1998) recently reviewed some of the assumptions and potential problems associated with using supraspecific terminal taxa in cladistic analyses.

Outgroup Taxa

I selected the incertae sedis genus Balanerpeton (middle Mississippian, Scotland) and the dendrerpetontid Dendrerpeton (early Pennsylvanian, North America and Europe) as outgroups because the osteology of each is well documented and both are widely regarded as relatively basal temnospondyls (Carroll, 1967; Milner, 1980, 1996; Godfrey et al., 1987; Milner and Sequeira, 1994; Holmes et al., 1998). My coding for Dendrerpeton is founded on the type and best known species, D. acadianum Owen, whereas my coding for Balanerpeton is based on the type and only known species, B. woodi Milner and Sequeira.

Ingroup Taxa

I chose the ten ingroup taxa for the following reasons: (1) Apateon and Doleserpeton Bolt because each has been hypothesized to be the sister-taxon of lissamphibians (Bolt, 1977; Milner, 1988, 1993b; Trueb and Cloutier, 1991; McGowan and Evans, 1995) and to assess whether the Albanerpetontidae might lie outside of the Lissamphibia; (2) the crown-clades Apoda Oppel, Anura Rafinesque, and Urodela because these taxa are appropriate for the level of resolution required for my study and to minimize the number of taxa and characters; (3) the respective stem-taxa Eocaecilia Jenkins and Walsh, Triadobatrachus (Piveteau), and Karauridae because fossil stem-taxa can provide new character states, suggest different polarities, and show that certain character states are convergent or more widespread than would have been evident if the crown-clades alone were included (see Wilson, 1992); (4) the crown-clades and stem-taxa listed under the previous two points to assess whether albanerpetontids might nest within the Gymnophiona, Caudata, or Salientia; and (5) Albanerpeton and Celtedens to test for monophyly of the Albanerpetontidae and, if supported, to examine the position the clade.

Dissorophoid-grade Temnospondyls—Among non-lissamphibian temnospondyls, genera within the Mississippian–Permian (Milner, 1993a) dissorophoid-grade families Amphibamidae Moodie and Branchiosauridae are generally regarded as including the immediate relatives of lissamphibians (see reviews by Milner, 1990, 1993b). Neither family is assuredly monophyletic, especially relative to the Lissamphibia (Trueb and Cloutier, 1991; Milner, 1993b; Clack and Milner, 1993) and, at present, there are too many conflicting character states and poorly known taxa to satisfactorily judge which family or genus is most closely related to lissamphibians (Milner, 1993b). The Early Permian genera Doleserpeton from Oklahoma and Apateon from Germany are appropriate representatives for the Amphibamidae and Branchiosauridae, respectively, because both genera have been postulated as the sister-taxon of lissamphibians (Bolt, 1969, 1977, 1991; Milner, 1988; Trueb and Cloutier, 1991; McGowan and Evans, 1995) and the osteology of each is reasonably well documented (Bolt, 1969, 1974, 1977, 1979, 1991; Bolt and Lombard, 1985; Boy, 1978, 1986, 1987; Werneburg, 1989; Schoch, 1992; Daly, 1994). My coding decisions for Doleserpeton are based on the type and only known species, D.

annectens Bolt, and for *Apateon* on two well known species, *A. caducus* Ammon and the type species *A. pedestris* Meyer.

Apoda Oppel—I follow Trueb and Cloutier (1991:296) and Trueb (1993:fig. 6.3) in restricting the name Apoda to the extant crown-group caecilians and use the name Gymnophiona for the more inclusive clade containing Apoda plus the Jurassic stem-gymnophionan *Eocaecilia*. Cannatella and Hillis (1993) favored the opposite arrangement of names. Monophyly of the Apoda is strongly supported by such synapomorphies as a greatly reduced orbit, maxilla and palatine fused to form a compound maxillopalatine, and lack of limbs and girdles (Trueb and Cloutier, 1991; Jenkins and Walsh, 1993). As there is broad agreement that the Ichthyophiidae Taylor and Rhinatrematidae Nussbaum are basal apodans (e.g., Nussbaum, 1977; Duellman and Trueb, 1986; Nussbaum and Wilkinson, 1989; Hedges et al., 1993), I followed Trueb and Cloutier (1991) in using these families to score the plesiomorphic apodan condition.

***Eocaecilia micropodia* Jenkins and Walsh**—*Eocaecilia* is represented by a series of incomplete skeletons from the Early Jurassic of Arizona. Jenkins and Walsh (1993) presented a preliminary description of the species; a more detailed description is in preparation by Jenkins and colleagues (Carroll, 1998:205). In having the maxilla and palatine unfused and in retaining limbs, girdles, and a relatively unreduced orbit, *Eocaecilia* is more primitive than apodans and is justifiably regarded as a stem-gymnophionan (Trueb and Cloutier, 1991; Milner, 1994).

Anura Rafinesque—The Anura or crown-clade frogs include *Vieraella* Reig, *Notobatrachus* Reig, and all fossil and living frogs most closely related to these two genera. Here I use the name Salientia for the more inclusive clade of *Triadobatrachus* (*Czatkobatrachus* Evans and Borsuk-Białynicka + Anura); this is essentially the arrangement advocated by Milner (1988) and Ford and Cannatella (1993), although *Czatkobatrachus* was then unknown. Monophyly of anurans is well supported by such synapomorphies as ten or fewer presacral vertebrae, caudal vertebrae fused to form a urostyle, fused radius and ulna, fused tibia and fibula, and elongate tibiale and fibulare (Milner, 1988; Ford and Cannatella, 1993; Báez and Basso, 1996; Sanchíz, 1998). The Jurassic genera *Notobatrachus* and *Vieraella* and the extant genera *Ascaphus* Stejneger and *Leiopelma* Fitzinger are widely regarded as basal anurans (e.g., Duellman and Trueb, 1986; Ford and Cannatella, 1993; Báez and Basso, 1996; Sanchíz, 1998) and I relied on these taxa to score the plesiomorphic condition for the Anura.

Triadobatrachus massinoti (Piveteau)—Triadobatrachus is represented by an incomplete, natural mould of a skeleton from the Early Triassic of Madagascar. Rage and Roček (1989) and Sanchíz (1998) provided the most recent accounts for the taxon. The phylogenetic status of Triadobatrachus has long been debated (see reviews by Estes and Reig, 1973; Rage and Roček, 1989; Trueb and Cloutier, 1991), but most contemporary workers (Milner, 1988; Trueb and Cloutier, 1991; Cannatella and Hillis, 1993; Ford and Cannatella, 1993; Báez and Basso, 1996) regard the genus as the sister-taxon of the Anura.

Evans and Borsuk-Białynicka (1998) recently named a second stem-salientian, Czatkobatrachus polonicus, for isolated postcranial elements from Poland. According to these authors, the new genus is slightly younger (ca. five Ma) than Triadobatrachus and is the immediate sister-taxon of the Anura. Although Czatkobatrachus is too poorly known to be meaningfully included in my analysis, the genus is informative for showing that one character state (atlas lacks foramen for exit of first spinal nerve) that cannot be determined for Triadobatrachus was already established in the stem leading to anurans.

Urodela Duméril—I follow Milner (1988, 1993a, b) and Evans and Milner (1996) in restricting the name Urodela to the crown-clade salamanders (i.e., most recent common ancestor of all living salamanders and all its descendants) and in using the name Caudata for the more inclusive clade containing Urodela plus the Middle Jurassic stem-salamanders Karaurus, Kokartus Nessov, and Marmorerpeton Evans et al. Others (e.g., Trueb and Cloutier, 1991; Cannatella and Hillis, 1993; Trueb, 1993) favoured the opposite arrangement for the names Urodela and Caudata. Monophyly of the Urodela is supported by at least one synapomorphy: the muscle adductor mandibulae internus superficialis extends posteriorly over the dorsal surface of the skull and originates on the exoccipital or, occasionally, the atlas (Carroll and Holmes, 1980; Estes, 1981; Milner, 1988; Trueb and Cloutier, 1991). Evans and Milner (1996) also identified the absence of a quadratojugal and the presence of a spinal foramen in the atlas as synapomorphies for the Urodela. The polarities of the last two characters for urodeles are difficult to judge: among described stem-caudates the presence of a quadratojugal can be demonstrated only for Karaurus (Ivachnenko, 1978:fig. 1a), whereas the absence in the atlas of a spinal foramen can be demonstrated only in Marmorerpeton (Evans et al., 1988:figs. 1, 3). In any case, it is clear that neither of these character states are unique to the Urodela among lissamphibians because the quadratojugal is also absent in anurans (Báez and Basso, 1996) and the spinal foramen occurs in albanerpetontids (Estes and Hoffstetter, 1976; this study) and gymnophionans (Norris and Hughes, 1918; Wake, 1980a). There is unanimous agreement that the Cryptobranchidae Fitzinger and Hynobiidae Cope are basal urodeles (e.g., Milner, 1983; Duellman and Trueb, 1986; Larson and Dimmick, 1993; Hay et al., 1995), and I followed Trueb and Cloutier (1991) in using these families to score the plesiomorphic condition for urodeles. Using cryptobranchids for this purpose is potentially problematic, because the family exhibits numerous paedomorphic and novel morphological features—many of the latter are cranial novelties involved in asymmetric suction feeding (Elwood and Cundall, 1994). Given that these modifications affect just two of the characters (1 and 8) in my analysis and that cryptobranchids otherwise are morphologically primitive, I believe the family remains informative for assessing the primitive urodelan condition.

Karauridae Ivachnenko—The Karauridae include two poorly known Middle Jurassic species: *Karaurus sharovi* Ivachnenko, represented by an exquisitely preserved skeleton from Kazakhstan, and *Kokartus honorarius* Nessov, known by isolated skull and postcranial elements from Kirghizia. Both species have an extensively ornamented squamosal (see Ivachnenko, 1978:fig. 1a; Nessov, 1988:fig. 2:1) and this is strong evidence that the muscle adductor mandibulae internus superficialis did not extend posteriorly across the dorsal surface of the skull as in urodeles (Carroll and Holmes, 1980; Estes, 1981; Evans and Milner, 1996). In this regard, *Karaurus* and *Kokartus* are more primitive than urodeles and both genera are widely regarded as stem-caudates (Milner, 1988, 1994; Evans and Milner, 1996). *Kokartus* is too poorly known to include as a separate terminal taxon, yet it alone provides critical information on the structure of the tooth pedicels and atlas. I thus follow Duellman and Trueb (1986), Milner (1993a, 1994), and Evans and Milner (1996) in provisionally allying *Karaurus* and *Kokartus*, even though monophyly of the Karauridae has yet to be demonstrated.

I have not included the other named stem-caudate, *Marmorerpeton* (Middle Jurassic, England; Evans et al., 1988), because this genus is not particularly well known and there is the suspicion that some jaws originally referred to the genus pertain to another, undescribed stem-caudate (Evans and Milner, 1994:311 and 1996:643).

Nevertheless, *Marmorerpeton* is instructive for showing aspects of atlantal and dental structure in stem-caudates that cannot be determined from published accounts for karaurids.

Albanerpeton Estes and Hoffstetter—The type genus of the Albanerpetontidae is known from the Early Cretaceous-Palaeocene of North America and Miocene of Europe (Estes and Hoffstetter, 1976; Estes, 1981; Fox and Naylor, 1982; Gardner, 2000a). Seven species are currently recognized (Gardner, 1999a–c, 2000a, in press b), each represented by disarticulated and occasional articulated elements. Monophyly of *Albanerpeton* is supported by the unique triangular outline of the fused frontals (Gardner, 2000a; here:Chapter 7). Although *A*. *arthridion* Fox and Naylor is the inferred basalmost species in the genus (Gardner, 1999b; here:Chapter 7), I used the type species *A*. *inexpectatum* Estes and Hoffstetter for my scoring decisions because the latter is known by more extensive collections (Estes and Hoffstetter, 1976; Estes, 1981; Gardner, 1999a) and characters used in my analysis do not vary within the genus.

Celtedens McGowan and Evans—The exclusively European genus *Celtedens* includes two Early Cretaceous species, both represented by skeletons (Estes, 1981; McGowan and Evans, 1995). The genus is also reliably known by isolated elements from other Lower Cretaceous and Upper Jurassic sites (McGowan and Ensom, 1997; McGowan, 1998a; Gardner, 2000a). Monophyly of *Celtedens* is supported by the unique bulbous shape of the anteromedian internasal process on the fused frontals (Gardner, 2000a). The holotype and only specimen of the type species *C*. *megacephalus* (Costa) is a poorly preserved skeleton that is difficult to interpret. My scoring decisions for the genus instead relied on McGowan and Evans' (1995) preliminary description of skeletons of the Spanish Barremian species *C*. *ibericus* McGowan and Evans and on firsthand examination of disarticulated elements, including those reported by McGowan and Ensom (1997), of an indeterminate congener from the Berriasian of England.

CHARACTER ANALYSIS AND DESCRIPTIONS

Character Analysis

My analysis employs 51 binary and eight multistate characters, representing 67 derived states. As nine of the 12 terminal taxa in my analysis are known only from skeletal remains, all but one of my characters are osteological. For the single non-osteological character (36), the primitive and derived states can be identified reliably by osteological markers. I polarized characters against the basal temnospondyls Dendrerpeton and Balanerpeton following the outgroup comparison method of Watrous and Wheeler (1981), Maddison et al. (1984), and Bryant (1991). My analysis is conservative, in the sense that I ran all characters as unweighted and most as unordered. I ran three characters (18, 20, and 47) as ordered because, as explained in the respective accounts below, I interpret the states in each character as forming a transformation series. Running these characters as unordered did not alter the topology of the shortest tree.

Many characters were taken from previously published studies and are referenced accordingly in the accounts below. Where appropriate, I revised and rescored such characters. Fifteen characters are common to Trueb and Cloutier's (1991) and McGowan and Evans' (1995) analysis; a further 18 characters are derived from the former study and nine are from the latter. Fourteen characters are adapted from other studies and three characters are new. I excluded a number of previously published characters that proved to be uninformative for my analysis. These characters either were invariant among or too poorly known for terminal taxa or were autapomorphic for a particular terminal taxon. I also rejected characters having states that are too subjectively or ambiguously defined, or both, to be applied with any confidence. Particularly problematic in this regard are characters used by Trueb and Cloutier (1991), McGowan and Evans (1995), and Laurin and Reisz (1997) to describe the shape and proportions of the parasphenoid. Finally, because palatal bones are undescribed for albanerpetontids, I retained only eight palatal characters (17–23 and 42) that appear particularly promising for assessing lissamphibian relationships.

My scoring decisions for characters were based on specimens and literature reported in Appendix 8-1. To permit comparisons with Trueb and Cloutier's (1991) analysis, I generally followed these authors in using the same inferred basal members to score the plesiomorphic conditions for the Apoda, Urodela, and Anura. Where the primitive and derived state of a character occurred in a terminal taxon and I was not able to confidently identify the plesiomorphic condition (characters 2 and 11 for Apoda; characters 1 and 25 for Urodela), I recorded the condition as polymorphic; such records account for less than one percent of the values in my matrix. I also recorded inapplicable and unknown character states as, respectively, "N" and "?;" these collectively account for about a further 18 percent of the values in my data matrix. An inapplicable score is used in situations where, for example, a character describes the form of a process on a bone, but the bone is absent in the terminal taxon of interest. Although the use of polymorphic and inapplicable scores is a more accurate way to score characters, this approach unfortunately results in some lost information because PAUP 3.1.1 interprets these types of records as unknown character states (Swofford, 1993).

Character Descriptions

Characters are described and evaluated below as necessary. To conserve space, in citations for characters I use the following abbreviations: B, Bolt (1991); E, Estes (1981); ES, Estes and Sanchíz (1982); FN, Fox and Naylor (1982); JW, Jupp and Warren (1986); LR, Laurin and Reisz (1997); Md, McCord (1999); ME, McGowan and Evans (1995); M88, Milner (1988); M93, Milner (1993b); NW, Nussbaum and Wilkinson (1989); PW, Parsons and Williams (1963); TC, Trueb and Cloutier (1991:data set II).

Skull (characters 1–27; Figs. 8-2 to 8-4)

1. Lacrimal (FN, LR, Md, TC): 0, present; 1, absent—If present the lacrimal lies laterodorsally in the snout, where the bone primitively contacts the maxilla lateroventrally, septomaxilla or external narial opening anteriorly, nasal and prefrontal medially, and orbital margin posteriorly. The lacrimal is unequivocally absent in anurans and cryptobranchid urodeles. The absence of a lacrimal in cryptobranchids may be paedomorphic (Elwood and Cundall, 1994), because this is one of the last skull bones to ossify in metamorphosed urodeles (Duellman and Trueb, 1986). Hynobiids retain the lacrimal and I conservatively score this character as polymorphic for basal urodeles. Scoring the lacrimal as primitively present for urodeles does not alter the topology of the shortest tree or the distribution of apomorphies. Adult apodans lack a discrete lacrimal. Some early workers (e.g., Peter, 1898; Marcus et al., 1935) claimed that the lacrimal appears ephemerally before fusing ontogenetically with the maxillary component of the maxillopalatine, but more recent studies have not reported a centre of ossification for the lacrimal (see Wake and Hanken, 1982:table 2; Reiss, 1996). Nussbaum (1977:11) suggested that the "lacrimal" identified by Marcus et al. (1935) may instead be the anlage of the prefrontal. As there is little solid evidence for the presence of a lacrimal in apodans, I score the element as absent (contra Trueb and Cloutier, 1991).

2. **Prefrontal** (LR, Md, TC): 0, present; 1, absent—Where present the prefrontal primitively contributes to the anteromedian margin of the orbit and contacts the lacrimal lateroanteriorly, nasal and frontal medially, and postfrontal posteriorly. As the prefrontal is absent in rhinatrematids and present in ichthyophiids (Nussbaum, 1977), I score this character as polymorphic for basal apodans. Anurans consistently lack a prefrontal. The prefrontal is retained in Albanerpeton, where the bone is incompletely fused with the lacrimal in at least some individuals of A. inexpectatum and, presumably, is also present in Celtedens (Gardner, 2000b; contra McGowan, 1998a:fig. 2).

3. **Maxillary arcade** (B, Md, ME, TC): 0, closed posteriorly; 1, open posteriorly—The posterior end of the maxilla primitively articulates with the jugal, quadratojugal, and, occasionally, the squamosal, resulting in a closed maxillary arcade. The maxillary arcade remains closed in Celtedens (McGowan, 1998a:fig. 2). Isolated Albanerpeton maxillae have a facet posteriorly and labiodorsally for contact with a more posterior element (Fox and Naylor, 1982; Gardner, 1999a). This implies that the maxillary arcade was also closed posteriorly in Albanerpeton (contra Trueb and Cloutier, 1991), not open as shown in Estes and Hoffstetter's (1976:fig. 4) cranial reconstruction for A. inexpectatum. The posterior end of the maxilla in Karaurus and basal urodeles is free of bony contacts, resulting in a posteriorly open maxillary arcade. The condition in Vieraella is uncertain (Estes and Reig, 1973; Báez and Basso, 1996), but in Notobatrachus, Leiopelma, and Ascaphus the posterior end of the maxilla is free; I regard this as the plesiomorphic anuran condition (contra Trueb and Cloutier, 1991). The holotype of Triadobatrachus preserves an impression of the posterior end of the maxilla on both sides, but it is unclear whether this bone was in contact posteriorly with one or more elements.

4. **Jugal** (B, LR, Md, ME, TC): 0, present; 1, absent—If present the jugal lies in the cheek, where the bone primitively forms the ventral margin of the orbit and contacts the maxilla ventrally, squamosal and quadratojugal posteriorly, and postorbital

posterodorsally. The jugal occurs in Eocaecilia and Celtedens and its presence can be inferred for Albanerpeton (contra Trueb and Cloutier, 1991) based on the labiodorsal facet along the posterior end of the maxillae. All other lissamphibians lack the jugal.

5. Frontal and parietal (E, FN, LR, Md, M88, TC): 0, frontals and parietals paired; 1, frontal and parietal fused on either side of midline; 2, frontals fused across midline, parietals paired—Frontals and parietals primitively are paired, median roofing bones. In salientians the frontal and parietal on either side of the midline fuse ontogenetically to form a compound frontoparietal; fusion of the paired frontoparietals into an azygous median element is a derived condition within anurans (Cannatella, 1985). In albanerpetontids the frontals fuse to form an azygous median bone, but the parietals remain paired. I interpret the salientian and albanerpetontid patterns as having been derived independently from the inferred primitive condition.

6. Form and contacts of internasal process on frontals (new): 0, absent or weakly developed; 1, prominent and partly separates paired nasals—In most temnospondyls the anterior margin of the frontal varies from shallowly concave to convex in dorsal outline. Near its medial limit, the anterior edge of the frontal occasionally bears a short, anteriorly directed prong that may barely extend between the posteriormost ends of the paired nasals. In the same position, fused frontals in albanerpetontids bear a more prominent median process that is about one-quarter the total midline length of the frontals and extends anteriorly between about the posterior one-half of the paired nasals (Gardner, 2000b). This process, termed the internasal process by McGowan and Evans (1995), evidently is unique to albanerpetontids among temnospondyls.

7. Frontal-nasal and -prefrontal contact (new): 0, nasal and prefrontal abut against or suture with frontal; 1, nasal and prefrontal fit into complementary slots on frontal—The posterior edges of the nasal and, where present, the prefrontal primitively abut or suture against the anterior edge of the frontals. These contacts are more complex in albanerpetontids and involve a pair of slots that lie to either side of the midline in the fused frontals (Gardner, 2000b). The first slot opens anteriorly between the bases of the internasal and anterolateral processes, to receive the posterior end of the nasal. The second slot is located more posterolaterally between the base of the latter process and the orbital margin, and opens anterolaterally to receive the posterior end of the prefrontal. To my knowledge, the mortise and tenon pattern of frontal-nasal and -prefrontal contact in albanerpetontids is unique among vertebrates.

8. Contribution of frontal to orbital margin (LR, Md, ME, TC): 0, excluded by pre- and postfrontals; 1, contributes to orbital margin—Where present the prefrontal and postfrontal primitively contact one another along the dorsal margin of the obit, thereby excluding the frontal from the orbit. This is the pattern in Balanerpeton, Dendrerpeton, and Eocaecilia. Reduction or loss of the prefrontal and postfrontal allows the frontal to contribute to the orbit in all other ingroup taxa, except apodans and cryptobranchid urodeles. Although the pre- and postfrontals are lost in most apodans, reduction in orbital size and dorsal expansion of the maxillary component of the maxillopalatine conspire to exclude the frontal from the orbit. This pattern is not homologous with the primitive temnospondyl condition and I scored the character as inapplicable for apodans. The postfrontal is absent in cryptobranchids, but the narrow frontals are excluded from the orbital margin by an anterior extension of the parietal that wraps around the lateral edge of the frontal and contacts the prefrontal. As this pattern of frontal exclusion appears to be unique among temnospondyls, I relied on hynobiids to score the primitive urodelan condition.

9. Parietal foramen (LR, Md, TC): 0, present; 1, absent—The parietal foramen primitively opens dorsally in the junction between the paired parietals in non-lissamphibian temnospondyls and, according to Rage and Roček (1989), between the paired frontoparietals in Triadobatrachus. Anurans lack a discrete palatal foramen, but in basal members the parietal organ is nonetheless exposed dorsally in a fontanelle between the medial edges of the paired frontoparietals. As it is unclear whether this fontanelle is homologous with the parietal foramen (Trueb and Cloutier, 1991), I record the character as unknown for anurans. The parietal foramen is absent and the parietal organ roofed dorsally by bone in other lissamphibians.

10. Sclerotic ring (M88): 0, present; 1, absent—Temnospondyls primitively have a ring composed of up to 30 sclerotic plates in the orbit. The presence or absence of a sclerotic ring cannot be determined for Albanerpeton, but Celtedens and all other lissamphibians lack these plates.

11. Postfrontal (B, Md, ME, TC): 0, present; 1, absent—Where present the postfrontal primitively forms the dorsoposterior margin of the orbit and contacts the postorbital medioposteriorly, inter- or supratemporal posteriorly, parietal and frontal medially, and prefrontal anteriorly. Among lissamphibians, the postfrontal is present only in Eocaecilia and some basal apodans. Given that isolated frontals and parietals of Albanerpeton and Celtedens bear no evidence for having laterally contacted a bone in the region primitively occupied by the postfrontal, I assume that albanerpetontids also lack a postfrontal.

12. Postorbital (B, LR, Md, ME, TC): 0, present; 1, absent—Where present the postorbital primitively forms the posterior edge of the orbit and contacts the jugal lateroventrally, squamosal lateroposteriorly, and supratemporal, intertemporal, and postfrontal medially. The postorbital is absent in apodans, caudates, and salientians. This also appears to be the case in Celtedens, judging by McGowan and Evans' (1995) scoring decision for albanerpetontids and McGowan's (1998a:fig. 2) cranial reconstruction for C. ibericus. Contrary to Trueb and Cloutier (1991), the condition in Albanerpeton cannot be demonstrated based on currently available specimens, but it presumably is the same as in Celtedens.

13. Intertemporal (B, LR, TC): 0, present, 1, absent—If present the intertemporal is a small temporal roofing bone surrounded by the postfrontal anteriorly, postorbital laterally, supratemporal posteriorly, and parietal medially. Where this character can be reliably scored, all ingroups lack the intertemporal.

14. Supratemporal (B, LR, Md, ME, TC): 0, present; 1, absent—The supratemporal, if present, lies more posteriorly on the skull roof and is surrounded by the intertemporal or postfrontal anteriorly, postorbital lateroanteriorly, squamosal lateroposteriorly, tabular posteriorly, and parietal and postparietal medially. The supratemporal is absent in gymnophionans, caudates, and salientians. The bone is also absent in Celtedens judging by McGowan and Evans' (1995) scoring decision for albanerpetontids and McGowan's (1998a:fig. 2) cranial reconstruction for C. ibericus. The condition in Albanerpeton is uncertain (contra Trueb and Cloutier, 1991), although it presumably is identical to that in Celtedens.

15. Postparietal (B, LR, Md, ME, TC): 0, present; 1, absent—If present the postparietal lies at the posterior end of the skull roof, where it contacts the posterior edge of the parietal and forms the dorsomedian part of the occiput. The distribution of states for this character follows character 14.

16. Tabular (B, LR, Md, ME, TC): 0, present; 1, absent—If present the tabular forms the posterolateral edge of the skull roof, where it articulates with the postparietal medially, supratemporal anteriorly, and squamosal laterally and contributes to the laterodorsal part of the occiput. The distribution of states for this character follows character 14.

17. Palatine (Md, TC): 0, present as a discrete element; 1, absent; 2, fused with adjacent element—The palatine primitively is a discrete palatal bone that forms the posterior margin of the internal narial margin and articulates with the maxilla laterally, ectopterygoid posteriorly, pterygoid medially, and vomer anteromedially. The palatine is modest in size in the non-lissamphibian terminal taxa and Eocaecilia, but evidently reduced to a splinter in Triadobatrachus (Rage and Roček, 1989:text-fig. 28). In apodans the palatine fuses ontogenetically with the maxilla to form the compound maxillopalatine (e.g., Wake and Hanken, 1982; Reiss, 1996). The palatine is absent in anurans, Karaurus, and basal urodeles. I regard fusion and loss of the palatine as independently derived states. The condition in albanerpetontids is unknown.

18. Ectopterygoid (LR, Md, ME, M88, TC): 0, unreduced; 1, reduced; 2, absent—Where present the ectopterygoid is a lateroposterior palatal bone that primitively contacts the maxilla laterally, palatine anteriorly, and pterygoid medially. The relative size of the ectopterygoid may be described using three states, which I regard as forming a transformation series leading to loss of the element. Primitively in temnospondyls, including Balanerpeton and Dendrerpeton, the ectopterygoid is relatively large, being comparable in length and breadth to the palatine. Apateon exhibits the inferred intermediate condition, in which the ectopterygoid is reduced to a narrow strip. The ectopterygoid is absent in Doleserpeton, gymnophionans, caudates, and salientians. The condition in albanerpetontids is unknown.

A comment is warranted here about the identity of the so-called ectopterygoid in apodans. In adults of most apodan species, two bones connected by a ligament lie in sequence between the posterior end of the maxillopalatine and the quadrate. The more anterior of these bones variously has been interpreted as the ectopterygoid (e.g., Parsons and Williams, 1963; Taylor, 1969; Carroll and Currie, 1975) or pterygoid (Nussbaum, 1977; Trueb, 1993), whereas the more posterior bone has been identified as either the pterygoid (Parsons and Williams, 1963; Taylor, 1969; Carroll and Currie, 1975) or the pterygoid process of the quadrate (Nussbaum, 1977; Trueb, 1993). Reiss (1996) has recently shown in an ontogenetic study of the rhinatrematid Epicrionops Boulenger that the two synostically united bones in question are actually the anterior and posterior parts of the pterygoid, which divides at metamorphosis in most individuals.

19. Anterior ramus of pterygoid in contact anteriorly (Md, TC): 0, yes; 1, no—The pterygoid is a triradiate palatal bone that braces the suspensorium and maxillary arcade against the braincase. The anterior ramus of the pterygoid primitively articulates anteriorly with some combination of the palatine, vomer, maxilla, and ectopterygoid. This is the condition in most of the terminal taxa for which the pterygoid is known. Caudates exhibit the inferred derived pattern, in which the anterior ramus of the pterygoid is not in bony contact anteriorly. As the pterygoid is unknown for albanerpetontids, this and the next four characters (20-23) cannot be scored for albanerpetontids.

20. Contact between anterior ramus of pterygoid and palatine (Md, TC): 0, articulates along medial edge of palatine; 1, articulates along posterior end of palatine; 2, no contact with palatine—This character is inapplicable for caudates and anurans, because these lack the palatine. Among the remaining terminal taxa for which the pattern of pterygoid-palatine contact can be determined, I recognize three states that I interpret as forming a transformation series leading to loss of contact between the two bones. Balanerpeton, Dendrerpeton, and Apateon show the inferred primitive condition, in which the elongate anterior ramus of the pterygoid articulates broadly along the medial edge of the palatine. The inferred intermediate state is seen in Doleserpeton, Eocaecilia, and apodans, where loss of the ectopterygoid and reduction in length of the anterior ramus of the pterygoid allows the process to articulate along the posterior edge of the palatine in the first two taxa and along the posterior edge of the palatine portion of the maxillopalatine in apodans. The inferred derived state occurs only in Triadobatrachus, where the pterygoid and reduced palatine are broadly separated.

21. Contact between anterior ramus of pterygoid and vomer (Md, TC): 0, present; 1, absent—Balanerpeton and Dendrerpeton exhibit the inferred primitive pattern, in which the elongate anterior ramus of the pterygoid articulates anteriorly with the large vomer. In all other terminal taxa for which this character can be scored, the anterior end of the pterygoid fails to contact the vomer.

22. Contact between anterior ramus of pterygoid and maxilla (LR; Md and TC in part): 0, absent; 1, present—As the pattern of pterygoid-maxillary contact is more complex than implied by Trueb and Cloutier (1991), I divided their character 32 into two separate characters (22 and 23). The first of these characters describes the absence or presence of pterygoid-maxillary contact. This contact is convincingly absent in Balanerpeton, Dendrerpeton, Apateon, gymnophionans, urodeles, and, probably, in Karaurus. Ivachnenko's line drawing (1978:fig. 1b) of the holotype skull of Karaurus in ventral view shows the anterior ramus of the pterygoid on both sides in contact with the outline of an unidentified lateral element that Estes (1981:10) evidently interpreted as the maxilla. However, Ivachnenko's more detailed figures (1978:fig. 1a and pl. 9) of the skull and skeleton in dorsal view show that the unidentified lateral element is instead part of the lower jaw. Even allowing for the slight postmortem displacement of bones that has occurred in the holotype skull, the maxilla and anterior ramus of the pterygoid appear too short to have been in contact, although the two elements likely approached one another closely as in many extant salamanders. In Doleserpeton and salientians the anterior ramus of the pterygoid articulates broadly along the more posterior part of the lingual face of the maxilla.

23. Manner in which pterygoid-maxillary contact fails to occur (Md and TC in part): 0, prevented by ectopterygoid and palatine; 1, prevented by elongate palatine alone; 2, pterygoid and maxilla reduced—Among taxa in which pterygoid-maxillary contact fails to occur, three patterns are seen. Primitively in temnospondyls contact between the anterior ramus of the pterygoid and maxilla is prevented by both the ectopterygoid and palatine. Gymnophionans lack the ectopterygoid, but the pterygoid remains wholly, or almost completely, excluded from the maxilla in Eocaecilia by the posteriorly elongate palatine and from the maxillary portion of the maxillopalatine in apodans by the posteriorly elongate palatine portion of the maxillopalatine. I interpret the gymnophionan pattern as a discrete state. Caudates exhibit a different pattern in which lack of contact between the pterygoid and maxilla is not due to any intervening element(s), but to the reduced lengths of the maxilla and pterygoid. Although not in direct bony contact, the posterior end of the maxilla and anterior end of the anterior ramus of the pterygoid in extant urodeles are united, in life, by a thick and tough pterygomaxillary ligament (see Elwood and Cundall, 1994:fig. 3; here:Fig. 8-4A, B) that presumably acts to stabilize the two bones. As there is no obvious transformation series among the three states of this character, I regard the gymnophionan and caudate patterns as independently derived.

24. Relationship between parasphenoid and neurocranium (LR, Md, TC): 0, parasphenoid discrete; 1, parasphenoid fused with other neurocranial bones—Primitively in temnospondyls the parasphenoid is a discrete, elongate median palatal bone. In gymnophionans the parasphenoid fuses early in ontogeny (Wake and Hanken, 1982; Reiss, 1996) with the exoccipitals, prootics, opisthotics, and pleurosphenoids to form a compound braincase called the os basale (De Beer, 1937; see Carroll and Currie, 1975:fig. 4D-G).

25. Stapedial foramen (LR, Md, TC): 0, present; 1, absent—Primitively in temnospondyls the proximal part of the stapes is perforated ventrally or posteriorly by a stapedial foramen that carries the stapedial artery, hyomandibular trunk of cranial nerve VII, or both (Trueb and Cloutier, 1991). The stapedial foramen occurs in non-lissamphibian temnospondyls, Eocaecilia, and Karaurus. The condition in Triadobatrachus is uncertain (contra Trueb and Cloutier, 1991), owing to poor preservation of the holotype skull and orientations of the impressions of the stapes. Despite Bolt and Lombard's (1985) claim that all extant lissamphibians lack a stapedial foramen, the foramen occurs in the basal apodan families Ichthyophiidae and Rhinatrematidae (Nussbaum, 1977) and, perhaps, in at least one basal urodele, the hynobiid Ranodon Kessler (see Schmalhausen, 1968:fig. 135). All anurans, however, appear to lack a stapedial foramen. The character cannot be scored for albanerpetontids, because a stapes has yet to be identified for the family.

26. Relative position of jaw articulation (Md, ME, TC): 0, posterior to level of occipital condyle; 1, in line with or anterior to level of occipital condyle—Primitively in temnospondyls the articulation between the skull and lower jaw lies well behind the level of the posterior face of the occipital condyle. In Apateon and ingroup taxa for which this character can be scored, the articulation is displaced forward and is level with or in front of the occipital condyle.

27. Form of occipital condyle (LR, ME, M88, M93): 0, single condyle; 1, bilobed condyle—Primitively in post-Devonian tetrapods, including Balanerpeton and Dendrerpeton, the occipital condyle is a single articular surface formed by a large basioccipital and paired exoccipitals (Milner and Sequeira, 1994). In certain temnospondyls the occipital condyle is bilobed: the basioccipital contribution is reduced or lost and the enlarged exoccipitals form a pair of lateral condyles that articulate with complementary cotyles on the anterior face of the atlantal centrum. All ingroup taxa exhibit the latter condition.

Mandible (characters 28–36; Fig. 8-5)

28. Composition of mandible (M88, NW): 0, multiple bones with discrete dentary; 1, mandible formed by two compound ossifications—The temnospondyl mandible primitively consists of ten bones: a dentary, angular, surangular, prearticular, and articular, two splenials, and three coronoids. There is a trend towards reducing the number of bones and occasional fusion of adjacent bones among lissamphibians, but in most groups fusion is not extensive and the dentary is always discrete. Gymnophionans are unique among temnospondyls in having the mandibular ramus formed entirely by two compound bones. Ontogenetic studies of extant apodans (e.g., Marcus et al., 1935; De Beer, 1937; Wake and Hanken, 1982) indicate that the anterior pseudodentary is composed of the fused dentary, splenial, coronoid, surangular, and mentomeckelian, whereas the posterior pseudoangular is composed of the fused angular, prearticular, articular, and an element of uncertain homology, called the complementale. The pseudodentary and pseudoangular in Eocaecilia structurally resemble those of apodans and presumably are composed of the same fused elements.

29. Surangular (LR, Md, TC): 0, present; 1, absent—Where present the surangular occupies much of the posterodorsal part of the labial surface of the ramus and contacts the dentary anteriorly, angular ventrally, and articular posteriorly. Among terminal taxa for which the status of the surangular can be determined, the element is absent in anurans, Albanerpeton, urodeles, and, evidently, Karaurus.

30. Splenials (LR, Md, TC): 0, present; 1, absent—Primitively a pre- and post-splenial lie in series along the ventral margin of the dentary, forming the ventrolingual part of the ramus anterior to the angular. Among terminal taxa for which the status of the splenials can be assessed, these bones are lacking in albanerpetontids, urodeles, and, apparently, Karaurus. The splenials may contribute to the angulosplenial in salientians, but because the homology of the latter element is uncertain I score the character as unknown for anurans and Triadobatrachus.

31. Coronoids (LR, M88, M93): 0, present; 1, absent—A series of three coronoids primitively extends along the lingual surface of the dentary from the symphysis to the articular fossa, lingual and ventral to the dentary tooth. Teeth may occur in patches or rows on some or all of the coronoids. Among the ingroup taxa coronoids are absent in albanerpetontids, anurans, and basal urodeles and appear to be absent in Karaurus and Triadobatrachus.

32. Mentomeckelian bone (B): 0, absent; 1, present—Primitively in temnospondyls the dentary forms the anterior end of the mandible. If present the mentomeckelian (= mentomandibular of some authors) is a small bone that ossifies from the anterior end of the Meckelian cartilage and lies at the anterior or anteromedial end of the mandible, where it contributes to the intermandibular joint. The mentomeckelian is reliably known for anurans, urodeles, and apodans (Parsons and Williams, 1963; Bolt, 1991). The status, function, and timing of ossification of the mentomeckelian varies among and, to a lesser extent within, each extant lissamphibian crown-clade. In anurans the mentomeckelian is among the last bones to appear at metamorphosis (see review by Trueb, 1985). The mentomeckelian remains discrete in most anuran taxa, where movement of these paired bones aids both in depressing the symphysis during protrusion of the tongue for feeding (Gans and Gorniak, 1982) and in closing the external nares during respiration (Gans and Pyles, 1983). The absence of an ossified mentomeckelian in some pipoids is derived within anurans and is associated with modifications to the tongue (Trueb and Cannatella, 1982). In apodans and urodeles the mentomeckelian appears to serve no documented function. The mentomeckelian ossifies and fuses with the dentary well before metamorphosis in apodans (e.g., De Beer, 1937; Wake and Hanken, 1982:table 1), whereas in salamanders, depending on the taxon, ossification and fusion occurs just before (e.g., Triturus Rafinesque; De Beer, 1937) to well after metamorphosis (e.g., Salamandra Laurenti; Francis, 1934). Carroll and Currie (1975) questioned the homology of the mentomeckelian in anurans and caudates based on functional differences, but because the element has the same ontogenetic origin in both groups I concur with Bolt (1991) that it is homologous. Although there is no evidence of a mentomeckelian in albanerpetontids and non-lissamphibian temnospondyls, it should be emphasized that because of its small size and tendency to fuse ontogenetically with the dentary the mentomeckelian may be difficult to identify in some fossils. Nevertheless, skeletons of several fossil frogs, including Notobatrachus (Báez and Basso, 1996:fig. 11 bottom) and some Miocene palaeobatrachids (Špinar, 1972:pl. 29) preserve distinct mentomeckelians.

33. Symphyseal prongs (E, ES, FN, ME, M88): 0, absent; 1, present—Regardless of whether the dentaries, mentomeckelians, or both are involved in the intermandibular joint, contact between the anterior or symphyseal ends of the mandibles primitively is in the form of a simple butt joint. The anterior part of the intermandibular joint in albanerpetontids involves the same butt-type joint, but posteriorly the contact is more elaborate. In this region the symphysis bears up to three medially directed processes. One or two of these processes are prominently developed into prongs and participate in an interlocking or mortise and tenon joint at the symphysis. The single prong on one dentary acts as a tenon that fits into the slot or mortise between a pair of complementary prongs on the opposite dentary (see Fox and Naylor, 1982:fig. 4c, b). Additional prongs, if present, are markedly smaller and contribute little to the symphyseal joint. Symphyseal prongs and the resultant mortise and tenon style intermandibular joint are unique to albanerpetontids among gnathostomes.

34. Form of articular surface on mandible (FN, JW): 0, concave facet; 1, convex condyle—Primitively in temnospondyls the articular surface on the mandible consists of a concave facet or groove that receives a complementary, convex condyle from the quadrate. Urodeles and anurans exhibit the opposite configuration: the articular surface of the articular in urodeles and of the angulosplenial in anurans is developed into a dorsally convex condyle that fits into a concave cotyle on the quadrate.

35. Orientation of articular surface on lower jaw (new): 0, faces dorsally-dorsoposteriorly; 1, faces posteriorly—Primitively in tetrapods the articular surface on the mandible faces dorsally-dorsoventrally to articulate with a ventrally-ventroanteriorly directed condyle or cotyle on the quadrate. To my knowledge, albanerpetontids are unique among temnospondyls in having the articular surface on the mandible facing posteriorly and only slightly dorsally. Isolated albanerpetontid quadrates (Estes and Hoffstetter, 1976; McGowan, 1996; McGowan and Ensom, 1997) indicate that the corresponding articular condyle on the quadrate was directed anteriorly and slightly ventrally in a complementary fashion. The mandibular-skull articulation in albanerpetontids thus lies in a nearly vertical, rather than horizontal, plane of orientation. McGowan (1998a:190) erroneously stated that this joint was nearly horizontal in albanerpetontids.

36. Dual jaw-closing mechanism (NW): 0, absent; 1, present—Primitively in temnospondyls the adductor muscles insert onto the lower jaw in front of the articulation with the skull and pull upwards to close the jaw. A retroarticular process may extend some distance posterior to the articular surface on the lower jaw. Even where prominently developed, as in amphiumid urodeles (see Erdman and Cundall, 1984:fig. 3), the process accounts for no more than about one-tenth the overall length of the ramus and serves simply to increase the area of attachment for the depressor muscles. Otherwise, the structure of the posterior part of the mandible is unremarkable. Gymnophionans have a unique dual jaw-closing mechanism, described in detail by Nussbaum (1983) and Bemis et al. (1983), that relies on three sets of ancestral internal adductors and a novel lateral adductor. Two distinctive osteological features, both of which occur in mandibles of Eocaecilia and extant apodans, are functionally associated with this dual jaw-closing mechanism: (1) a prominent retroarticular process, accounting for about one-third of the total jaw length, increases the area of attachment for the set of ancestral internal adductors that have shifted posteriorly and for the novel lateral adductor and (2) a prong-like and medially projecting process on the lingual surface of the ramus, below the articular facet, acts as a pulley to re-direct the force of one of the ancestral internal adductors.

Dentition (characters 37–42; Figs. 8-2 to 8-6)

37. Marginal teeth folded (B, LR): 0, folded; 1, not folded—Folded teeth (sensu Schultze, 1970) are those in which the orthodentine wall is infolded into the pulp cavity, forming a pattern called plicidentine. Various patterns of plicidentine are recognized among tetrapods (see Schultze, 1970; Warren and Davey, 1992) and one of these, the labyrinthodont pattern (pulp cavity free; folds relatively simple and unbranched; bone of attachment at tooth base rarely extends between folds), is regarded as primitive for tetrapods (Vorobyeva and Schultze, 1991). Plicidentine develops ontogenetically in Apateon (Schoch, 1992); this may be true for other non-lissamphibian temnospondyls as well. In Doleserpeton and all other ingroup taxa for which the structure of the marginal teeth can be determined, the teeth have smooth walls that lack any evidence of plicidentine. Bolt's (1991) suggestion that loss of plicidentine may be related to small body size is supported, to some extent, by Warren and Davey's (1992) observation that plicidentine among non-lissamphibian temnospondyls becomes more pronounced as absolute jaw size increases.

38. Marginal teeth pedicellate (B, E, EH, FN, LR, Md, ME, M88, PW, TC): 0, non-pedicellate; 1, pedicellate—Tetrapod teeth primitively are undivided or non-pedicellate, with no demarcation between the basal pedicel and distal crown. This is the pattern in the outgroups and, contrary to Trueb and Cloutier (1991), in Apateon. Divided or pedicellate teeth have an asymmetrical ring of uncalcified or weakly calcified tissue that separates the pedicel from the crown (e.g., Oltmanns, 1952; Parsons and Williams, 1962; Schultze, 1970) and allows the crown to bend slightly lingually, but not labially (Greven and Clemen, 1980; Bemis et al., 1983; Beneski and Larsen, 1989). Among the terminal taxa pedicellate teeth occur in Doleserpeton, gymnophionans, and basal anurans and urodeles. Pedicellate teeth operate in a passive ratchet-like fashion, with the crown bending inwards as prey moves into the mouth, then returning to the more nearly vertical "at rest" position when prey struggles or is manipulated (Larsen and Guthrie, 1975; Greven and Clemen, 1980; Bemis et al., 1983; Moury et al., 1985; Beneski and Larsen, 1989). Pedicellate teeth may also assist in more rapid and less traumatic tooth replacement (e.g., Larsen and Guthrie, 1975; Beneski and Larsen, 1989), for when the resorption pit in the lingual face of the pedicel reaches the division plane, the crown breaks away cleanly with little damage to surrounding tissues. Ontogenetic studies of extant lissamphibian show that pedicellate teeth develop metamorphically from non-pedicellate teeth (e.g., Parker and Dunn, 1964; Wake, 1980b; Greven and Clemen, 1985; Beneski and Larsen, 1989). The occasional presence among lissamphibians of teeth that are weakly pedicellate (e.g., proteid urodeles; see Schultze, 1970:fig. 3A) or non-pedicellate (e.g., batrachosauroidid urodeles; see Hinderstein and Boyce, 1977:fig. 2B–F), is widely regarded as being derived for or within these groups (Estes, 1981; Duellman and Trueb, 1986). All albanerpetontid jaws bear non-pedicellate teeth. I also provisionally score this as the condition for karaurids based on Nessov's (1988) statement that palatal teeth in Kokartus are non-pedicellate.

39. Crowns on marginal teeth (B, E, EH, FN, LR, Md, ME, M88, PW, TC): 0, monocuspid; 1, labiolingually bicuspid; 2, labiolingually compressed and mesiodistally tricuspid—Marginal teeth in tetrapods primitively are conical, with the crown terminating in a single point. This monocuspid pattern occurs in the outgroups and Apateon. I recognize two independently derived crown patterns among the remaining terminal taxa.

The first derived state accommodates teeth having a bicuspid crown comprised of a pointed labial and lingual cuspule, separated by a mesiodistally elongate sulcus. This is the condition in Doleserpeton, Eocaecilia, and basal apodans, anurans, and urodeles. The structure of tooth crowns in karaurids and Triadobatrachus is unknown. Ontogenetic studies of extant lissamphibians demonstrate that bicuspid teeth develop metamorphically from monocuspid teeth (e.g., Parker and Dunn, 1964; Wake, 1980b; Greven and Clemen, 1985; Beneski and Larsen, 1989). Although bicuspid teeth are accepted as primitive for lissamphibians (e.g., Parsons and Williams, 1962; Duellman and Trueb, 1986; Milner, 1988; Bolt, 1991; Trueb and Cloutier, 1991; Laurin and Reisz, 1997) and are widely distributed within the clade, it should be appreciated that a variety of adult tooth crown patterns exist. Within urodeles, for example, crowns are monocuspid in proteids and sirenids (Means, 1972:figs. 1, 2, respectively), whereas some species of the ambystomatid Ambystoma Tschudi have labiolingually bicuspid crowns with club-shaped cuspules or labiolingually tricuspid crowns (see Beneski and Larsen, 1989:fig. 5f, G, respectively).

Previous cladistic analyses have treated albanerpetontids as having monocuspid teeth (Trueb and Cloutier, 1991; McGowan and Evans, 1995; McCord, 1999). This is incorrect. Marginal teeth in albanerpetontids have tooth crowns that are chisel like, labiolingually compressed, and terminate in three weakly developed and mesiodistally aligned cuspules. This pattern is more derived than the primitive monocuspid condition and differs fundamentally from the labiolingually bicuspid lissamphibian/amphibamid pattern. For these reasons, I have erected a second, independently derived state to accommodate the albanerpetontid tooth crown pattern.

40. Marginal teeth on dentary (LR, M88): 0, present; 1, absent—The major tooth-bearing element of the lower jaw in temnospondyls is the dentary. This bone primitively bears a marginal (i.e., labial) row of moderate-sized teeth extending from the symphysis to the adductor fossa. The dentary is edentulous in Triadobatrachus and basal anurans.

41. Symphyseal teeth (B, LR): 0, present; 1, absent—The dentary in temnospondyls primitively bears one or a few symphyseal teeth (= parasymphyseal teeth of some authors) at the anterior end of the dentary and lingual to the marginal tooth row. I concur with Bolt (1991) that loss of the symphyseal teeth is derived among temnospondyls, although the level at which this occurred is not clear. A row of so-called "splenial teeth" (sensu Taylor, 1977) primitively occurs on the lower jaw in gymnophionans (Nussbaum and Wilkinson, 1989; Jenkins and Walsh, 1993), in approximately the same position as symphyseal teeth in non-lissamphibian temnospondyls. Based on the position of the splenial teeth and his belief (Bolt, 1991:217) that these teeth are borne on the dentary component of the pseudodentary, Bolt (1991) interpreted the splenial teeth of gymnophionans as primitively retained symphyseal teeth. In my opinion, the homologies of these two sets of teeth are unproven. As Bolt (1991:210) acknowledged earlier in the same paper, it is unclear whether the splenial teeth in gymnophionans are borne on the dentary or, as DeBeer (1937:195) stated, on the coronoid component of the compound pseudodentary. Until developmental studies can be brought to bear on this issue, I consider it best to regard the homology of the splenial teeth in gymnophionans as unresolved. The status of symphyseal teeth in karaurids is uncertain based on published descriptions, but such teeth are lacking in albanerpetontids, salientians, and all but one urodele—the purported sirenid Kababisha humarensis Evans et al. from the Early Cretaceous of Sudan (see Evans et al., 1996:text-figs. 3A, 4A, B).

42. Palatal dentition (B, LR, Md, M88, ME): 0, palatal fangs present; 1, palatal fangs absent—Primitively in temnospondyls the vomer, palatine, and, where present, ectopterygoid each bear a pair of fangs that are larger than the marginal teeth on the upper and lower jaws. If smaller palatal teeth are also present, as in Apateon, these are arranged in series with the fang pairs. In Doleserpeton and lissamphibians for which the pattern of palatal dentition can be determined, palatal teeth are similar in size to the marginal teeth and are arranged in rows or clumps.

Axial Skeleton (characters 43–49; Fig. 8-7)

43. Number of presacral vertebrae (modified from LR, Md, ME, M93): 0, 20–26; 1, more than 40; 2, less than 20—Where counts can be determined directly or estimated with confidence, 20 to 26 presacral vertebrae occur in the outgroup taxa, Apateon, and Doleserpeton. Celtedens ibericus also falls within this range, with a presacral count of 22 (McGowan and Evans, 1995). Two independently derived states are seen among other lissamphibians. Elongation of the presacral region in gymnophionans is concomitant with a marked increase in the number of vertebrae. Eocaecilia has an estimated minimum of 42 presacrals (Jenkins and Walsh, 1993) and extant apodans have 96–286 presacrals (Duellman and Trueb, 1986). Conversely, the presacral region is shortened and the number of presacral vertebrae reduced, at least primitively, in batrachians. For example, Karaurus has 15 presacrals (Ivachnenko, 1978) and the basal urodele Cryptobranchus Leuckart has 19 presacrals (Reese, 1906). The number of presacral vertebrae is secondarily increased to nearly 60 in some elongate urodeles, such as amphiumids and sirenids. Reduction in the number of presacral vertebrae is most pronounced in salientians, with presacral counts of 14 in Triadobatrachus, ten in Vieraella, nine in Notobatrachus, Ascaphus, and Leiopelma, and eight in other anurans (Rage and Roček, 1989; Báez and Basso, 1996).

44. Odontoid process on atlas (LR, Md, ME, M88, TC): 0, absent; 1, present—The odontoid process (= tuberculum interglenoideum of some authors) is an anteriorly directed shelf or nipple-like structure that arises from between the paired atlantal cotyles and fits into the floor of the foramen magnum, thereby providing an additional point of articulation between the atlas and skull. Among temnospondyls an odontoid process occurs in Eocaecilia, albanerpetontids, and basal urodeles. Reduction and loss of the odontoid process within the urodele family Batrachosauroididae Auffenberg is regarded as a secondarily derived condition (Estes, 1981; Duellman and Trueb, 1986). Contrary to Trueb and Cloutier (1991), the condition of the process in Karaurus is uncertain because the atlas and skull of the holotype are preserved in articulation and the atlas has not been figured in ventral view. However, an odontoid process is present on the referred atlas figured by Nessov (1988:fig. 2:4) for Kokartus. Judging by the impression left by the ventral face of the displaced atlas in the holotype of Triadobatrachus, no odontoid process is present. Apodans and anurans also lack a true odontoid process. A superficially similar structure occurs in certain apodans and anurans (e.g., some species of the anuran genus Pipa Laurenti; see Trueb and Cannatella, 1986:fig. 11D, F), where the medioventral edges of the paired atlantal cotyles are confluent and project anteriorly; in contrast to Laurin and Reisz (1997), I do not regard these structures as the homologue of the odontoid process.

45. Foramen for exit of first spinal nerve in atlas (ES, Md, M88): 0, foramen absent; 1, foramen present—Primitively in temnospondyls the first spinal nerve exits intervertebrally between the atlas and first trunk vertebra. Where the first spinal nerve exits intravertebrally, it does so through a foramen in the junction between the neural arch wall and centrum of the atlas. This foramen occurs in apodans (Norris and Hughes, 1918; Wake, 1980a), Eocaecilia (Jenkins and Walsh, 1993), and urodeles (Edwards, 1976). The foramen for the first spinal nerve occurs in all albanerpetontid specimens I have seen, including atlantes of A. arthridion (Gardner, 1999b) and an atlas of A. inexpectatum (Estes and Hoffstetter, 1976:pl. 6, fig. 14; here:Fig. 8-7E, F), yet McGowan (1998b) claimed the foramen was absent in atlantes of A. inexpectatum and Celtedens spp. available to him. Considering that the foramen for the first spinal nerve is consistently present in atlantes of all urodeles and apodans, I would be surprised if the foramen was variably present among albanerpetontids, especially within one genus or species. Nevertheless, as I have not seen the Celtedens atlantes that McGowan (1998b) examined, I scored the foramen for the first spinal nerve as unknown for the genus. The status of this foramen is also unknown for karaurids and Triadobatrachus. All anurans lack a foramen for the first spinal nerve.

46. Structure and contacts of anteriormost vertebrae (E, EH, ES, FN, ME, M88): 0, generalized temnospondyl pattern; 1, albanerpetontid pattern—Primitively in temnospondyls the atlas and first trunk vertebra are the anteriormost two vertebrae. There are three points of contact between these vertebrae. Ventrally, the centra articulate across intervertebral cartilages that infill the smooth-walled posterior cotyle of the atlas and the anterior cotyle of the first trunk vertebra. Dorsally, the paired postzygapophyses on the atlantal neural arch extend posteriorly to overlap onto complementary, anteriorly directed prezygapophyses on the neural arch of the first trunk vertebra. This basic pattern holds true regardless of whether one or both vertebrae are primitively multipartite, as in Triadobatrachus and Balanerpeton, respectively, or are composed of a single centrum fused with the neural arches, as in Doleserpeton and extant lissamphibians. In albanerpetontids the atlas and first trunk vertebra are separated by a small centrum that lacks a neural arch. McGowan (1998b) interpreted this archless centrum as a neomorph, and I follow him and Fox and Naylor (1982) in calling this structure the "axis." The centra of the axis and atlas contact in a unique manner: the anterior face of the axis has three slightly convex facets, one dorsally and one each ventrolaterally, that fit into complementary facets in the walls of the concave posterior cotyle of the atlantal centrum.

Contact more posteriorly between the axis and anterior cotyle of the first trunk vertebra is unremarkable, although the two bones fuse in some individuals of at least one species, Albanerpeton inexpectatum (Estes and Hoffstetter, 1976; McGowan, 1998b). The usual tetrapod pattern of contact between the neural arches on the atlas and first trunk vertebra does not occur in albanerpetontids, because these elements lack, respectively, the post- and prezygapophyses. Instead, the leading edge of the neural arch on the first trunk vertebra is developed into an anteriorly projecting process that fits into a V-shaped notch in the posterior edge of atlantal neural arch. Because the structure and patterns of contacts among the first three vertebrae in albanerpetontids undoubtedly acted in concert to enhance flexibility and rigidity of the "cervical" region (McGowan, 1998b; this study), I regard morphological novelties of these vertebrae as forming a single, complex character.

47. Intercentra in postatlantal vertebrae (B, LR, Md, ME): 0, Intercentrum larger than pleurocentra; 1, intercentra smaller than pleurocentrum; 2, intercentra absent—The vertebral centrum in most lissamphibians consists of a single element, the homology of which has long been uncertain. Here I follow Williams (1959) and Bolt (1991) in regarding this element as the homologue of the pleurocentrum. I recognize three states that form a linear transformation series leading to loss of the intercentra. Primitively in temnospondyls the vertebral centrum consists of a large, anterior intercentrum and a pair of smaller, posterior pleurocentra. Doleserpeton and Eocaecilia exhibit the intermediate state in which tiny, paired intercentra are retained and the pleurocentrum is the dominant element. In all other lissamphibians the intercentra are absent and the pleurocentrum forms the entire centrum.

48. Basapophyses on trunk vertebrae (ES, Md, ME, M88): 0, absent; 1, present—Basapophyses are paired ventral processes that primitively are lacking from the trunk centra of temnospondyls. Where present basapophyses arise ventrolaterally on trunk vertebrae, near the rim of the posterior or anterior cotyles or both. Basapophyses in albanerpetontids and, where present, in basal urodeles are small bony nubs that do not extend any appreciable distance past the margin of the centrum and are not involved in articulating with the ribs. Intraspecific variation in the position, size, and presence of basapophyses along the trunk region has been documented in urodeles (Naylor, 1978) and inferred, based on a urodelan model, for albanerpetontids (Estes and Hoffstetter, 1976;

Estes, 1981; Estes and Sanchíz, 1982). Basapophyses are intimately associated with the ventral trunk musculature in more advanced urodeles, but less so in hynobiids and cryptobranchids (Naylor, 1978). This probably was true for albanerpetontids as well, judging by their similarly weak basapophyses. The presence of basapophyses in Eocaecilia is uncertain, but trunk vertebrae in crown-clade gymnophionans anteroventrally bear enlarged, modified basapophyses (= parapophyseal process of some authors) that extend forward to grip the preceding vertebral centrum and serve as major points of origin for trunk muscles and associated ligaments. Apodan basapophyses thus are important for maintaining a strong, yet flexible vertebral column (Naylor and Nussbaum, 1980; Nussbaum and Naylor, 1982) and additionally provide a point of articulation for the ventral head of the rib (Wake, 1980a).

49. Number of rib heads (Md, ME, TC): 0, two; 1, one—Temnospondyl ribs primitively bear two proximal heads, one dorsally and one ventrally, for articulation with the centrum. These paired rib heads may be obscured by an interconnecting web of bone, as in Balanerpeton and Dendrerpeton, or closely appressed, as in some basal urodeles. Ribs in Celtedens, Triadobatrachus, and, where free, in basal anurans have a single proximal head.

Appendicular Skeleton (characters 50–58)

50. Scapulocoracoid (LR, Md, ME, M88): 0, one ossification; 1, separate scapular and coracoid ossifications—The scapulocoracoid develops as a single unit in most temnospondyls and forms the lateral part of the pectoral girdle. In anurans, Triadobatrachus, and Celtedens the dorsal and ventral components of the ancestral scapulocoracoid ossify separately as, respectively, the scapula and coracoid. This character is inapplicable for apodans because all members lack the pectoral girdle.

51. Interclavicle (LR, Md, ME, M88, TC): 0, present; 1, absent—Where present the interclavicle primitively forms a broad, ventromedian plate in the pectoral girdle. Urodeles, anurans, and apodans lack the interclavicle. This also appears to be the case in Karaurus, Triadobatrachus, and Celtedens judging by published figures of skeletons.

52. Cleithrum (LR, Md, TC): 0, present; 1, absent—If present in the pectoral girdle, the cleithrum lies along the anterodorsal edge of the scapulocoracoid and contacts the distal end of the interclavicle. The cleithrum is absent in apodans, anurans, and urodeles. Judging by published figures of the respective holotype skeletons, Triadobatrachus and Karaurus also appear to lack the cleithrum. The status of this character in albanerpetontids is unknown.

53. Clavicle (LR, Md, TC): 0, present; 1, absent—The clavicle in temnospondyls primitively is an L-shaped element comprised of a broad, horizontal ventral plate that underlies the interclavicle and a narrow, dorsally directed process that articulates along the anterior edge of the scapulocoracoid. Trueb and Cloutier (1991) regarded reduction and loss of the clavicle as separate derived states. As I have found it difficult to describe the relative size of the clavicle, the only states I recognize here are the presence and absence of the bone. The latter condition occurs in apodans and urodeles. Published figures of skeletons of Karaurus and Celtedens also show no evidence of a clavicle.

54. Proportions of humerus (ME, M93): 0, stout and short; 1, slender and elongate—The humerus in temnospondyls primitively is stout and relatively short, with the length only about two to three times the maximum width across the distal head. This is the condition seen in Balanerpeton and Dendrerpeton. Where known in other terminal taxa the humerus is relatively longer and more slender or gracile in build, although the proportions in cryptobranchids (see Reese, 1906:fig. 10A) approach those seen in more basal temnospondyls. Humeri in the holotype of Karaurus lack the distal and proximal articular ends (Ivachnenko, 1978) and, thus, underestimate the proportions of the bone.

55. Form of radial condyle on humerus (Md, ME): 0, low ridge; 1, ball-shaped—Primitively in temnospondyls the distal end of the humerus bears a low, broad, ridge-like radial condyle for articulation with the radius. Among ingroups for which the form of the radial condyle can be established, the condyle is developed into a ball in urodeles, anurans, and albanerpetontids.

56. Entepicondylar foramen in humerus (LR, M88, 93): 0, present, 1, absent—Where present in temnospondyls the entepicondylar foramen perforates the humerus medially at about the midpoint of the shaft. The foramen is absent in all ingroups for which this character can be scored.

57. Form of iliac blade (LR, Md, M88, TC): 0, short, club-shaped, directed posterodorsally–dorsally; 1, elongate, slender, directed anterodorsally—Where present the ilium articulates dorsally with the sacral vertebra to brace the pelvic girdle against the vertebral column. Primitively in temnospondyls the ilium is relatively short, club-shaped, and extends posterodorsally, as in Dendrerpeton (Holmes et al., 1998:fig. 9), or more dorsally, as in Apateon (Schoch, 1992:text-fig. 15). In anurans and Triadobatrachus the ilium is elongate, narrow, and extends anterodorsally. The unique configuration of the ilium in salientians is functionally related to hopping or saltation (Jenkins and Shubin, 1998).

58. Pubis (Md, ME): 0, ossified; 1, unossified—Primitively in temnospondyls the pubis is ossified as the ventroanterior element of the pelvic girdle. Among terminal taxa for which this character can be scored the pubis is present, but unossified in caudates and salientians.

Miscellaneous Character

59. Dermal scales (Md, ME, M88, TC): 0, present; 1, absent—Temnospondyls primitively have dermal scales embedded in the skin. As these scales are often tiny and develop late in ontogeny, they may be difficult to identify in fossils. This is the situation for the four non-lissamphibian temnospondyls and three of the fossil lissamphibians included in my analysis. Dermal scales are reliably known for apodans (e.g., Zylberberg et al., 1980) and albanerpetontids (McGowan and Evans, 1995), but are absent in basal urodeles and anurans.

RESULTS

Shortest Tree

The branch-and-bound search yielded one shortest tree of 96 steps (Fig. 8-8). Albanerpeton and Celtedens are identified as sister-taxa and the resultant monophyletic Albanerpetontidae nests in the Lissamphibia as the sister-taxon of the Batrachia. The topology of this tree thus agrees with McGowan and Evans' (1995) shortest tree, but differs from all 12 of Trueb and Cloutier's (1991) shortest trees and McCord's (1999) shortest tree in finding no support for a closer relationship between albanerpetontids and caudates. Figure 8-8 shows that the less inclusive clades identified in the shortest tree are relatively well supported: these clades are recovered in at least 74% of 2000 bootstrap replicates and require two to eight extra steps to collapse. Figure 8-9 shows distributions of apomorphies as mapped by the ACCTRAN and DELTRAN character state optimizations. Below I report on the synapomorphies and support for each of the nine less inclusive clades identified in the shortest tree. Additional comments on certain clades and character states appear in the "Discussion."

Node A, unnamed clade: Apateon (Doleserpeton (Gymnophiona (Albanerpetontidae (Caudata + Salientia))))—Seven synapomorphies reliably support clade A: 8(1), frontal contributes to orbital margin; 13(1), intertemporal absent; 18(1), ectopterygoid reduced; 21(1), no pterygoid-vomer contact; 27(1), bilobed occipital condyle; 54(1), humerus relatively elongate and slender; and 56(1), humerus lacking entepicondylar foramen. Neither palatal character can be scored for albanerpetontids. Character 8 subsequently reverts to the primitive state either in gymnophionans according to ACCTRAN or in Eocaecilia according to DELTRAN (see account below for Gymnophiona).

None of the remaining three synapomorphies identified by ACCTRAN convincingly support the clade. Reduced intercentra [47(1)] and a ball-shaped radial condyle [55(1)] are problematic synapomorphies because the former character cannot be scored for Apateon, whereas the latter cannot be scored for Apateon, Doleserpeton, and Eocaecilia. Judging by the condition in other branchiosaurids and amphibamids (e.g., Boy, 1978; Daly, 1994), derived states of both characters probably arose at less inclusive nodes along the stem, as suggested by DELTRAN. Character 26 can be scored for all relevant taxa, but two equally parsimonious arrangements are possible on the shortest tree: a more anteriorward jaw articulation [26(1)] either arose once at node A and subsequently reversed in Doleserpeton (ACCTRAN) or arose convergently in Apateon and at node C (DELTRAN).

Along with the Lissamphibia and Albanerpetontidae, clade A is one of the most robust clades identified in my analysis. Clade A is recovered in all 2000 bootstrap replicates and it is tied with the Lissamphibia in having the second highest decay index (seven steps).

Node B, unnamed clade: Doleserpeton (Gymnophiona (Albanerpetontidae

(Caudata + Salientia)))—Six unambiguous synapomorphies are identified for the clade of Doleserpeton + Lissamphibia: 18(2), ectopterygoid absent; 20(1), palatine articulates posteriorly with pterygoid; 37(1), marginal teeth not folded; 38(1), marginal teeth pedicellate; 39(1), crowns on marginal teeth labiolingually bicuspid; and 42(1), palatal fangs absent. Character 20 is inapplicable to anurans and caudates because these taxa primitively lack the palatine. Characters 18, 20, and 42 currently cannot be scored for albanerpetontids and character 38 reverses independently in karaurids and albanerpetontids. The latter group also exhibits the alternative, derived pattern of three mesiodistally aligned tooth cuspules [39(2)]. As implied in the previous account, the DELTRAN arrangement is more conservative and probably correct in postulating reduced intercentra [47(1)] as a further synapomorphy for node B.

ACCTRAN postulates that loss of the interclavicle [51(1)], cleithrum [52(1)], and clavicle [53(1)] occurred at node B. The positions occupied by these apomorphies on the shortest tree are problematic because none of the three characters can be scored for Doleserpeton and Eocaecilia, and character 52 also cannot be scored for albanerpetontids. Considering that other amphibamids retain the interclavicle, cleithrum, and clavicle, DELTRAN is probably correct in postulating that these elements were lost at one or more less inclusive nodes, but it is uncertain at which node(s) these losses occurred.

Support for Clade B is marginally less than for clade A, Lissamphibia, and Albanerpetontidae. Clade B has the second highest bootstrap value (98%) and third highest decay index (six steps).

Node C, Lissamphibia: Gymnophiona (Albanerpetontidae (Caudata + Salientia))—The Lissamphibia are supported by seven unambiguous synapomorphies in this analysis: 9(1), parietal foramen absent; 10(1), sclerotic ring absent; 14(1), supratemporal absent; 15(1), postparietal absent; 16(1), tabular absent; 45(1), foramen for spinal nerve in atlas; and 48(1), basapophyses present. Each of these characters can be scored for one or both albanerpetontid genera. Accepting the last character as a lissamphibian synapomorphy is problematic because the condition in Eocaecilia is uncertain. Characters 9, 45, and 48 subsequently reverse to their respective primitive states at some level in salientians (see salientian account below). I follow the ACCTRAN optimization in regarding the odontoid process on the atlas [44(1)] as an additional lissamphibian synapomorphy, because this arrangement requires that the process be gained only once at the base of the Lissamphibia. This interpretation necessitates that the odontoid process subsequently was lost independently in apodans and salientians; I do not consider this unreasonable, because reduction and loss of the process has occurred elsewhere within the urodelan family Batrachosauroididae (Estes, 1981). The alternative and, in my opinion, biologically less probable DELTRAN arrangement demands that the odontoid process evolved independently three times among lissamphibians—once each in Eocaecilia, albanerpetontids, and caudates.

None of the other eight putative synapomorphies reliably support the Lissamphibia. Loss of the symphyseal teeth [41(1)] as postulated by ACCTRAN and of the interclavicle [51(1)], cleithrum [52(1)], and clavicle [53(1)] as postulated by DELTRAN are problematic synapomorphies because the relevant characters cannot be scored for some critical taxa. Two equally parsimonious, and evidently equally biological probable, arrangements are possible for the derived states of characters 26 and 32 on the shortest tree. An anteriorward jaw articulation [26(1)] either arose convergently at node C and in Apateon (DELTRAN), or appeared once at node A and reversed in Doleserpeton (ACCTRAN). The mentomeckelian [32(1)] either evolved once at node C and was secondarily lost in albanerpetontids (ACCTRAN), or arose convergently in apodans and batrachians (DELTRAN). Ambiguity over the position of the mentomeckelian on the shortest tree is due, in part, to the fact that this character cannot be scored for stem-gymnophionans, -caudates, or -salientians. ACCTRAN places loss of the postorbital [12(1)] and intercentra [47(2)] at node C, but I reject both as lissamphibian synapomorphies because such an arrangement requires the biologically problematic re-appearance of both bones in Eocaecilia. DELTRAN postulates a more realistic arrangement, in which both bones are lost twice at less inclusive levels—once each in apodans and at node E. I thus interpret the postorbital and reduced intercentra in Eocaecilia as primitively retained elements.

The Lissamphibia are one of the three most robust clades identified in my analysis, with a bootstrap value of 100% (tied with both clade A and the Albanerpetontidae) and the second highest decay index (seven steps; tied with clade A).

Node D, Gymnophiona: Eocaecilia + Apoda—Five unambiguous synapomorphies support the Gymnophiona: 23(1), palatine prevents pterygoid-maxilla contact; 24(1), parasphenoid contributes to compound os basale; 28(1), mandible formed by pseudodentary and pseudoangular; 36(1), dual jaw closing mechanism; and 43(1), more than 40 presacral vertebrae. Accepting the first apomorphy as a gymnophionan synapomorphy admittedly is hindered by the fact that the pattern of pterygoid-maxillary contact remains unknown for albanerpetontids.

Both optimizations interpret exclusion of the frontal [8(0)] from the orbital margin as a reversal from the more derived condition at node A and either a synapomorphy of the Gymnophiona (ACCTRAN) or an autapomorphy of Eocaecilia (DELTRAN). As character 8 is inapplicable for apodans, the DELTRAN arrangement is more conservative, but it too may be misleading. Although large compared to apodans (Jenkins and Walsh, 1993), the orbit in Eocaecilia still appears to be relatively smaller than in other temnospondyls. Considering that the reduced orbit in Eocaecilia may contribute to the frontal failing to contact the orbit, the pattern of frontal exclusion in this stem-gymnophionan may not be homologous with that seen in the outgroups, where exclusion of the frontal from the orbit primitively is due entirely to broad contact between the pre- and postfrontals.

The Gymnophiona are one of the four least robust clades identified in my analysis: the clade has the third lowest bootstrap value (78%) and second lowest decay index (three steps; tied with clade E).

Node E, unnamed clade: Albanerpetontidae (Caudata + Salientia)—Of the 11 synapomorphies identified for this clade, just three are unambiguous: 29(1), surangular absent; 30(1), splenials absent; and 31(1) coronoids absent. Loss of the postfrontal [11(1)] is a homoplasy convergent with non-rhinatrematid apodans. For reasons given above in the account for node C, I follow the DELTRAN optimization in regarding loss of the postorbital [12(1)] and intercentra [47(2)] as homoplasies of clade E and apodans.

None of the other five putative synapomorphies convincingly support clade E. ACCTRAN postulates loss of the palatine [17(1)] as a synapomorphy for the clade, but this is difficult to accept, in part, because the status of the palatine in albanerpetontids is uncertain and, in part, because this arrangement requires the re-appearance of a reduced palatine in Triadobatrachus. DELTRAN postulates the more conservative and, in my opinion, biologically realistic arrangement in which the palatine is lost independently in caudates and anurans. As discussed in the account above for Lissamphibia, loss of symphyseal teeth [41(1)] is an equivocal synapomorphy for either the Lissamphibia

(ACCTRAN) or, more conservatively, clade E (DELTRAN). Single-headed ribs [49(1)] and separate coracoid and scapular ossifications [50(1)] occur in salientians, Celtedens (McGowan and Evans, 1995), and, judging by the conservative postcranial morphology of albanerpetontids, almost certainly in Albanerpeton as well. Two equally parsimonious arrangements are possible: single-headed ribs and separate coracoid and scapular ossifications either arose once at node E, with both characters subsequently reversing to their respective primitive states in caudates (ACCTRAN), or the derived state for each character arose convergently in Celtedens (probably in albanerpetontids as a whole) and salientians (DELTRAN). As noted in the account above for node A, character 55 is problematic because I have not been able to score it for Apateon, Doleserpeton, and Eocaecilia. The derived state for this character, a ball-shaped radial condyle [55(1)], thus could be placed at any of nodes A–C or E, with ACCTRAN and DELTRAN postulating the extreme positions (nodes A and E, respectively). Judging by other branchiosaurids and amphibamids, a ball-shaped radial condyle probably arose at either node C or E, depending on the condition in Eocaecilia.

Clade E is among the four least robust clades identified in my analysis. The clade has the second lowest bootstrap value (76%) and is tied with the Gymnophiona in having the second lowest decay index (three steps).

Node F, Albanerpetontidae: Albanerpeton + Celtedens—Seven unambiguous synapomorphies support the Albanerpetontidae: 5(2), azygous frontals and paired parietals; 6(1), prominent internasal process on frontals; 7(1), posterior ends of paired nasals and prefrontals fit into complementary slots in azygous frontals; 33(1), symphyseal prongs on dentary; 35(1), articular surface on mandible for contact with skull faces posteriorly; 39(2), crowns on marginal teeth labiolingually compressed and mesiodistally tricuspid; and 46(1), unique configuration of anteriormost vertebrae. I interpret an eighth apomorphy, non-pedicellate marginal teeth [38(0)], as a reversal potentially convergent with karaurids.

I follow the ACCTRAN optimization in regarding the odontoid process [44(1)] in albanerpetontids as a retained lissamphibian symplesiomorphy, rather than a homoplasy convergent with Eocaecilia and caudates as postulated by DELTRAN. The lack of a mentomeckelian [32(0)] is either a reversal from the inferred primitive lissamphibian condition and, therefore, derived for albanerpetontids (ACCTRAN), or a retained temnospondyl symplesiomorphy (DELTRAN).

The Albanerpetontidae are the most robust clade identified in my analysis, with a bootstrap value of 100% (tied with clade A and Lissamphibia) and a decay index of eight steps.

Node G, Batrachia: ((Karauridae + Urodela) (Triadobatrachus + Salientia))—The Batrachia are supported by five unambiguous synapomorphies: 3(1), maxillary arcade open posteriorly; 34(1), mandible bears convex condyle for articulation with skull; 43(2), presacral count less than 20; 58(1), pubis unossified; and 59(1), dermal scales absent. Of these, character 3 cannot be scored for Triadobatrachus and characters 34 and 59 cannot be scored for stem-salientians or stem-caudates. A sixth apomorphy, jugal absent [4(1)], is convergent with apodans.

Neither of the two putative synapomorphies identified by DELTRAN confidently supports the Batrachia. The shortest tree infers that basal batrachians have a mentomeckelian [32(1)], but this is uncertain because the condition in stem-caudates and stem-salientians is unknown. DELTRAN postulates that the mentomeckelian evolved convergently in batrachians and apodans, whereas ACCTRAN interprets the bone as a lissamphibian symplesiomorphy. Lack of pterygoid–palatine contact [20(2)] cannot realistically be regarded as a batrachian synapomorphy because all batrachians, except Triadobatrachus, lack the palatine. I prefer the more conservative ACCTRAN optimization, which views lack of contact between the pterygoid and palatine as an autapomorphy for Triadobatrachus.

The Batrachia are among the four least robust clades recovered in my analysis. The clade has the lowest bootstrap value (74%) and the third lowest decay index (four steps; tied with Salientia).

Node H, Caudata: Karauridae + Urodela—Monophyly of the Caudata is supported by two synapomorphies: anterior ramus of pterygoid free of bony contacts anteriorly [19(1)] because the ramus is shortened [23(2)]. Although neither character can presently be scored for albanerpetontids, I provisionally regard the derived states of both characters as caudate synapomorphies because these otherwise are absent among taxa included in my analysis. When described in detail, skulls now available for Celtedens ibericus may help clarify whether albanerpetontids actually retain the primitive state for each of these two characters.

As discussed in the account above for node E, I follow the DELTRAN optimization in regarding loss of the palatine [17(1)] as a homoplasy convergent with anurans. Because I regard the odontoid process as a lissamphibian synapomorphy, I interpret the presence of this process [44(1)] in caudates as a symplesiomorphy, rather than the homoplasy postulated by the DELTRAN optimization. Caudates appear to be unique within the more inclusive clade E in having double-headed ribs [49(0)] and one scapulocoracoid ossification [50(0)]. As implied in the account above for node E, the relative apomorphies of these character states are uncertain for the Caudata: these character states are either reversals from node E and, therefore, derived for the Caudata (ACCTRAN), or are retained temnospondyl symplesiomorphies (DELTRAN).

The Caudata are among the four least robust clades identified in my shortest tree. Bootstrap and decay analyses reveal different levels of relative support. Although the clade has the fourth highest bootstrap value (80%), it has the lowest decay index and collapses after only two steps. Failure to recognize a more robust Caudata is not surprising, as few compelling caudate synapomorphies have previously been identified (see Milner, 1988; Trueb and Cloutier, 1991). A potential autapomorphy for caudates is the presence of elongate, doubled-headed or bicipital transverse processes, for articulation with ribs, on at least the anterior trunk vertebrae (Fig. 8-7C). I have not been able to include in my analysis a character that describes the relative length (short versus long) and number (one or two) of transverse processes, because homologies of these processes among temnospondyls are uncertain (see Gamble, 1922; Naylor, 1978).

Node I, Salientia: Triadobatrachus + Anura—Fusion of the frontal and parietal into a compound frontoparietal [5(1)], absence of marginal teeth on the dentary [40(1)], and an elongate, anteriorly directed ilium [57(1)] are unambiguous synapomorphies for the Salientia. Two and, probably, four homoplasies also support the clade. According to both character state optimizations pterygoid–maxilla contact [22(1)] is convergent with Doleserpeton, whereas lack of basapophyses [48(0)] is a reversal from the inferred primitive lissamphibian condition. I follow the ACCTRAN optimization in viewing the odontoid process as having been lost [44(0)] secondarily and convergently in salientians and apodans. Although the status of the foramen for the first spinal nerve cannot be determined for Triadobatrachus, the foramen is absent in a referred atlas figured by Evans and Borsuk-Białynicka (1998:fig. 3G) for Czatkobatrachus. The condition in the latter stem-salientian suggests that ACCTRAN may also be correct in identifying loss of the spinal foramen [45(0)] as a reversal for salientians as a whole, rather than anurans alone as proposed by DELTRAN.

Although identified by both ACCTRAN and DELTRAN, the presence of clavicles [53(0)] as a salientian homoplasy should be viewed with suspicion because this requires the problematic re-appearance of the clavicle in salientians. None of the other five putative synapomorphies reliably support the Salientia. As discussed in the account above for clade E (Albanerpetontidae + Batrachia), the positions of single-headed ribs [49(1)] and separate coracoid and scapular ossifications [50(1)] on the shortest tree are equivocal. These apomorphies either arose convergently in salientians and albanerpetontids (DELTRAN) or once at the base of clade E, then reversed to their respective primitive states in caudates (ACCTRAN). ACCTRAN interprets the parietal foramen [9(0)] as a reversal for salientians, but because the homologies of the parietal foramen and anuran frontoparietal fontanelle are uncertain, I follow the more conservative DELTRAN arrangement in viewing the parietal foramen as a reversal for _Triadobatrachus_ alone. Another two salientian homoplasies identified by ACCTRAN are better regarded as anuran homoplasies by DELTRAN, because neither character can be scored for _Triadobatrachus_: loss of the lacrimal [1(1)] is convergent with apodans and many urodeles, whereas loss of the stapedial foramen [25(1)] is convergent with post-rhinatrematid and -ichthyophiid apodans, and most, if not all, urodeles.

Support for the Salientia in my analysis is moderate, falling between clades A, B, Lissamphibia, and Albanerpetontidae on one hand and the remaining four clades on the other hand. The Salientia have the third highest bootstrap value (92%) and the third lowest decay index (four steps; shared with Batrachia).

Next Longest Trees

Although longer trees are often ignored because they are less parsimonious, such trees may be insightful for revealing alternative patterns that are only slightly less well supported than those recovered in the shortest tree(s). Searches for longer trees using my data matrix show that other arrangements of terminal taxa require a minimum of two extra steps (Fig. 8-10). None of these alternative topologies are compelling, because these require even more character state conflicts than the shortest tree. Topologies of the next longest trees (two 98 step trees; i.e., minimum + 2 steps) differ only in identifying a paraphyletic Caudata (Fig. 8-10B). The placement of albanerpetontids is first altered in one of two 99 step trees (i.e., minimum + 3 steps), where this clade and the Gymnophiona reverse positions (Fig. 8-10C). Successively longer trees show other arrangements for the Albanerpetontidae (Fig. 8-10D–I).

DISCUSSION

Monophyly of the Albanerpetontidae

My analysis corroborates monophyly of the Albanerpetontidae. The relatively high bootstrap and decay values and suite of eight synapomorphies identified for the clade attest to the strength of this corroboration. The two albanerpetontid dental synapomorphies evidently are associated with feeding and I concur with previous suggestions (Estes, 1981; Fox and Naylor, 1982; McGowan, 1998b; Gardner, 1999a) that other cranial and vertebral features in the group, including the remaining six apomorphies identified here, strengthened and enhanced the mobility of the skull and cervical region for feeding, burrowing, or some combination of these. Elsewhere, I (Gardner, 1999a, c, in press a) have suggested that feeding and burrowing capabilities in some species of Albanerpeton were enhanced further to varying degrees by additional modifications to the frontals and jaws.

Albanerpetontid marginal teeth are distinctive in being non-pedicellate and in having labiolingually compressed, mesiodistally tricuspid tooth crowns. The origins of these tooth morphologies deserve consideration, because pedicellate and bicuspid teeth are primitive at a more inclusive level for lissamphibians and at least some amphibamids. Ontogenetic studies of extant lissamphibians show that marginal teeth typically change around the time of metamorphosis, first from non-pedicellate monocuspids to pedicellate monocuspids, then to pedicellate bicuspids (for references see accounts above for characters 38 and 39). Bolt (1977, 1991) has argued for a similar pattern in the Early Permian amphibamid Tersomius Case, but his arguments should be treated cautiously because it remains unclear how many species are represented in his postulated growth series of specimens from Oklahoma and Texas (Milner, 1982; Clack and Milner, 1993). The role that ontogeny played in establishing the distinctive marginal teeth of albanerpetontids cannot be demonstrated directly. Judging by size and structure, all available albanerpetontid jaws appear to be from postmetamorphic individuals; this implies that non-pedicellate and chisel-like teeth are the adult condition. The observation that tooth crowns are consistently chisel shaped along these jaws further supports this interpretation, because jaws of metamorphosing urodeles often exhibit a transitional condition in which teeth with larval and incipient adult crowns alternate along the ramus (see Greven, 1984:fig. 2a; Beneski and Larsen, 1989:fig. 2E). Non-pedicellate teeth in albanerpetontids may have been retained from an earlier larval or premetamorphic stage, as appears to be the case for extant sirenid and proteid urodeles, or these teeth may have developed secondarily during ontogeny from pedicellate teeth, as reportedly occurs (Lehman, 1968) in the anuran Ceratophrys Wied. Given the difficulty in deriving a mesiodistally tricuspid crown from a labiolingually bicuspid crown, I suggest that the albanerpetontid crown pattern instead was derived from a more generalized, premetamorphic monocuspid crown. Although the ontogenetic scenarios I have presented here are necessarily somewhat speculative, they should be testable if albanerpetontid jaws become available from larval or metamorphic individuals.

Regardless of how the distinctive marginal teeth of albanerpetontids arose, I propose that both derived character states of these teeth are functionally related. Whereas marginal teeth in lissamphibians primitively have bicuspid crowns, with pointed labial and lingual cuspules that are well suited for piercing and holding prey, the chisel-shaped tooth crowns of albanerpetontids seem better adapted for vertical shearing. As I have not identified unequivocal wear facets on tooth crowns of albanerpetontid jaws available to me, shearing evidently did not involve precise occlusion of opposing teeth. While the ability of crowns on pedicellate teeth to buckle inwards is advantageous for holding and manipulating prey (see account above for character 38), such mobility compromises the efficiency of a shearing bite. During shear, the crown must be immobile to ensure that opposing tooth crowns slide past one another. Non-pedicellate teeth are ideal in this regard, because they ensure that crowns remain stable during biting.

Two albanerpetontid apomorphies relate to the mandibular joints. The unique mortise and tenon joint between the anterior ends of the paired dentaries presumably both strengthened and allowed for controlled movement about the intermandibular or symphyseal joint; these factors probably played a role in feeding, burrowing, or both. Large collections of albanerpetontid dentaries show that one or two major symphyseal prongs occur with approximately equal frequencies on left and right dentaries (Fox and Naylor, 1982; Gardner, 1999a, b, in press a). This antisymmetry in symphyseal prong counts suggests that development of the paired mandibles must have been tightly controlled to ensure that a functional intermandibular joint was maintained. For example, if an individual developed one major symphyseal prong on the left dentary, then the right dentary would have to develop two major complementary prongs. To my knowledge, the nearly vertical joint between the mandible and skull is unique to albanerpetontids among temnospondyls. The functional significance of this modified joint is unclear to me. Considering that a similar condition occurs in amphisbaenids (see Montero and Gans, 1999:figs. 7, 8), a highly fossorial group of squamates, a nearly vertical mandibular-skull joint may be associated with burrowing. Re-orientation of this joint in both albanerpetontids and amphisbaenids requires that the mandible shorten to provide room for the more nearly horizontal quadrate, but this condition is considerably less pronounced in albanerpetontids. Osteological modifications about the intermandibular and mandibular-skull joints in albanerpetontids must have been accompanied by changes in jaw musculature.

Three albanerpetontid apomorphies describe the form and articulation of the frontals. Fusion of the frontals occurs with growth in albanerpetontids (Gardner, 1999a) and results in a solid, azygous median roofing element. The prominent internasal process and two pairs of slots in the leading edge of the azygous frontals evidently strengthened the skull roof by increasing the area of contact between this element and the more anterior paired nasals and prefrontals. The posterior ends of the last two pairs of bones act as tenons that fit into complementary slots (mortises) in the frontal. These mortise and tenon style joints undoubtedly strengthened the skull roof further. I suspect these joints were also capable of limited anterior-posterior movement, based on the observation that the inner walls of both pairs of slots and the complementary posterior end of the prefrontal (isolated nasals remain undescribed for albanerpetontids) are relatively smooth. The albanerpetontid skull is additionally strengthened by two primitively retained elements: the large lacrimal braces the skull roof against the maxilla and the jugal strengthens the maxillary arcade by acting as a bony bridge between the posterior end of the maxilla and squamosal. Strengthening of the skull and the potential development of a mobile frontal-nasal and -prefrontal joint presumably are also related to feeding, burrowing, or a combination of both.

The final albanerpetontid apomorphy involves the unique structure of the anteriormost three vertebrae. McGowan (1998b) recently proposed that the tripartite atlanto-axial joint enhanced neck mobility by permitting medial-lateral movement, thereby allowing albanerpetontids to swing their head from side to side without having to pivot the anterior part of the body. Although not noted by McGowan (1998b), albanerpetontids have a second unique contact in the cervical region. The anterior end of the neural arch on the first trunk vertebra extends craniad to fit into a complementary, median notch on the posterior edge of the atlantal neural arch. With the atlantal neural arch thus braced posteriorly against the neural arch of the first trunk vertebra, the cervical region would have been able to resist posteriorly directed compression, such as would be generated during head-first burrowing.

A number of other osteological features may be derived for albanerpetontids, but I have excluded these from my analysis either because I have not been able to determine homologies or because I could not reliably establish the condition in Celtedens. The most notable of these probable apomorphies are the following: bony boss on labial face of premaxillary pars dorsalis; suprapalatal pit opens in lingual face of pars dorsalis and associated palatal foramen perforates pars palatinum in premaxilla (see Gardner, 2000a); pars dentalis on maxilla developed anteriorly into a prominent process (= premaxillary lateral process of Gardner, 1999a) that labially overlaps and fits into complementary facet on premaxilla; lacrimal contributes to dorsal margin of external naris, articulates anteriorly with premaxilla, and fuses with prefrontal; Meckelian canal in dentary closed anteriorly; and prominent ventrolateral crest on underside of frontals extends posteriorly to underlap parietal.

Phylogenetic Position of the Albanerpetontidae

Albanerpetontids as Non-batrachian Lissamphibians—Cladistic analyses by Trueb and Cloutier (1991), McGowan and Evans (1995), McCord (1999) and myself (this study) agree in nesting albanerpetontids within the Lissamphibia, crownward of the Gymnophiona. In the context of all of these analyses albanerpetontids are placed within the more inclusive Temnospondyli. Trueb and Cloutier (1991) identified a clade of post-Dendrerpeton temnospondyls (their clade D) comprised of numerous taxa, including all of the ingroup taxa used here that were included in their analysis. Trueb and Cloutier's (1991) clade is supported by one synapomorphy: mediolateral, rather than vertical, replacement of marginal teeth. I have not used this character because patterns of tooth replacement are too poorly documented among non-lissamphibian temnospondyls. Nevertheless, in the context of placing albanerpetontids within the Temnospondyli, it is worth noting that undescribed Upper Cretaceous albanerpetontid jaws from North America appear to preserve evidence of mediolateral tooth replacement.

In contrast to studies by Trueb and Cloutier (1991) and McCord (1999), my analysis identifies the branchiosaurid Apateon and the amphibamid Doleserpeton as successively more closely related sister-taxa of the Lissamphibia. The clade of Apateon + (Doleserpeton + Lissamphibia) in my study is supported by seven cranial and postcranial synapomorphies that involve modifications to the humerus, the first loss of a temporal bone, and alterations to contacts about the orbit, in the palate, and at the cranial-cervical joint. Although these character states are identified as unambiguous synapomorphies based on the limited number of non-lissamphibian temnospondyls included here, it should be recognized that more comprehensive analyses for temnospondyls (e.g., Milner, 1990, 1993b; Trueb and Cloutier, 1991; Milner and Sequeira, 1994) and intra-familial analyses for dissorophoid-grade temnospondyls (e.g., Werneburg, 1989; Milner, 1993b; Clack and Milner, 1993) indicate that distributions of most of the character states are more complex. Only the reduced ectopterygoid appears to support a branchiosaurid + amphibamid + lissamphibian clade; the remaining six apomorphies actually support more inclusive nodes that lead towards a branchiosaurid–amphibamid–lissamphibian level of organization. Additionally, some of the latter apomorphies appear to have arisen multiple times among dissorophoid-grade temnospondyls. For example, entrance of the frontal into the orbit has evolved convergently in amphibamids, branchiosaurids, and micromelerpetontids (Werneburg, 1989; Milner, 1993b). Milner (1993b) listed another two synapomorphies, neither of which I have used here, to unite branchiosaurids, amphibamids, and lissamphibians: skull table reduced and interclavicle reduced, poorly ossified, and minimally overlapped by clavicle.

Doleserpeton and the Lissamphibia are united in my analysis by six synapomorphies relating to the structure of the palate and teeth, as well as one probable synapomorphy associated with simplifying the structure of the vertebral centra. Two of these synapomorphies—marginal teeth pedicellate and having labiolingually bicuspid crowns—have long been regarded as evidence for a close relationship between lissamphibians and amphibamids (Bolt, 1969, 1977, 1979, 1991; Milner, 1988, 1993b; McGowan and Evans, 1995). Such teeth appear to enhance prey handling and I suggest that this functional advantage was a key adaptation in the success of the amphibamid–lissamphibian clade. I have three major comments about these teeth.

First, divided teeth in which the division occurs between the crown and pedicel, rather than between the tooth base and the underlying bone as in some squamates (Savitzky, 1983; Patchell and Shine, 1986), are reliably known among tetrapods only in the amphibamids Doleserpeton, Amphibamus Cope (middle Pennsylvanian, USA) and Tersomius (Bolt, 1977, 1979, 1991; Clack and Milner, 1993) and primitively in lissamphibians. Two amphibamid genera, Platyrhinops (middle Pennsylvanian, USA and Czech Republic) and Eoscopus Daly (late Pennsylvanian, USA), have non-pedicellate teeth (Clack and Milner, 1993; Daly, 1994). Tooth structure cannot be determined for the final amphibamid genus, Milneria Hunt et al. (late Pennsylvanian, USA), because tooth-bearing sections of jaws are obscured in the only known skeleton (Hunt et al., 1996). The variable presence of pedicellate teeth among amphibamids is an interesting problem with potentially significant phylogenetic implications, but these matters cannot be explored further until the osteology and systematics of amphibamid genera are better documented and the monophyletic status of the family is resolved.

Published reports of pedicellate teeth in two other tetrapod taxa, both temnospondyls, are unsubstantiated. The first case involves a skull (FMNH PR892) identified by Bolt (1977) as pertaining to cf. Broiliellus Williston, an Early Permian genus of dissorophoid-grade temnospondyl. Published figures (Bolt, 1977:text-fig. 7) of the specimen are uninformative, because these show only the crown of a vomerine fang tooth, and published comments by Bolt (1977, 1991) are contradictory: Bolt (1977:242) originally stated "there is no evidence for pedicely of either fang teeth or marginal teeth in this specimen," but in his 1991 paper he first implied that pedicellate teeth are present (201, lines 18–21), then stated that the specimen has "marginal and fang teeth that may or may not be pedicellate" (201, lines 33–34). The second case involves Apateon, a genus that Trueb and Cloutier (1991:appendix II) scored as having pedicellate teeth. They justified their scoring decision as follows (1991:266): "Apateon is considered to have pedicellate teeth based on illustrations of Boy (1978:Fig. 5, 1987:Fig. 27)." The former figure in Boy's (1978) paper depicts a dentary fragment of Branchiosaurus sp., cf. petrolei Gaudry (= A. pedestris; Boy, 1986:135) without a single complete tooth. The surviving pedicels are too incomplete to convincingly show features suggestive of pedicely—i.e., pedicels uniform in height along ramus and each having a smooth dorsal rim for fibrous contact with the crown (see Fig. 8-5C). The second figure cited by Trueb and Cloutier (1991) does not exist in Boy's (1987) paper. To my knowledge, pedicellate teeth have never convincingly been demonstrated for Apateon nor any other branchiosaurid. Trueb and Cloutier's (1991) hypothesis that Apateon and lissamphibians are sister-taxa thus cannot be supported, because this inferred relationship hinged entirely on the presumed, shared presence of pedicellate teeth.

Second, among tetrapods, marginal teeth having bicuspid crowns with the labial and lingual cuspule separated by a mesiodistal sulcus occur only in the amphibamids Amphibamus, Doleserpeton, Platyrhinops, and Tersomius and primitively in lissamphibians (Bolt, 1977, 1979, 1991; Clack and Milner, 1993). The amphibamid Eoscopus appears to have monocuspid teeth, judging by figure 2 in Daly's (1994) paper. The condition in Milneria is uncertain because no teeth are exposed in the sole reported skeleton (Hunt et al., 1996). Bicuspid crowns have been reported for a variety of other tetrapods (e.g., Bolt, 1977, 1980; Langston and Olson, 1986; Laurin and Reisz, 1997) but upon closer examination such teeth prove to be structurally different from and clearly not homologous with those of amphibamids and lissamphibians. For example, bicuspid teeth in the brachystelechid microsaur Carrolla Langston and Olson (Early Permian, USA) have the cuspules arranged mesiodistally (Langston and Olson, 1986), not labiolingually. Superficially labiolingually bicuspid teeth have been reported in the same referred skull (FMNH PR892) mentioned above for cf. Broiliellus (Bolt, 1977) and in isolated jaws of two paracontemporaneous, unnamed tetrapod taxa from Oklahoma, USA (Bolt, 1980). However, published figures (Bolt, 1977:text-fig. 7; 1980:fig. 2) reveal that the crowns differ from the usual lissamphibian/amphibamid pattern in lacking a sulcus between the lingual and labial cuspules. Instead, the "'cuspules' are little more than the end points on a straight ridge which runs labiolingually across the crown" (Bolt, 1977:242).

Given that various kinds of bicuspid and superficially bicuspid teeth occur among tetrapods, crown patterns obviously need to be evaluated carefully for use in phylogenetic analyses. Contrary to the implications of Laurin and Reisz's (1997) scoring decisions for their character 97, the bicuspid marginal teeth of lissamphibians, Tersomius, and Amphibamus are homologous neither with those of brachystelechid microsaurs nor procolophonid reptiles. Trueb and Cloutier's (1991) use of "bicuspid or multicuspid" crowns as the derived state for their character 57 is equally inappropriate. In encompassing a diverse array of markedly different crown patterns, the state "bicuspid or multicuspid" obscures most, if not all, of the phylogenetically informative variation in crown patterns among dissorophoid-grade temnospondyls and lissamphibians.

Third, while I favour the interpretation that pedicellate, labiolingually bicuspid marginal teeth arose just once in more crownward temnospondyls, Laurin and Reisz's (1997) recent phylogenetic hypothesis implies that such teeth instead evolved at least twice among tetrapods—once in amphibamids (represented by Amphibamus and Tersomius in their analysis) and again in lissamphibians.

The Lissamphibia in my analysis are supported by eight synapomorphies, each of which can be identified in one or both albanerpetontid genera and, thus, supports placing albanerpetontids within the Lissamphibia. Loss of the sclerotic bones, postparietal, supratemporal, tabular, and parietal foramen and presence of an odontoid process previously have been advanced as lissamphibian synapomorphies (Milner, 1988; Trueb and Cloutier, 1991; McGowan and Evans, 1995; Laurin and Reisz, 1997). The first four synapomorphies involve losses of cranial elements, a trend that began in post-Dendrerpeton/Balanerpeton temnospondyls with the loss of the intertemporal and continued further in each of the less inclusive lissamphibian clades. The presence of a spinal foramen in the atlas and basapophyses on the trunk vertebrae have not previously been postulated as lissamphibian synapomorphies. Although the eight synapomorphies recognized here are derived within the Temnospondyli, none is assuredly unique to the Lissamphibia among tetrapods. For example, various groups of lepospondyls lack many of the same skull bones and a parietal foramen and possess a lissamphibian-like atlas (see

Carroll et al., 1998). Considerable work is needed to determine whether such resemblances are homologous and, thus, indicative of a close relationship between lissamphibians and lepospondyls or are convergences related to reduced body size and presumably similar lifestyles.

Over 30 more osteological synapomorphies for the Lissamphibia have been proposed by Parsons and Williams (1963), Duellman and Trueb (1986), Milner (1988), Bolt (1991), Trueb and Cloutier (1991), Trueb (1993), McGowan and Evans (1995), Reiss (1996), and Laurin and Reisz (1997), among others. Although detailed consideration of these putative synapomorphies is not essential for my purposes here, the following three comments are warranted:

(1) Loss of the postorbital, palatine, jugal, and lacrimal are not lissamphibian synapomorphies as some authors have suggested (e.g., Milner, 1988; Trueb and Cloutier, 1991; Trueb, 1993; Laurin and Reisz, 1997). The presence of all four elements in the stem-gymnophionan Eocaecilia (Jenkins and Walsh, 1993), of a reduced palatine in the stem-salientian Triadobatrachus (Rage and Roček, 1989), of the jugal and lacrimal in albanerpetontids (Estes and Hoffstetter, 1976; Fox and Naylor, 1982; McGowan and Evans, 1995), and of the lacrimal in the stem-caudate Karaurus (Ivachnenko, 1978) and certain basal (hynobiids) and more crownward (Dicamptodon Strauch and Rhyacotriton Dunn) urodeles (Larson, 1991) argues for each of the four bones having been lost several times at less inclusive levels within the Lissamphibia.

(2) At least four character states previously regarded as lissamphibian synapomorphies (Parsons and Williams, 1986; Duellman and Trueb, 1986; Milner, 1988; McGowan and Evans, 1995; Laurin and Reisz, 1997) are better viewed as lissamphibian symplesiomorphies that are synapomorphic at more inclusive levels: double-headed ribs are primitive for temnospondyls; marginal teeth that are pedicellate and have bicuspid crowns with a labial and lingual cuspule separated by a sulcus are synapomorphic for lissamphibians plus at least some amphibamids (see Clack and Milner, 1993); and the lack of palatal fangs is synapomorphic for Doleserpeton and lissamphibians.

(3) The status of many putative lissamphibian synapomorphies remains unresolved for a variety of reasons. Often the relevant characters cannot be scored for critical taxa. For example, the presence or absence of a clavicle, interclavicle, and cleithrum (Milner, 1988; Trueb and Cloutier, 1991; McGowan and Evans, 1995; Laurin and Reisz, 1997) is

not reliably known for Doleserpeton and Eocaecilia. For some characters, as with the symphyseal teeth of non-lissamphibian temnospondyls and splenial teeth of gymnophionans (Bolt, 1991), homologies are uncertain. In other cases, characters can be scored for critical taxa and the homologies are seemingly secure (e.g., mentomeckelian bone; Bolt, 1991), yet character state distributions conflict on the shortest tree(s).

McGowan and Evans' (1995) analysis and my study agree in postulating that albanerpetontids are the sister-taxon of the Batrachia. Alternative arrangements for the position of albanerpetontids using my unmodified data matrix are considerably less robust. For example, reversing the positions of albanerpetontids and gymnophionans requires three extra steps (Fig. 8-10C) and the resultant, less inclusive clade of Gymnophiona + Batrachia is recovered in less than five percent of 2000 bootstrap runs. A further step (i.e., minimum + 4 steps) is required to force albanerpetontids more crownward within the Batrachia.

Albanerpetontids and batrachians share six synapomorphies describing loss of the intercentra, postorbital, postfrontal, surangular, splenials, and coronoids. The first three of these are convergent with at least some apodans, whereas the remainder are uniquely derived among temnospondyls. Loss of these elements continues the trends towards simplifying and consolidating the vertebral centra and reducing the number of skull bones. McGowan and Evans (1995) earlier identified loss of the intercentra, postorbital, and postfrontal as synapomorphies for albanerpetontids and batrachians. These authors also listed basapophyses as a synapomorphy for the clade, but because I homologize the basapophyses of albanerpetontids and caudates with the so-called parapophyses of gymnophionans (see account above for character 48), I instead regard basapophyses as a lissamphibian synapomorphy. Both interpretations require the subsequent loss of basapophyses in salientians, an event evidently associated with the modification and reduction of trunk musculature that accompanied shortening of the presacral column for jumping. Although a sister-group relationship between albanerpetontids and batrachians is more robust than the alternatives, support for this more inclusive clade is not overwhelming at present. For this reason, I have refrained from formally naming the clade of Albanerpetontidae + Batrachia.

Albanerpetontids lack six synapomorphies that unite caudates and salientians: jugal and dermal scales lost (both present in albanerpetontids); maxillary arcade open posteriorly (closed posteriorly in albanerpetontids); pubis unossified (ossified in albanerpetontids); convex articular facet on mandible (concave in albanerpetontids); and less than 20 presacral vertebrae (22 presacrals in albanerpetontids). McGowan and Evans (1995) identified the first four apomorphies and another two character states, neither of which I have used, as batrachian synapomorphies. In my opinion a wide parasphenoid (their character 20) is too ambiguously defined, whereas an ossified opercular (their character 22) is problematic because the character cannot reliably be scored for Triadobatrachus, karaurids, and albanerpetontids. One batrachian synapomorphy, loss of the jugal, is convergent with apodans, and is a continuation of the lissamphibian trend towards reducing the number of skull bones. The convex articular facet on the mandible and posteriorly open maxillary arcade are uniquely derived for batrachians among lissamphibians, but for temnospondyls as a whole the former character state is convergent with metoposaurids (Jupp and Warren, 1986) and the latter character state is convergent with the branchiosaurid Schoenfelderpeton (Boy, 1987:fig. 7d). Both apomorphies involve modifications to the jaws that presumably are related to feeding. A decrease in the number of presacral vertebrae has been carried to an extreme in anurans, in which shortening of the trunk is functionally related to hopping. Presacral counts are more labile in caudates and have increased secondarily in various urodele lineages, particularly aquatic forms such as sirenids and amphiumids. The functional significance of an unossified pubis and loss of dermal scales is unclear.

Albanerpetontids as Caudates—I find little support for the hypothesis (e.g., Estes and Hoffstetter, 1976; Estes, 1981; Estes and Sanchíz, 1982; Trueb and Cloutier, 1991; McCord, 1999) that albanerpetontids are caudates. None of the 17 character states listed in Table 8-2 are convincing synapomorphies, either for placing the Albanerpetontidae within the Caudata or for allying the two groups as sister-taxa. Characters A–D can be dismissed because these involve three bones—pterygoid (A, B), squamosal (C), and stapes (D)—that are unknown for albanerpetontids. Two other characters (E and F) have been misinterpreted for albanerpetontids: the maxillary arcade (E) is primitively complete (see account above for character 3) and transverse processes on trunk vertebrae (F) are single-headed or unicipitate (see McGowan, 1996:fig. 12). Four characters (G–J) are better interpreted as lissamphibian synapomorphies. The distribution of one character state (K: clavicle absent) is problematic (see accounts above for nodes B and C) and is likely synapomorphic at a more inclusive level. The remaining six characters require the following comments:

Character L: movable quadrate. Estes and Sanchíz (1982) stated, without explanation, that the quadrate was movable in Albanerpeton and they regarded this as a synapomorphy shared with caudates. McCord (1999), also without explanation, accepted the character and regarded a movable quadrate as synapomorphic for "albanerpetontines" + urodeles. Facets on isolated albanerpetontid quadrates (Estes and Hoffstetter, 1976:pl. 5, fig. 5; McGowan, 1996:fig. 6; McGowan and Ensom, 1997:fig. 1e, f) indicate that the quadrate articulated posteriorly and dorsally with a bone, presumably the squamosal. The latter element remains undescribed for albanerpetontids. Judging by the structure of facets on the quadrate, particularly the groove along the dorsal surface of the posteriorly projecting process, the bone may have been capable of at least limited anterior–posterior movement relative to the squamosal, but this is not certain. Nor is it clear to me that the quadrate–squamosal joint in caudates is particularly mobile. The nature of the quadrate–squamosal joint in stem-caudates is unknown and I have not detected any notable movement about this joint when manipulating jaws of extant urodele specimens available to me. In fact, Elwood and Cundall (1994) stated that the quadrate is firmly united with the squamosal in Cryptobranchus, a basal urodele having an otherwise highly kinetic skull. Until the distribution and relative polarity of a movable quadrate–squamosal joint is better documented among temnospondyls, I see no justification for accepting a movable quadrate as a synapomorphy for albanerpetontids and caudates.

Character M: articular discrete. Trueb and Cloutier (1991) regarded the articular as discrete in caudates and albanerpetontids, and they interpreted this as a reversal from the inferred primitive lissamphibian pattern in which the articular fuses with one or more adjacent elements. My observations regarding the distribution of these character states differ. The articular is unknown for stem-caudates and where ossified in basal urodeles (e.g., Cryptobranchus; Reese, 1906:fig. 4A) the bone may fuse with the angular, at least in older individuals. The articular and angular are also fused in well-preserved mandibles of Albanerpeton inexpectatum (Estes and Hoffstetter, 1976; Gardner, 1999a:pl. 2F; here:Fig. 8-5F). Thus, instead of having a discrete articular (i.e., the inferred derived state within the Lissamphibia), at least some albanerpetontids and basal urodeles retain an articular that is primitively fused with an adjacent element.

Character N: muscle adductor mandibulae internus superficialis extends posteriorly across dorsal surface of skull. Estes (1981) and Estes and Sanchíz (1982) interpreted the smooth trough extending anterolaterally-posteromedially across the dorsal surface of the parietal—not the squamosal as reported incorrectly by McCord (1999: his character 28)—in albanerpetontids as evidence that the muscle adductor mandibulae internus superficialis extended posteriorly onto the dorsal surface of the skull. Estes (1981) and Estes and Sanchíz's (1982) interpretation suffers from circular reasoning: the condition in urodeles was used to interpret the condition in albanerpetontids, with the latter then being used to argue for a close relationship between albanerpetontids and urodeles. Although the position and structure of the trough along the dorsal surface of the parietal strongly argues for it having carried one or more adductor muscles, I see no basis for determining which muscle(s) were actually involved. Consequently, I regard extension of the muscle adductor mandibulae internus superficialis onto the skull as an unproven and, at best, speculative synapomorphy for albanerpetontids and urodeles. This character potentially could be salvaged by limiting it to the absence (primitive) and presence (derived) of the dorsal trough on the parietal, without reference to which adductor muscles(s) were involved. Yet even the derived state of this redefined character remains an unconvincing synapomorphy for albanerpetontids plus urodeles, because a similar trough crosses the parietal portion of the frontoparietal in some anurans.

Character O: prefrontal contributes to external narial margin. If present the prefrontal in temnospondyls primitively is excluded from the external narial margin by the nasal, septomaxilla, lacrimal, or some combination of these. Trueb and Cloutier (1991) and McCord (1999) identified contribution of the prefrontal to the external narial margin as a synapomorphy for albanerpetontids + urodeles. I believe these authors misinterpreted this character in both groups. In all figures and specimens of hynobiids and cryptobranchids available to me, the prefrontal is primitively excluded from the external narial margin. This also appears to be the case for Albanerpeton (contra Trueb and Cloutier, 1991), judging by a referred specimen (MNHN.LGA 1226, maxilla and incompletely fused lacrimal and prefrontal; Gardner, 2000b:figs. 4, 5) of A. inexpectatum in which the large lacrimal would have excluded the smaller prefrontal from the external narial margin in life. Albanerpetontids and basal urodeles thus exhibit the inferred primitive, not the derived, state of prefrontal-external narial contact.

Contribution of the prefrontal to the external narial margin may instead be autapomorphic for Karaurus. Contacts about the external naris are admittedly difficult to interpret for this taxon, because the holotype and only skull is flattened and the bones are slightly displaced, but the published photograph (Ivachnenko, 1978:pl. 9) of the skeleton in dorsal view supports Estes's (1981) statement that the prefrontal minimally contributes to the naris (contra Trueb and Cloutier, 1991).

Character P: teeth non-pedicellate. Even assuming that Karaurus had non-pedicellate teeth (see account above for character 38), non-pedicely does not compelling support a sister-pair relationship between Karaurus and albanerpetontids, as Trueb and Cloutier (1991) proposed, because this putative synapomorphy is incongruent with six synapomorphies that unite caudates and salientians to the exclusion of albanerpetontids. Further, it is evident that non-pedicely has arisen numerous times among lissamphibians. In my opinion, non-pedicellate teeth are better regarded as having evolved convergently in albanerpetontids and Karaurus.

Character Q: teeth monocuspid. There are two problems with this character state. First, Trueb and Cloutier's (1991) claim that monocuspid teeth are a synapomorphy either for a Caudata that includes Albanerpeton or for uniting Karaurus + Albanerpeton within the Caudata (their topological variants 3A and 3B, respectively) is based on the belief that tooth crowns in Karaurus are monocuspid. To my knowledge, the structure of tooth crowns in Karaurus and Kokartus has never been described, nor can this information be determined from published figures of specimens (see Ivachnenko, 1978; Nessov, 1988). Considering that bicuspid teeth are reliably known for the stem-caudate Marmorerpeton (Evans et al., 1988) and basal urodeles, I suspect that bicuspid teeth are probably primitive for caudates. Second, using the term "monocuspid" to describe the crown pattern in albanerpetontids is misleading, because this implies that albanerpetontids exhibit the primitive tetrapod pattern of conical tooth crowns. As I argued in the account above for character 39, crowns on the marginal teeth in albanerpetontids are, in fact, unique among temnospondyls in being labiolingually compressed and terminating in three mesiodistally aligned cuspules.

FINAL COMMENTS

The results of my study support Fox and Naylor's (1982) and McGowan and Evans' (1995) contention that albanerpetontids are distinct from caudates and the latter authors' suggestion that albanerpetontids are members of the Lissamphibia. My interpretations are admittedly based on incomplete information, but when new evidence becomes available it can be used to assess the ideas proposed here. Once described in detail, the well-preserved albanerpetontid skeletons reported by McGowan and Evans (1995) from the Early Cretaceous of Spain can be expected to play a key role in shaping and testing our concept of albanerpetontid relationships.

Information on the palate probably will prove critical for these purposes, because palatal characters historically have been important for assessing relationships among lissamphibians. McGowan (1994) identified fragmentary palatal bones in the holotype and referred skeletons of Celtedens ibericus, but his interpretations have not been formally published. The only published, unequivocal report of an albanerpetontid palatal element is Estes' (1981) brief mention of the narrow, anteriorly elongate cultriform process of the parasphenoid in the holotype skeleton of C. megacephalus. Although there is little direct information on palatal structure in albanerpetontids, some constrained predictions can be made based on the structure of marginal jaws and comparisons with other temnospondyls. Albanerpetontid maxillae and premaxillae bear clear evidence in the form of lingual facets and suture marks for having contacted palatal bones (Fox and Naylor, 1982; Gardner, 1999a, b, in press a). Comparisons with other temnospondyls suggest that, besides the parasphenoid, the albanerpetontid palate included paired vomers, pterygoids and, probably, palatines. Articular surfaces on the lingual faces of premaxillae and maxillae argue for these having articulated in a complex fashion with at least some of the paired palatal bones. Fox and Naylor (1982:123) even speculated that the articulation between the pars palatinum on the premaxilla and the presumed vomer was movable. Comparisons with other temnospondyls also suggest that some or all of the albanerpetontid palatal bones bore teeth arranged in rows or clumps. Like the teeth on the upper jaws, palatal teeth probably were non-pedicellate. Considering that albanerpetontid marginal teeth appear specialized for shearing, I would not be surprised if palatal teeth lack the distinctive chisel-like crowns and, instead, have simpler crowns.

This may explain why palatal bones have yet to be recognized in collections from screenwashed microvertebrate sites where albanerpetontids otherwise are well represented by other elements. The possible exception was an apparent palatal bone (UCM 38762) from the late Maastrichtian (Lancian) Laramie Formation of Colorado, USA, that Carpenter (1979:43 and fig. 15) identified as a "?pterygopalatine," possibly referrable to Albanerpeton. Unfortunately, this specimen has been lost (P. Murphy, pers. comm., 1997).

Albanerpetontid specimens from the Bathonian (Middle Jurassic) to middle Miocene attest to the remarkably conservative structure of albanerpetontids over the approximately 155 million years of their known record. Phylogenetic inference, regardless of whether the Lissamphibia are nested within temnospondyls (e.g., Trueb and Cloutier, 1991; Milner, 1993b) or lepospondyls (Laurin and Reisz, 1997), and stratigraphic occurrences (Milner, 1993a) imply that the Lissamphibia originated by at least the earliest Triassic and probably earlier (Milner, 1988, 1993b). As such, even the oldest known albanerpetontid fossil, an atlantal centrum originally considered to be late Bajocian in age (Seiffert, 1969), but now regarded as early Bathonian (Kriwet et al., 1997), from France is too young to provide insights into the origin and early evolution of the group. As useful as Middle Jurassic to Miocene fossils have been, and will continue to be, for assessing albanerpetontid relationships, geologically older fossils are necessary to better document and provide insights into the first one-third or more of albanerpetontid history.

CONCLUSIONS

Cladistic analysis of 59 characters scored for the albanerpetontid genera Albanerpeton and Celtedens, stem- and crown-clade gymnophionans, caudates, and salientians, and select non-lissamphibian temnospondyls yields the following conclusions:

(1) Albanerpeton and Celtedens are each others' closest relatives and together constitute a robustly monophyletic Albanerpetontidae. Synapomorphies of the Albanerpetontidae involve dental modifications associated with a shearing bite and modifications to the mandibles, skull roof, and anteriormost vertebrae that increased the strength and mobility in these regions for feeding, burrowing, or both.

(2) Nested sets of osteological synapomorphies place the Albanerpetontidae within the Lissamphibia, crownward of the Gymnophiona as the sister-taxon of the Batrachia (i.e., Caudata plus Salientia). There are no synapomorphies that compelling support a closer relationship between albanerpetontids and caudates, as some authors have advocated.

(3) Albanerpetontids thus are best recognized not as aberrant caudates, but as a distinct clade in which numerous specializations are superimposed on a relatively primitive lissamphibian body plan.

TABLE 8-1. Data matrix of the 59 characters among two outgroup taxa (*Balanerpeton* and *Dendrerpeton*) and ten ingroup taxa. Conventions: a, polymorphic for states 0 and 1 and the primitive condition is not interpreted; 9, inapplicable character; ?, state unknown. Final column is percentage of missing records (i.e., unknown + inapplicable).

	00000	00001	11111	11112	22222	22223
	12345	67890	12345	67890	12345	67890
Balanerpeton	00000	00000	00000	00000	00000	00000
Dendrerpeton	00000	00000	00000	00000	00000	00000
Apateon	00000	00100	00100	00100	10000	110?0
Doleserpeton	00000	00100	00100	00201	11900	010?0
Apoda	1a010	00911	a1111	12201	10110	11100
Eocaecilia	00000	00011	00111	10201	10110	111??
Urodela	a0110	00111	11111	11219	1020a	11011
Karauridae	00110	00111	11111	11219	10200	11011
Anura	11111	001?1	11111	11209	11901	1101?
Triadobatrachus	?0?11	00101	11111	10202	1190?	110??
Albanerpeton	00002	1111?	1????	?????	?????	?1011
Celtedens	0?002	11111	11111	1????	???0?	110?1

	33333	33334	44444	44445	55555	5555	Missing
	12345	67890	12345	67890	12345	6789	Records
Balanerpeton	00000	00000	00000	00000	00000	000?	02%
Dendrerpeton	00000	00000	000??	?0000	00000	000?	07%
Apateon	00000	?0000	?00??	???00	0001?	100?	17%
Doleserpeton	00000	?1110	01000	01000	?????	1???	17%
Apoda	01000	11110	?1101	02109	11199	9990	14%
Eocaecilia	??000	11110	?1111	01?00	???1?	????	24%
Urodela	11010	01110	11211	02100	11111	1011	02%
Karauridae	1?0??	??0?0	?121?	02?00	1111?	?01?	22%
Anura	11010	01111	11200	02011	11011	1111	07%
Triadobatrachus	1?0??	????1	1?20?	02011	1101?	?11?	31%
Albanerpeton	10101	01020	1??11	121??	??11	1??0	42%
Celtedens	10101	01020	1?01?	12111	1?111	1000	22%

TABLE 8-2. Seventeen proposed synapomorphies of albanerpetontids and caudates. Character states are: A, anterior ramus of pterygoid not in bony contact anteriorly; B, quadrate ramus of pterygoid directed laterally in palatal view; C, squamosal embayment; D, stapedial foramen; E, maxillary arcade open posteriorly; F, trunk vertebrae bearing bicipital transverse processes (= "rib-bearers" of some authors); G, atlas bearing odontoid process; H, atlas pierced by foramen for first spinal nerve; I, trunk vertebrae bearing basapophyses; J, parietal foramen absent; K, clavicle absent; L, movable quadrate; M, articular discrete; N, muscle adductor mandibulae internus superficialis extends posteriorly across dorsal surface of skull; O, prefrontal contributes to external narial margin; P, teeth non-pedicellate; Q, teeth monocuspid.

I. Proposed synapomorphies for nesting Albanerpetontidae within Caudata:

Estes and Sanchíz (1982): characters F, H, I, L.
Trueb and Cloutier (1991:topology 3A): characters A, E, G, M, Q.
Trueb and Cloutier (1991:topology 3B): characters A, E, G, M.
McCord (1999): characters C, E, K.

II. Proposed synapomorphies of Albanerpetontidae + Urodela, within Caudata:

Estes and Sanchíz (1982): character N.
Trueb and Cloutier (1991:topology 3A): character O.
McCord (1999): characters G, I, L, N, O.

III. Proposed synapomorphies of Albanerpetontidae + Karaurus, within Caudata:

Trueb and Cloutier (1982:topology 3B): characters B, D, J, P, Q.

FIGURE 8-1. Shortest trees generated by previous analyses that included albanerpetontid taxa (boldface). **A**, Trueb and Cloutier's (1991) strict consensus of 12 shortest trees, with Albanerpeton in an unresolved trichotomy with the stem-caudate Karaurus and crown-clade salamanders Urodela (modified from Trueb and Cloutier, 1991:figs. 4, 8); reported tree statistics: tree length = 104 steps, CI = 0.583 (autapomorphies excluded). **B**, strict consensus of 56 shortest trees, with a different topology, obtained by re-analysing Trueb and Cloutier's (1991:appendix II) published data matrix and excluding their seven uninformative characters; tree statistics: tree length = 113 steps, CI = 0.628, HI = 0.372, RI = 0.787. **C**, McGowan and Evans' (1995) shortest tree, with the Albanerpetontidae as the sister-taxon of the Batrachia (modified from McGowan and Evans, 1995:fig. 3); reported tree statistics: tree length = 44 steps, CI = 0.720. Re-analysing McGowan and Evans' (1995) original matrix and excluding their five uninformative characters produces the same shortest tree with the following statistics: tree length = 38 steps, CI = 0.684, HI = 0.316, RI = 0.714. **D**, McCord's (1999) shortest tree, with "albanerpetontines" nested within the Caudata as the sister-taxon of the Urodela (modified from McCord, 1999:fig. 1); reported tree statistics: tree length = 108 steps, CI = 0.75. Re-analysing McCord's (1999) published matrix and excluding his 12 uninformative characters produces the same shortest tree with the following statistics: tree length = 89 steps, CI = 0.697, HI = 0.303, RI = 0.707. Outgroups are excluded from all trees. Numbers above and below branches in the last three trees (**B**–**D**) are indices of support, obtained by re-analysing published matrices with uninformative characters excluded, as follows: top = bootstrap value (%) for 200 (**B**) and 2000 (**C** and **D**) replicates; and bottom = decay value (steps). Decay values in excess of three steps could not be determined for the second tree (**B**) because the search for trees ≥ 116 steps reached the maximum limit of 32767 saved trees allowed in PAUP 3.1.1.

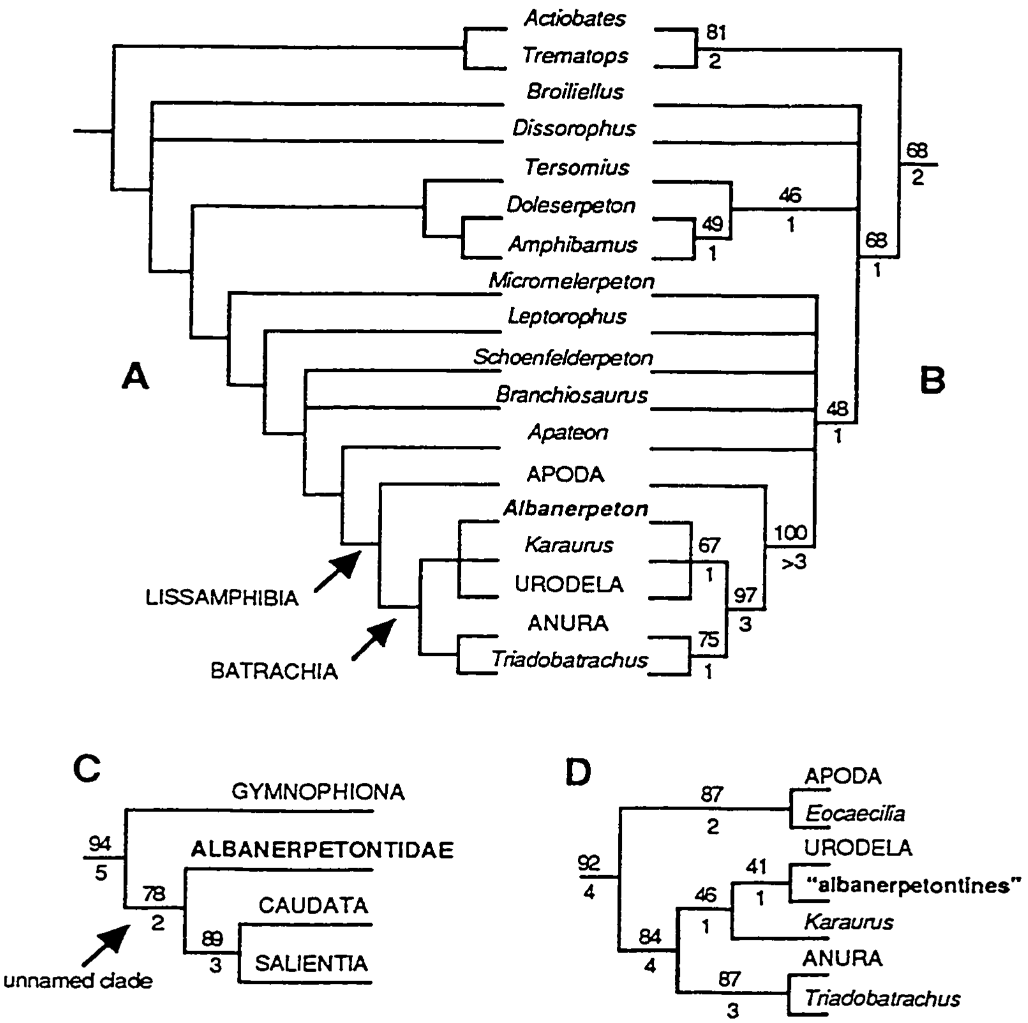
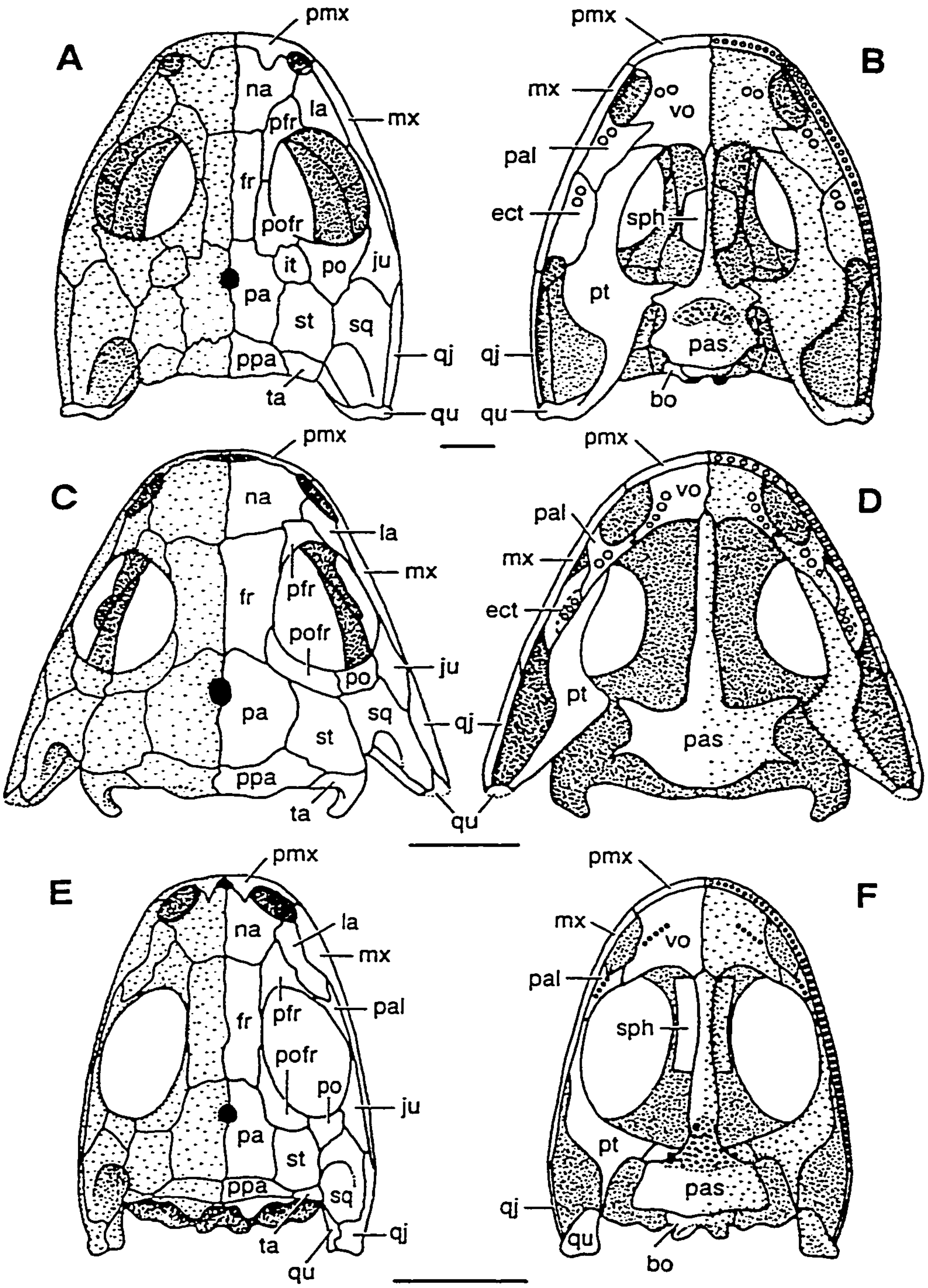

Actiobates
Trematops
Broiliellus
Dissorophus
Tersomius
Doleserpeton
Amphibamus
Micromelerpeton
Leptorophus
Schoenfelderpeton
Branchiosaurus
Apateon
APODA
Albanerpeton
Karaurus
URODELA
ANURA
Triadobatrachus
LISSAMPHIBIA
BATRACHIA
A
B
81
2
68
2
46
1
49
1
68
1
48
1
100
>3
67
1
97
3
75
1
C
GYMNOPHIONA
ALBANERPETONTIDAE
CAUDATA
SALIENTIA
94
5
78
2
89
3
unnamed clade
D
APODA
Eocaecilia
URODELA
"albanerpetontines"
Karaurus
ANURA
Triadobatrachus
87
2
92
4
41
1
46
1
84
4
87
3

FIGURE 8-2. Skulls of representative non-lissamphibian temnospondyls. **A, B,** Balanerpeton woodi Milner and Sequeira, reconstruction in (**A**) dorsal and (**B**) ventral views; basal temnospondyl, Early Carboniferous; modified from Milner and Sequeira (1994:fig. 5A, B), with anterior ends of frontals based on Milner and Sequeira (1994:fig 3C). **C, D,** Apateon pedestris Meyer, reconstruction in (**C**) dorsal and (**D**) ventral views; Branchiosauridae, Early Permian; modified from Boy (1987:figs. 2c, 3c) and Schoch (1992:text-fig. 26). **E, F,** Doleserpeton annectens Bolt, reconstruction in (**E**) dorsal and (**F**) ventral views; Amphibamidae, Early Permian; modified from Bolt (1977:text-fig. 1 and 1991:fig. 2, respectively). Skulls depicted without ornament and with marginal teeth excluded from right upper jaws. Figures at different scales. Scale bars: top (**A, B**), middle (**C, D**), and bottom (**E, F**) bars = 5 mm.


A
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pt
pas
E
pmx
la
na
mx
pal
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pfr
pofr
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sph
pt
pas
qj
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FIGURE 8-3. Skulls of representative lissamphibians. **A, B,** Eocaecilia micropodia Jenkins and Walsh, reconstruction in (**A**) dorsal and (**B**) ventral views; stem-gymnophionan, Early Jurassic; modified from Jenkins and Walsh (1993:fig. 2B), with mandible excluded. **C, D,** Epicrionops petersi Taylor, in (**C**) dorsal and (**D**) ventral views; basal apodan (Rhinatrematidae), extant; modified from Nussbaum (1977:fig. 1) and Reiss (1996:figs. 1, 2). **E, F,** Notobatrachus degiustoi Reig, reconstruction in (**E**) dorsal and (**F**) ventral views; basal anuran, Early Jurassic; modified from Estes and Reig (1973:figs. 1-4, 1-5, respectively), with mandible excluded. Skulls depicted without ornament and with marginal teeth excluded from right upper jaws. Figures at different scales. Scale bars: top (**A, B**), middle (**C, D**), and bottom (**E, F**) bars = 5 mm.

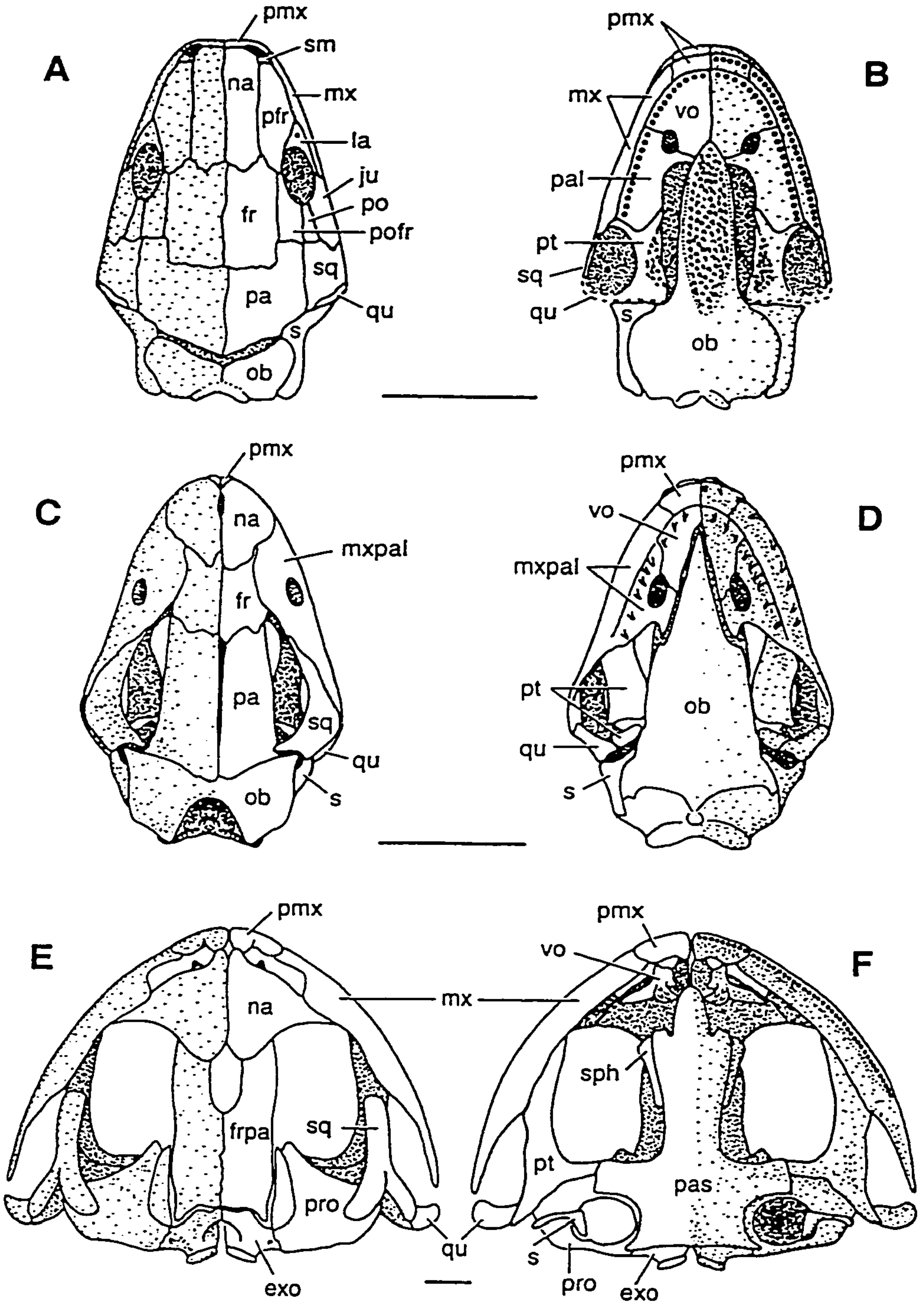
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FIGURE 8-4. Skulls of representative lissamphibians. **A**, **B**, Batrachuperus pinchonii (David), in (**A**) dorsal and (**B**) ventral views; basal urodele (Hynobiidae), extant; modified from Carroll and Holmes (1980:fig. 4B, as "B. sinensis" [Sauvage]), with marginal teeth excluded from right upper jaws. **C**, Albanerpeton inexpectatum Estes and Hoffstetter, reconstruction in dorsal view; Albanerpetontidae, middle Miocene; modified from Estes and Hoffstetter (1976:fig. 4B), with information from specimens in collections of the MNHN.LGA, configuration of jugal and squamosal from McGowan's (1998a:fig. 2) reconstruction for Celtedens ibericus McGowan and Evans, and ornament shown on left side. Cross-hatching (**A**, **B**) denotes dried pterygomaxillary ligament. Figures at different scales. Scale bars: top (**A**, **B**) and bottom (**C**) bars = 5 mm.

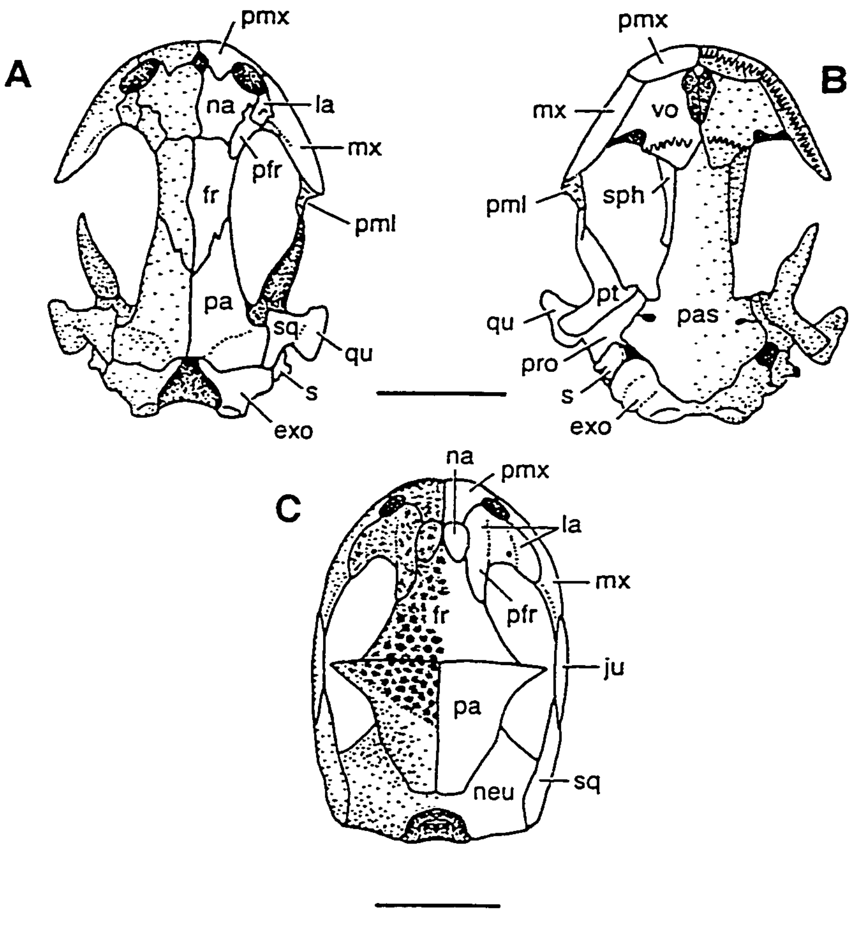
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FIGURE 8-5. Mandibles of representative temnospondyls. **A**, **B**, *Balanerpeton woodi* Milner and Sequeira, reconstruction of (**A**) right mandible in labial view and (**B**) left mandible in lingual view; basal temnospondyl, Early Carboniferous; modified from Milner and Sequeira (1994:fig. 5C, D). **C**, *Doleserpeton annectens* Bolt, OMNH 56863, anterior end of right dentary, lacking tooth crowns and preserving largely intact tooth pedicels, in lingual view; Amphibamidae, Early Permian. **D**, *Epicrionops petersi* Taylor, right mandible in occlusal view; basal apodan (Rhinatrematidae), extant; modified from Nussbaum (1977:fig. 2). **E**, *Cryptobranchus alleganiensis* (Daudin), UALVP 14327, right mandible, in lingual view; basal urodele (Cryptobranchidae), extant. **F**, **G**, *Albanerpeton inexpectatum* Estes and Hoffstetter, MNHN.LGA 1250, right mandible in (**F**) lingual and (**G**) occlusal views; Albanerpetontidae, middle Miocene. Figures at different scales. Scale bars: top (**A**, **B**), left middle (**C**), right middle (**D**), middle (**E**), and bottom (**F**, **G**) bars = 1 mm.

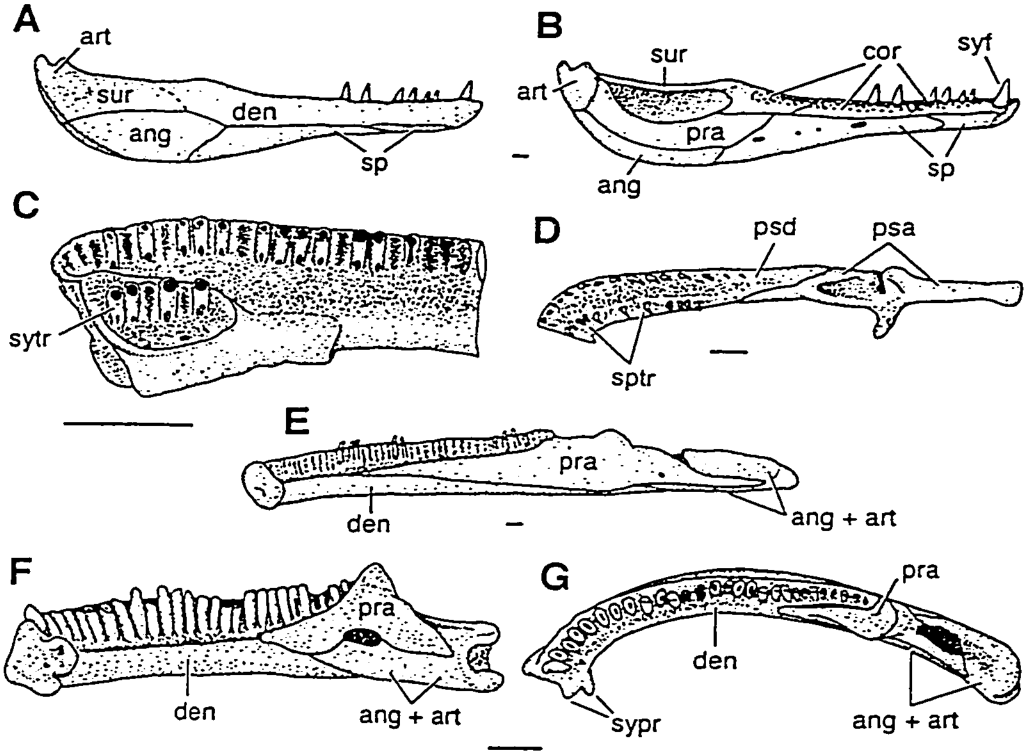
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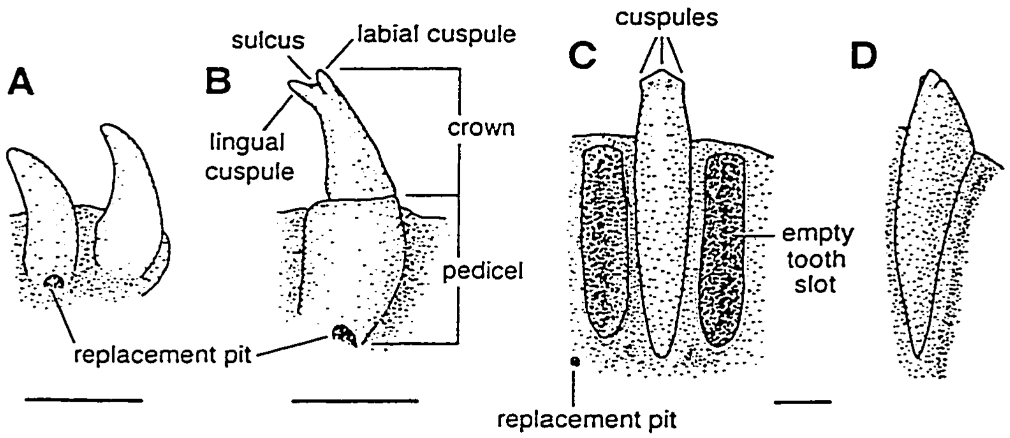
FIGURE 8-6. Representative marginal tooth morphologies in lissamphibians. **A**, Hynobius nebulosus Temminck and Schlegel, premaxillary teeth (inverted) in lingual and slightly mesial view, showing typical larval pattern of non-pedicely and monocuspid crowns; basal urodele (Hynobiidae), extant; drawn from a photograph (Greven and Clemen, 1985:fig. 1c). **B**, Onychodactylus japonicus (Houttuyn), premaxillary tooth (inverted) in distal and slightly lingual view, showing typical postmetamorphic pattern of pedicely and labiolingually bicuspid crown, with cuspules separated by a mesiodistal sulcus; basal urodele (Hynobiidae), extant; drawn from a photograph (Beneski and Larsen, 1989:fig. 5A). **C**, **D**, Albanerpeton inexpectatum Estes and Hoffstetter, MNHN.LGA 1207, premaxillary tooth (inverted), in (**C**) lingual and (**D**) distal and slightly lingual views, showing presumed postmetamorphic albanerpetontid pattern of non-pedicely and labiolingually compressed, chisel-like crown with three faint, mesiodistally aligned cuspules; Albanerpetontidae, middle Miocene. Figures at different scales. Scale bars: left (**A**), center (**B**), and right (**C**) bars each approximately 0.2 mm.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lingual cuspule
crown
pedicel
replacement pit
cuspules
empty tooth slot
replacement pit

FIGURE 8-7. Anterior vertebrae of representative temnospondyls. **A**, **B**, Doleserpeton annectens Bolt, reconstructed atlas in (**A**) anterior and (**B**) left lateral views; Amphibamidae, Early Permian; modified from Bolt (1991:fig. 4-5). **C**, Hynobius sp., cf. H. naevius (Temminck and Schlegel), UALVP 14321, articulated atlas and first trunk vertebra in left lateral view; basal urodele (Hynobiidae), extant. **D**, Dermophis mexicanus (Dumèril and Bibron), KU 105459, articulated atlas, first trunk vertebra (with rib removed), and anterior part of second trunk vertebra (with rib in place) in left lateral view; Apoda (Caeciliidae), extant. **E**, **F**, Albanerpeton inexpectatum, MNHN.LGA 1236, atlas, in (**E**) posterior view with arrow pointing to median notch in posterior face of roof of neural arch and (**F**) articulated with reconstructed co-ossified axis and first trunk vertebrae, all in left lateral view, with dotted line representing anterior end of neural arch on first trunk vertebra seated in complementary median notch in atlantal neural arch; Albanerpetontidae, middle Miocene; co-ossified axis and first trunk vertebra based on MNHN.LGA 176 (holotype) and MNHN.LGA 1241 (see Estes and Hoffstetter, 1976:figs. 1C, 2B and pl. 6, figs. 13, 15). Figures at different scales. Scale bars: top (**A**, **B**), middle (**C**, **D**), and bottom (**E**, **F**) bars = 1 mm.

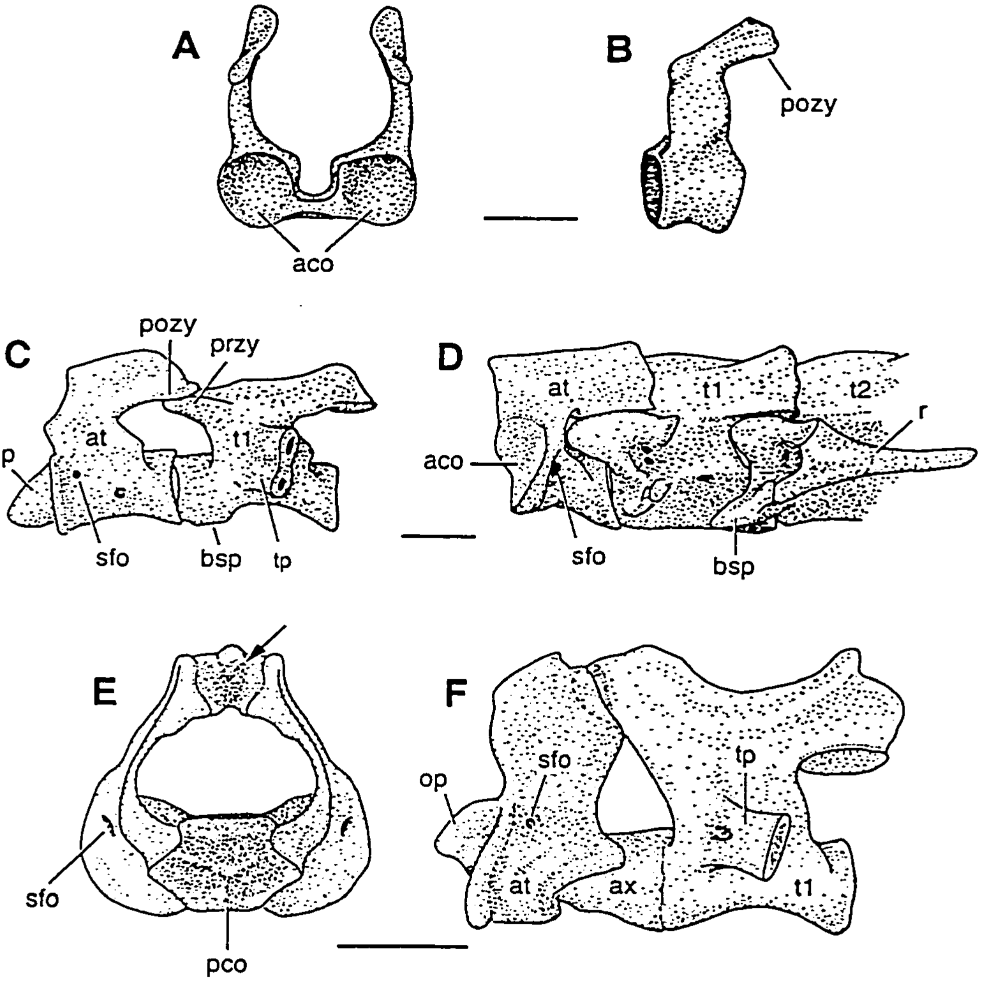
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FIGURE 8-8. Shortest tree generated in this analysis, based on 59 characters scored for two outgroup and ten ingroup taxa. Capital letters and names below branches identify, respectively, nodes and clades discussed in text. Indices of support for each clade are given above branches as follows: number of unambiguous synapomorphies/total number of synapomorphies, bootstrap value (%) for 2000 replicates, and decay index (steps). Tree statistics: tree length = 96 steps, CI = 0.792, HI = 0.208, and RI = 0.845.

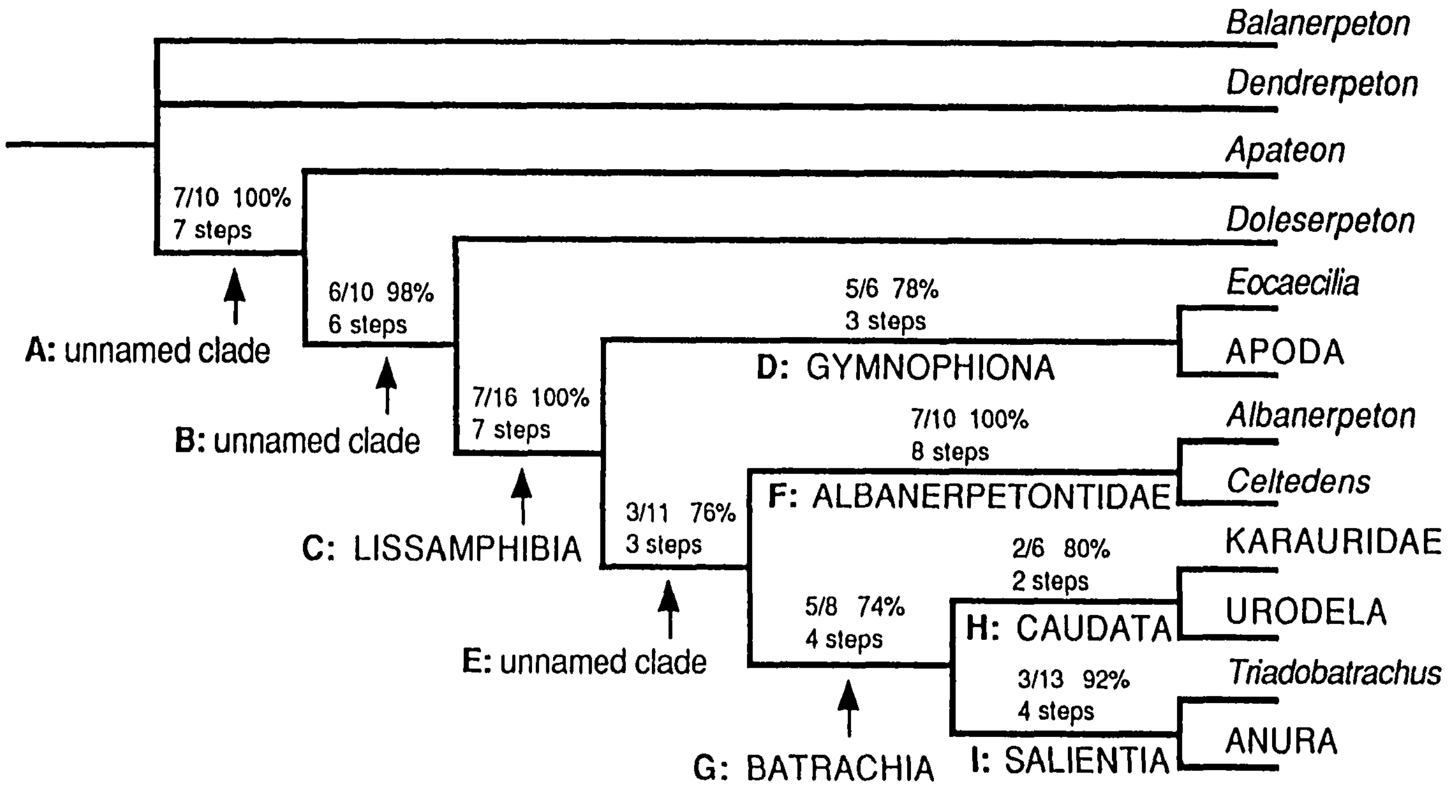
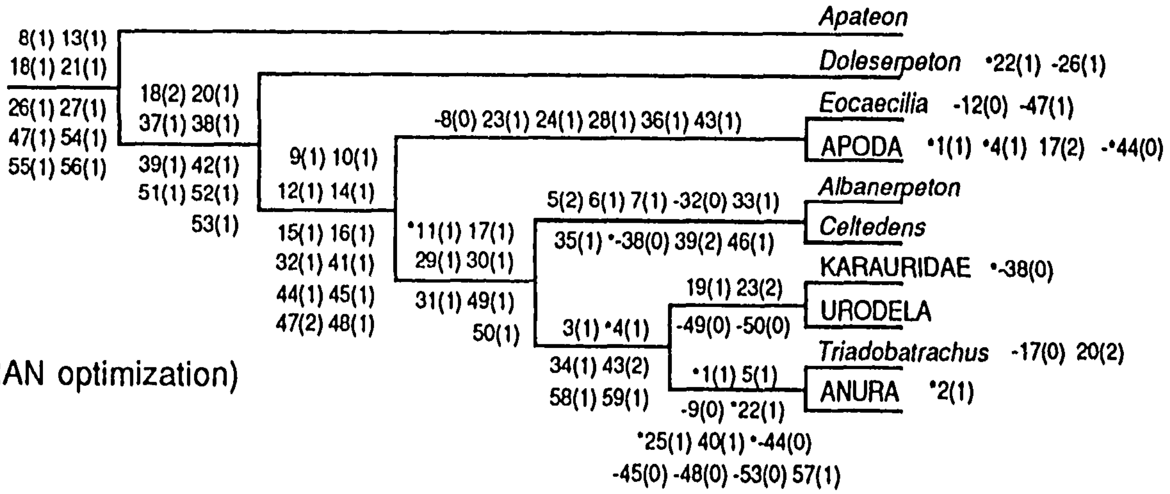
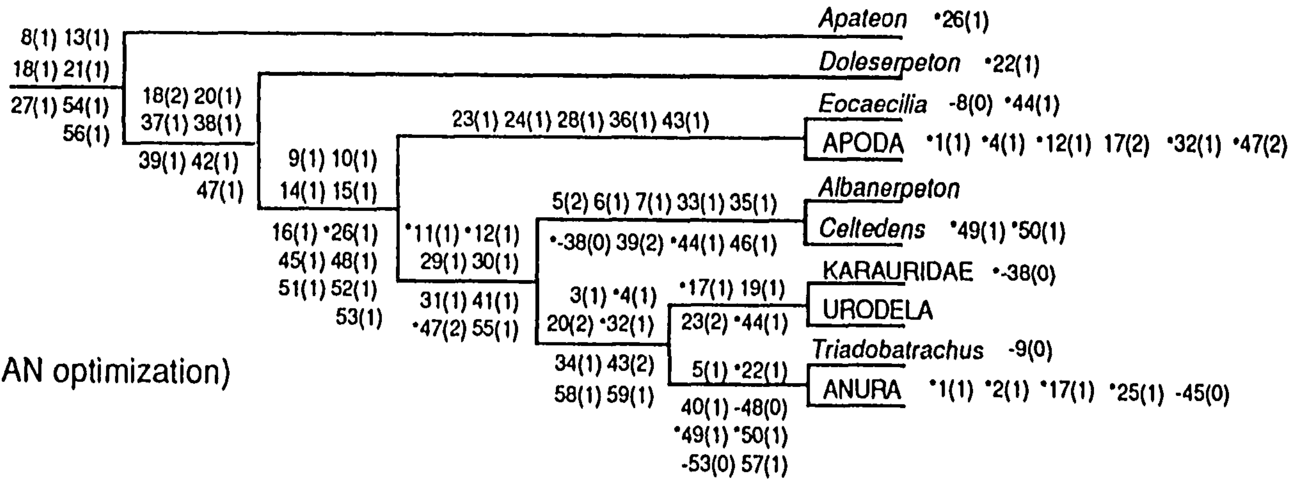

Balanerpeton
Dendrerpeton
Apateon
Doleserpeton
Eocaecilia
APODA
Albanerpeton
Celtedens
KARAURIDAE
URODELA
Triadobatrachus
ANURA
7/10 100%
7 steps
A: unnamed clade
6/10 98%
6 steps
B: unnamed clade
7/16 100%
7 steps
C: LISSAMPHIBIA
5/6 78%
3 steps
D: GYMNOPHIONA
3/11 76%
3 steps
E: unnamed clade
7/10 100%
8 steps
F: ALBANERPETONTIDAE
5/8 74%
4 steps
G: BATRACHIA
2/6 80%
2 steps
H: CAUDATA
3/13 92%
4 steps
I: SALIENTIA

FIGURE 8-9. Shortest tree generated in this analysis, with distribution of derived character states mapped by (A) ACCTRAN and (B) DELTRAN character state optimizations. An asterisk (*) denotes a convergent character state and a minus sign (-) denotes a reversal. Outgroups excluded and tree statistics as in caption for Figure 8-8.

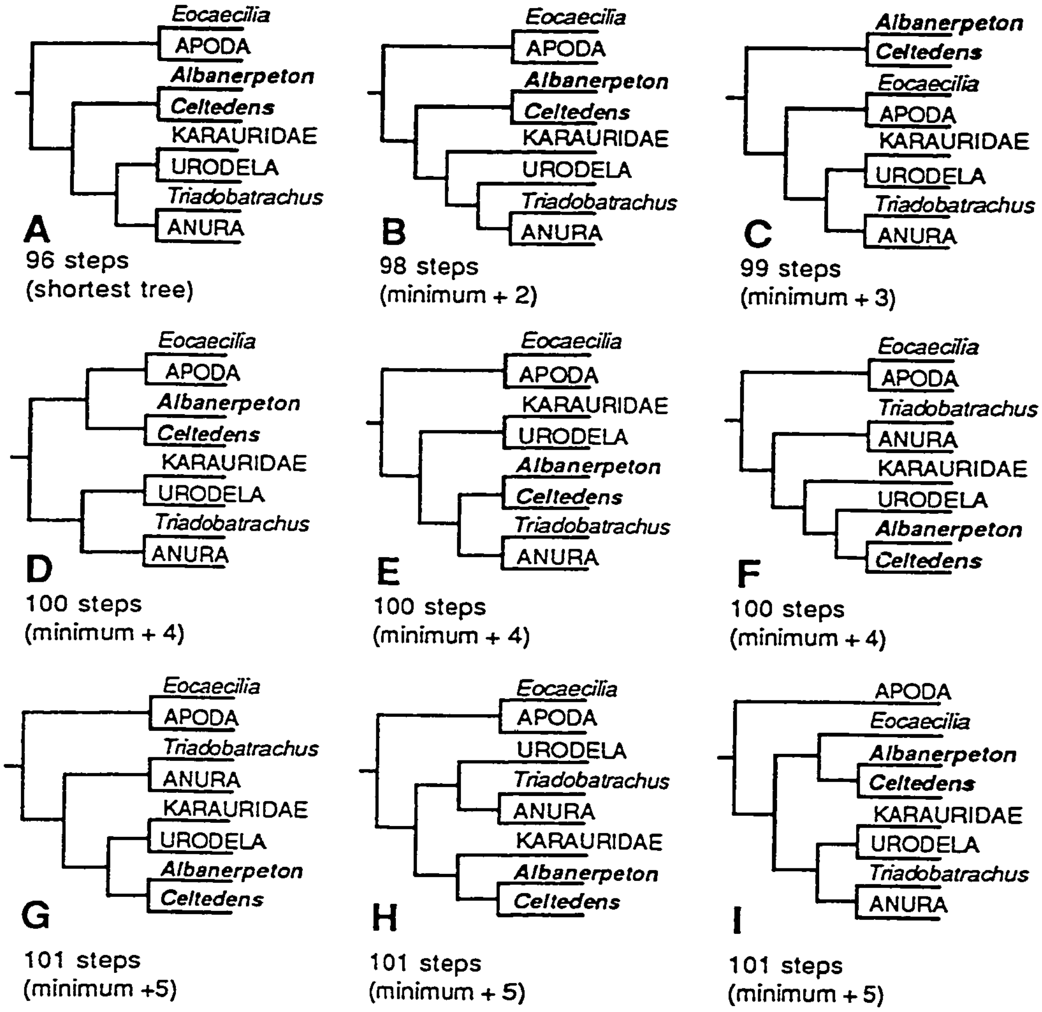


A (ACCTRAN optimization)



B (DELTRAN optimization)

FIGURE 8-10. Alternative placements for the Albanerpetontidae (boldface) within the Lissamphibia. **A**, shortest and preferred 96 step tree, with the Albanerpetontidae as the sister-taxon of the Batrachia. **B**, next longest tree (98 steps; minimum + 2 steps) showing essentially the same topology as the shortest tree, except for a paraphyletic Caudata. **C**, shortest tree (99 steps; minimum + 3 steps) in which position of the Albanerpetontidae is first altered, by reversing with Gymnophiona. **D–F**, shortest trees (100 steps; minimum + 4 steps) having the Albanerpetontidae as the sister-taxon of (**D**) Gymnophiona or (**E**) Salientia or (**F**) nested within Caudata. **G–I**, shortest trees (101 steps; minimum + 5 steps) having the Albanerpetontidae as the sister-taxon of (**G**) Caudata, (**H**) Karauridae exclusive of the Urodela, or (**I**) Eocaecilia exclusive of the Apoda. Tree statistics: 96 step tree (**A**): as in caption for Figure 8-8; 98 step trees (**B**): n = 2, CI = 0.776, HI = 0.224, RI = 0.829; 99 step trees (**C**): n = 2, CI = 0.768, HI = 0.232, RI = 0.822; 100 step trees (**D–F**): n = 8, CI = 0.760, HI = 0.240, RI = 0.814; 101 step trees (**G–I**): n = 17, CI = 0.752, HI = 0.248, RI = 0.806.



A 96 steps (shortest tree)

B 98 steps (minimum + 2)

C 99 steps (minimum + 3)

D 100 steps (minimum + 4)

E 100 steps (minimum + 4)

F 100 steps (minimum + 4)

G 101 steps (minimum +5)

H 101 steps (minimum + 5)

I 101 steps (minimum + 5)

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APPENDIX 8-1. Specimens and literature examined. Specimens and literature used to score characters are listed below. Symbols for specimens of extant taxa: *, cleared and stained; §, skeleton.

Balanerpeton: Milner and Sequeira (1994). *Dendrerpeton*: Carroll (1967), Milner (1980, 1996), Clack (1983), Godfrey et al. (1987), Holmes et al. (1998). *Doleserpeton*: Bolt (1969, 1974, 1977, 1979, 1991), Bolt and Lombard (1985), Daly (1994); OMNH 3149-3157 isolated jaws; OMNH 56844, 56846, associated skull and postcranial elements; OMNH 56845, isolated jaws; OMNH 56863, dentary. *Apateon*: Boy (1978, 1986, 1987), Werneburg (1989), Schoch (1992). Gymnophiona: *Eocaecilia*: Jenkins and Walsh (1993); Ichthyophiidae and Rhinatrematidae: Taylor (1969, 1977), Carroll and Currie (1975), Nussbaum (1977), Reiss (1996); Caeciliidae: *Dermophis mexicanus* (Dumèril and Bibron): KU 105459§, 125351§. Caudata: Karauridae: *Karaurus*: Ivachnenko (1978), Estes (1981); *Kokartus*: Nessov (1988); Cryptobranchidae: *Cryptobranchus alleganiensis* (Daudin): Reese (1906), Carroll and Holmes (1980), Naylor (1978), Elwood and Cundall (1994); UALVP 14327§, 14413*, 14414*; Hynobiidae: Carroll and Holmes (1980), Naylor (1978); *Hynobius naevius* (Temminck and Schlegel): UALVP 14111*; *H*. sp., cf. *H*. *naevius*: UALVP 14321§; *H*. *retardus* Dunn: UALVP 14410*; *Onychodactylus japonicus* (Houttuyn): UALVP 14405*-14409*; *Pachypalaminus boulengeri* Thompson: UALVP 14412*. Salientia: *Triadobatrachus*: Rage and Roček (1989); *Vieraella* and *Notobatrachus*: Estes and Reig (1973), Báez and Basso (1996); *Ascaphus truei* Stejneger: UMMZ 134982§, 152263§, USNM 62450§; *Leiopelma hochstetteri* Fitzinger, FMNH 51641§. Albanerpetontidae: *Albanerpeton inexpectatum*: catalogued and uncatalogued elements listed by Gardner (1999a) in collections of the MNHN.LGA; *Celtedens ibericus*: McGowan and Evans (1995); *Celtedens* sp. indet.: catalogued and uncatalogued elements, including specimens listed by McGowan and Ensom (1997), in collections of the DORCM.

CHAPTER 9 — PROAMPHIUMA CRETACEA ESTES FROM THE LATE MAASTRICHTIAN OF MONTANA AND RELATIONSHIPS AMONG AMPHIUMID SALAMANDERS

INTRODUCTION

The Amphiumidae Gray are a small family of paedomorphic, aquatic salamanders with a limited fossil record. Amphiumids are endemic to North America, where they are known from the Pleistocene–Recent of the southeastern USA, late Paleocene of Wyoming, late Maastrichtian of Montana and, possibly, the middle Miocene of Texas (e.g., Salthe, 1973a; Estes, 1981; this study). The three extant species in the type genus Amphiuma Garden range in maximum length from about 300–1015 mm (Conant and Collins, 1991) and are identified by their elongate, superficially eel-like body, a single gill slit but no external gills, and tiny fore- and hindlimbs with three or fewer toes (Salthe, 1973a; Conant and Collins, 1991; Duellman and Trueb, 1986). Amphiumids are widely regarded as crown-clade salamanders (= Urodela Duméril, sensu Milner, 1988; Evans and Milner, 1996) but there is no further consensus on the position of the family, largely because its members exhibit a confusing mixture of derived and paedomorphic character states superimposed on a relatively primitive body plan. Cladistic hypotheses (Edwards, 1976; Hecht and Edwards, 1977; Milner, 1983; Duellman and Trueb, 1986; Sever, 1991; Hedges and Maxson, 1993; Larson and Dimmick, 1993; Hay et al., 1995) and non-cladistic classifications (e.g., Cope, 1889; Dunn, 1922; Noble, 1931; Regal, 1966; Naylor, 1978; Estes, 1981) broadly agree in placing amphiumids at a post-cryptobranchid and hynobiid level of organization (however, see Larson, 1991), and many of these schemes have allied amphiumids with ambystomatids, plethodontids, and salamandrids or some combination thereof. Cope's (1889) belief that amphiumids were ancestral to gymnophionans, which he regarded as a degenerate family of salamanders, has not been seriously entertained since.

The geologically oldest reported amphiumid is Proamphiuma cretacea Estes. P. cretacea is the type and only species in the genus and was briefly described by Estes (1969) for 17 isolated, topotypic vertebrae from the late Maastrichtian (Lancian) Bug

Creek Anthills locality in the Hell Creek Formation, Montana. Little new information since has been presented for *Proamphiuma*: Estes (1981) provided a nearly verbatim rediagnosis and redescription, but listed no new specimens; Naylor (1978), in an unpublished Ph.D. thesis, briefly described a dentary from the Bug Creek Anthills; and Edwards (1976) reported on spinal foramina and identified four caudals among Estes' (1969) topotypic collection. The status of the taxon recently has been challenged by Rieppel and Grande (1998), who argued that the name *P. cretacea* is a *nomen dubium*. Here I present a revised diagnosis and expanded redescription for *P. cretacea* based on Estes's (1969) topotypic collection and additional, isolated specimens from the holotype locality. The latter collection triples the number of vertebral specimens known for *Proamphiuma* and includes the only skull element (a dentary) yet identified for the taxon. The 43 specimens now available provide new information on the status and osteology of *Proamphiuma* and insights into the evolutionary history of the Amphiumidae.

For reasons discussed below, I restrict membership in the Amphiumidae to *Amphiuma* (four species) and the monotypic *Proamphiuma*. Given uncertainty over the higher level affinities of the family, I conservatively follow Estes (1981) in placing the Amphiumidae within the monotypic Amphiumoidea Cope. For comparative purposes I examined skeletons of the extant species *A. pholeter* Neill (UALVP 14487), *A. tridactylum* Cuvier (UALVP 14364), and *A. means* Garden (FMNH 98657 and 196143) and a middle trunk vertebra dissected from an alcohol preserved specimen (UALVP 14507) of *A. means*. Mine is the first study to compare all three extant species of *Amphiuma* to *Proamphiuma*. I was not able to examine any fossil specimens of *Amphiuma*.

SYSTEMATIC PALEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order CAUDATA Scopoli, 1777
Crown-order URODELA Dumèril, 1806
Suborder AMPHIUMOIDEA Cope, 1889
Family AMPHIUMIDAE Gray, 1825 (amend. Gray, 1850)

Remarks—Salthe (1973a) presented a concise review of the early taxonomic and nomenclatural history of the Amphiumidae. The relevant points are that Gray (1825) originally proposed the familial name Amphiumidae to include Amphiuma and the North American cryptobranchid Cryptobranchus Leuckart. Tschudi (1838) disputed a close relationship between the two genera, leading Gray (1850) to eject Cryptobranchus and retain Amphiuma as the only genus in the Amphiumidae.

Monophyly of the Amphiumidae has never been disputed. The three extant Amphiuma spp., the late Paleocene A. jepseni Estes, and Proamphiuma are united by one derived vertebral character state that is unique among salamanders: trunk vertebrae and anterior caudals dorsally bear a pair of postzygapophyseal crests (Estes, 1969, 1981; Naylor, 1981; see additional comments below). Based on specimens of Amphiuma and Proamphiuma available to him, Edwards (1976) stated these genera were further unique among salamanders he surveyed in having intravertebral exit of postatlantal spinal nerves restricted to vertebrae in the posterior part of the caudal series. There are two problems with accepting this pattern as autapomorphic for amphiumids: first, caudals are unknown for A. jepseni and, second, a caudal that I describe below indicates that anterior caudals were also pierced by a spinal foramen in Proamphiuma. Numerous other character states explicitly or implicitly have been regarded as derived for amphiumids (e.g., Davison, 1895; Salthe, 1973a; Estes, 1981; Duellman and Trueb, 1986; Sever, 1991; Larson and Dimmick, 1993), yet many of these are not unique among salamanders to amphiumids and, more importantly, none can be determined for both fossil taxa. Fusion of the premaxillae, a posteriorly elongate premaxillary pars dorsalis (= premaxillary spine of some authors) completely separating the nasals and partly separating the frontals, a posteriorly elongate premaxillary vomerine process separating the nasals and partly bisecting the parasphenoid, absence of a lacrimal, and a single row of vomerine teeth paralleling the premaxillary and maxillary tooth rows all involve characters that can be scored only for species of Amphiuma, whereas a single external gill slit, reduced girdles and limbs, three or fewer toes, columella fused to skull, septomaxilla and ypsiloid cartilage absent, first ceratobranchial and hypobranchial fused, spermatheca present in all but most posterior part of cloacal chamber in females, and cloacal pit, dorsal pelvic, Kingsbury's, and vent glands present in cloaca of males all involve characters that can be scored only for extant Amphiuma spp. Elongation of the trunk and increased trunk vertebral counts cannot be observed directly for Proamphiuma or A. jepseni, but can be inferred from the unicipital transverse processes on trunk vertebrae in both taxa (see below, "Discussion").

The type genus Amphiuma includes four diagnosable species from the late Paleocene and Pleistocene–Recent. The extant species A. tridactylum, A. means, and A. pholeter have, respectively, three, two, and one toes per foot and are limited to the southeastern USA (Salthe, 1973a–c, Means, 1996). The fossil record of amphiumids is biased towards vertebrae. These elements are easily differentiated from vertebrae of other salamanders by the following combination of features (Figs. 9-1 to 9-3): notochordal pit retained; atlas has large, hemispherical, slightly laterally compressed, and deeply concave anterior cotyles, a prominent, scoop-shaped odontoid process with a raised facet to either side of ventral midline, and a robust neural arch with a posteriorly short roof; postatlantal vertebrae amphicoelous and all but posteriormost caudals have a pair of postzygapophyseal crests; and trunk vertebrae lack spinal foramina, bear a subcentral keel, an elongate and moderately high neural crest, a posteriorly bifurcate neural spine, and a pair of anterior basapophyses, and all but the anteriormost trunk vertebrae have unicipital transverse processes. Isolated amphiumid vertebrae from Holocene and Pleistocene sites in Florida (Brattstrom, 1953; Weigel, 1962; Hirschfield, 1969; Meylan, 1995) and the middle Pleistocene of Texas (Holman, 1965; Slaughter and McClure, 1965) have been referred to extant (usually A. means) and indeterminate species of Amphiuma. The fossil congener A. jepseni is represented by three incomplete skeletons from the upper Paleocene (Tiffanian in age) Polecat Bench Formation (= Fort Union Formation of some authors), Wyoming (Estes, 1969, 1975, 1981). Published figures of the crushed and incomplete topotypic skull of A. jepseni indicate the species differs from its extant congeners (cf., Estes, 1969:fig. 4 versus Erdman and Cundall, 1984:fig. 2) in having a relatively shorter and broader snout, a relatively shorter maxilla and vomer, with both bones having a correspondingly shorter tooth row, and, evidently, a relatively broader parasphenoid (Estes, 1969, 1981; Naylor, 1978; contra Rieppel and Grande, 1998). I thus disagree with Rieppel and Grande's (1998) proposal that the name A. jepseni is a nomen dubium. Names of the remaining two nominal species of Amphiuma are nomina dubia, as previous authors have suggested. The name A. antica Holman is founded on a poorly preserved middle Miocene (Barstovian) trunk vertebra (Holman, 1977:fig. 2) from the Fleming Formation, Texas, that neither differs significantly from trunk vertebrae of extant congeners (Estes, 1981; Rieppel and Grande, 1998) nor is it clear to me that the specimen is from an amphiumid. Albright (1994:1135) questionably assigned to the Amphiumidae an unfigured, fragmentary trunk vertebra from a stratigraphically lower site (early Miocene or Arikareean) in the same formation. The holotype parasphenoid (Brunner, 1956:abb. 7, fig. 4) and only specimen of A. nordica Brunner from the Pleistocene of Germany is likely from a teleost (Estes, 1965, 1969, 1981).

Rieppel and Grande (1998) recently named the new genus and species Paleoamphiuma tetradactylum on a skeleton from the lower Eocene part of the Green River Formation, Wyoming. These authors regarded Paleoamphiuma as a primitive amphiumid and listed four features to justify their familial assignment (Rieppel and Grande, 1998:702, 707–708): trunk elongate; limbs reduced; ribs present only in anteriormost part of trunk region; and postzygapophyseal crests on trunk vertebrae. The first three features are not compelling because each occurs in some other salamander families; the first two features also are less pronounced than in extant amphiumids. More critically, the supposed postzygapophyseal crests were misidentified. Trunk vertebrae of unequivocal amphiumids have a characteristic arrangement of dorsal crests on the neural arch (see Figs. 9-1G, L, R, 9-3B, D): the neural crest extends along the midline to the posterior edge of the roof and, to either side, the unique postzygapophyseal crest extends anteriorly and slightly medially along the postzygapophyseal process onto the roof, before grading into the roof at about the level of the base of the transverse process. At no point does the postzygapophyseal crest contact the neural crest. The former crest is associated with the modified dorsalis trunci epaxial trunk muscles in extant Amphiuma (Davison, 1895; Auffenberg, 1959; Naylor, 1978) and the same arrangement of postzygapophyseal and neural crests in A. jepseni (Estes, 1969:fig. 3c, f) and Proamphiuma (Fig. 9-3)—taxa that are older than Paleoamphiuma—attests to the early establishment of this vertebromuscular pattern in amphiumids (Estes, 1969, 1981; Naylor, 1978). Published figures (Rieppel and Grande, 1998:figs. 4, 5, respectively) of the third-fifth and seventh trunk vertebrae in the holotype of P. tetradactylum show a markedly different arrangement of crests, which implies a correspondingly different arrangement of trunk musculature. The structure regarded by Rieppel and Grande (1998) as the postzygapophyseal crest arises posteriorly on the dorsal surface of the postzygapophysis, but the crest extends anteromedially at a pronounced angle to join with the posterior end of the neural crest, which is limited to the anterior half of the neural arch. The three dorsal crests in Paleoamphiuma thus form a posteriorly open "Y," in dorsal view, instead of being separate and approximately parallel, as in Amphiuma and Proamphiuma. In this respect, trunk vertebrae of Paleoamphiuma more closely resemble those of sirenid salamanders and the "postzygapophyseal crest" of Rieppel and Grande (1998) is probably an aliform crest (see next chapter). Pending the outcome of a planned study of the holotype by Drs. Rieppel and Grande and myself, I exclude P. tetradactylum from the Amphiumidae.

Genus PROAMPHIUMA Estes, 1969

Type Species—Proamphiuma cretacea Estes.

Distribution—As for the type and only species.

Diagnosis—As for the type and only species.

PROAMPHIUMA CRETACEA Estes, 1969

(Figs. 9-2, 9-3, 9-4A-C)

Proamphiuma cretacea (Estes) nomen dubium Rieppel and Grande, 1998:707.

Holotype—MCZ 3504, incomplete trunk vertebra, from the middle trunk region, missing leading edge of neural crest, distalmost end of left prezygapophysis, entire right postzygapophysis, part of left postzygapophyseal crest, and most of transverse processes on both sides (Estes, 1969:fig. 1a–e; here:Fig. 9-3A, B).

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Hell Creek Formation; Bug Creek Anthills, McCone County, Montana, USA.

Referred Specimens—MCZ 3505, 3637, UALVP 40045, 43813–34816, atlantes; MCZ 3508, 3509, 3632, UALVP 43817, 43825, 43826, 43834, anterior trunk vertebrae; MCZ 3506, 3507, UALVP 43818, 43820-43824, 43827, 43828, 43830-43833, 43837-43839, middle trunk vertebrae; MCZ 3629, 3631, 3634, 3636, UALVP 43819, 43829, 43835, 43836, posterior trunk vertebrae; MCZ 3630, UALVP 43840, caudal vertebrae; UALVP 14316, dentary. All 42 referred specimens are from the holotype locality.

The above list excludes four of the 16 referred vertebrae listed by Estes (1969, 1981): MCZ 3627 is a trunk vertebra of the sirenid Habrosaurus Gilmore; MCZ 3635 is a trunk vertebra of the batrachosauroidid Opisthotriton Auffenberg; and MCZ 3633 and 3628 are, respectively, a trunk centrum and probable caudal that are not diagnostic beyond Caudata Indeterminate.

Distribution—Known only from the holotype locality. See "Remarks" below for unverified records from elsewhere.

Revised Diagnosis—Species of Amphiumidae primitively differing from Amphiuma in having atlas and postatlantal vertebrae with neural crest relatively lower, trunk vertebrae with subcentral keel relatively shallower and anterior basapophyses relatively shorter, and trunk vertebrae and more anterior caudals with postzygapophyseal crests relatively lower. Differs further from extant species of Amphiuma (conditions uncertain for late Paleocene A. jepseni) as follows: more derived in having atlas with indistinct postzygapophyseal processes and anterior caudals pierced by spinal foramen; more primitive in having postatlantal vertebrae with neural crest extending anteriorly to leading edge of neural arch roof, trunk vertebrae with leading edge of neural crest inclined more posteriorly, atlas with ventral rims of anterior and posterior cotyles approximately in line, and dentary with internal opening of mandibular canal lingual to posteriormost external nutritive foramen; and in two character states of uncertain polarities—dentary with internal opening of mandibular canal anterior to level of posterior end of tooth row and inferred middle trunk vertebrae with neural crest broadly rounded anteriorly and dorsal edge horizontal.

Description

None of the 43 specimens known for Proamphiuma are complete. Descriptions below are composites, unless indicated otherwise.

Atlas (Estes, 1969:fig. 1f–j; here:Fig. 9-2)—The seven specimens collectively document the structure of the atlas. The largest specimen (UALVP 43813) is about half again as large as the smallest (MCZ 3637). The centrum is broad and short, with an intercotylar width of about 2.8–4.1 mm (n=7) and ventral midline length, including the odontoid process, of about 1.9–2.5 mm (n=6). The paired anterior cotyles are relatively large and extend up about the ventral third to half of the neural arch. Each cotyle is laterally compressed (ratio of maximum height:width about 1.3–1.6) and hemispherical in anterior outline, with the medial edge nearly straight. The dorsal edge of the cotyle is tilted slightly posteriorly and, especially in larger specimens, the anterior face is deeply concave. The odontoid process is robust and moderately elongate, accounting for about 0.4 of the total midline length of the atlantal centrum. The process is a scoop-like projection that broadens anteriorly and the leading edge is truncate to shallowly concave in outline. To either side of the ventral midline, the odontoid process bears a low, shallowly convex condyle that is subcircular in outline. In life each of these condyles would have fit into a complementary, concave facet in the medial face of the occipital condyle on the skull.

In lateral view the ventral rim of the posterior cotyle lies approximately in line with or slightly higher than the ventral rim of the anterior cotyle. In posterior view the posterior cotyle is oval in outline, taller than wide, and tapers ventrally. The inner surface of the cotyle is shallowly concave and coated with a thin film of calcified cartilage. A small notochordal pit opens in the dorsal half of the cotyle. To either side of the ventral midline, a low ridge extends posteromedially between the ventral rims of the anterior and posterior cotyles. Between this pair of ridges the ventral surface of the centrum is pierced by one to three moderate sized pits or foramina. The foramen for exit of the first spinal nerve opens about midway up and in the lateral half of the posterior surface of the anterior cotyle. A second foramen opens more ventrally and posteriorly in the lateral wall of the centrum, in front of the rim of the posterior cotyle. No basapophyses or transverse processes are present.

The neural arch is moderately high and robust. The latter condition probably accounts for the high percentage of specimens (five of seven) that retain a substantial portion of the arch. The arch on MCZ 3505 is fragmented (Fig. 9-2B); judging by Estes' (1969:fig. 1f–j) drawings, this damage occurred after he figured the specimen. In anterior outline the neural canal is laterally compressed and oval, with the ventral part pinched between the anterior cotyles. With growth the canal becomes relatively broader and increases from about a third to half of the intercotylar width. The neural arch roof is anteroposteriorly short, extending just past the level of the posterior cotyle. The roof is relatively broad and tapers minimally towards the posterior end; damage to the lateroposterior edges of the neural arch on UALVP 43813 (Fig. 9-2E, F) creates the impression that arch is more tapered on this specimen. A median neural crest and a pair of laterodorsal accessory ridges extend posteriorly along the dorsal surface of the neural arch roof. On MCZ 3505 these three crests are low and indistinct. The neural crest is relatively taller on UALVP 43813–43815 (Fig. 9-2E, I, and M, respectively) and 40045, whereas on the last two specimens the accessory ridges are also relatively taller. The neural crest is inclined posteriorly at an angle of about 13° to 28° (n=4) and is steepest on the two largest specimens. The crest terminates posteriorly in a low and blunt neural spine that extends as a vertical ridge down the posterior face of the arch (Fig. 9-2K). To either side of the neural spine, the posterior face of the roof is indented by a tiny facet. Where preserved, the postzygapophyseal process is weakly developed and does not project ventrally or laterally any significant distance from the neural arch. The postzygapophyseal facet is flattened and indistinct.

Trunk Vertebra (Estes, 1969:figs. 1a–e, 2; here:Fig. 9-3A–U)—The 33 trunk vertebrae range in ventral midline length from about 2.4–4.6 mm (n=28) and show minor differences in the form of processes and muscle crests. These structures vary continuously along the trunk region in extant species of Amphiuma (Cope, 1889:pl. 10; Naylor, 1978; Estes, 1981) and it is probable that similar variation occurred in Proamphiuma. On vertebrae from the middle part of the trunk in Amphiuma the neural crest is relatively tall, the paired neural spines are low, posteriorly short, and lie adjacent to the midline, the postzygapophyseal crests are prominent and located laterally, and the subcentral keel is moderately deep. Based on these criteria, 18 of the trunk vertebrae at hand for Proamphiuma appear to be from the middle part of the trunk region. My description focuses on these specimens because middle trunk vertebrae are typical for the trunk region and include the holotype.

The most nearly complete and informative of the middle trunk vertebral specimens are the holotype MCZ 3504 (Estes, 1969:fig. 1a–e), MCZ 3506 (Estes, 1969:fig. 2c), MCZ 3507 (Estes, 1969:fig. 2a) and UALVP 43818, 43827, 43830, 43831, and 43839 (Fig. 9-3A–L). The centrum is amphicoelous and constricted medially midway along its length. Both cotyles are deeply concave, the inner walls are coated with a thin film of calcified cartilage, and the notochordal pit is relatively large and opens in about the center of the cotyle. The anterior cotyle is circular in outline, whereas the posterior cotyle tends to be laterally compressed and oval in outline, with the narrow end directed ventrally. The subcentral keel spans between the anterior and posterior cotyles, and varies from a narrow, distinct flange to a broad, shallow, indistinct ridge. The ventral edge of the keel is concave dorsally in lateral profile and lies approximately in line with or, more commonly, well dorsal to the ventral rims of the cotyles. Although absent on the holotype (Estes, 1969:fig. 1e), a prominent subcentral foramen typically opens on either side between the subcentral keel and the base of the transverse process. Midway along its length, the lateral face of the keel is variably indented by a faint vertical groove that, in life, carried a blood vessel from the subcentral foramen. The paired anterior basapophyses are small, narrow, ridge- or prong-like structures, each of which arises from about the midpoint of the centrum and extends anteroventrally and slightly laterally. The anterior end of the basapophysis occasionally projects slightly beyond the rim of the anterior centrum, but typically lies in line with or behind the rim. From about the midpoint of the vertebra, a stout and unicipital transverse process projects laterally and slightly ventroposteriorly. Where intact, the transverse process is blunt distally. The distal end of the process on two specimens (MCZ 3506 and UALVP 43839) has a pair of tiny indentations that, in life, presumably were finished in cartilage. Three alar processes are associated with the transverse process. The most prominent of these is the anterior alar process—this is a triangular flange that extends between the anterior wall of the centrum and the anteroventral edge of the transverse process. Estes' (1969:4, 1981:44) statement, "ventral lamina [= alar processes, here] of transverse process present but apparently not well developed anteriorly," is true only in relation to trunk vertebrae of extant Amphiuma means and A. tridactylum; in these species the anterior alar process is a prominent rectangular flange that extends along the length of the transverse process (Fig. 9-1G, H, L, M). The posterior alar process is small and best developed on UALVP 43830 (Fig. 9-3F) as a posteriorly narrow flange that extends along the proximal part of the posteroventral edge of the transverse process. The dorsal alar process is a low ridge that runs along the proximal half of the dorsoanterior surface of the transverse process to the wall of the centrum. No vertebrarterial or spinal foramina are present.

The neural canal is broad and low, and the roof is shallowly convex dorsally. In dorsal outline the roof of the neural arch is elongate and hourglass-shaped, with the lateral edge constricted medially above the base of the transverse process. No interzygapophyseal ridges are present. The pre- and postzygapophyseal processes are relatively elongate and narrow. Prezygapophyses taper distally to a gently rounded tip and project anterolaterally at 33°–46° from the midline. Postzygapophyses project posterolaterally at complementary angles, but typically are more blunt distally. The prezygapophyseal facet is elliptical in dorsal outline and faces dorsally or dorsomedially, whereas the facet on the postzygapophysis is more oval, with the distal end broader, and faces ventrally or ventromedially. The postzygapophyseal crest is a distinct, but low and mediolaterally narrow ridge. The crest extends anteromedially along the dorsal surface of the postzygapophysis onto the dorsolateral surface of the neural arch and grades anteriorly into the roof of the arch at about the level of the base of the transverse process. The neural crest is mediolaterally narrow and extends from just behind the leading edge of the roof of the neural arch to the posterior margin of the arch. The lateral profile of the neural crest varies, presumably with the position along the trunk series as in extant amphiumids. Where most prominently developed, as on MCZ 3507 (Estes, 1969:fig. 2a) and UALVP 43827, 43831 (Fig. 9-3I), and 43839 (Fig. 9-3K), the crest is relatively tall, the leading edge rises steeply in a broad curve, and the dorsal edge extends posteriorly in an essentially horizontal plane. On inferred more anterior middle trunk specimens, such as the holotype and UALVP 43818 (Fig. 9-3A and C, respectively), the neural crest is relatively lower anteriorly and ascends posteriorward at a shallower angle to its full height. The neural spine is low and developed as a pair of posteriorly bifurcate ridges. Each ridge arises from the lateral surface of the neural crest, near the posterior end of the latter, and extends lateroposteriorly for a short distance along the dorsoposterior edge of the neural arch roof. In dorsal view the posterior end of the neural crest and the lateral ends of the neural spines often project slightly past the posterior edge of the neural arch in a three-pronged arrangement. Between the neural crest and the neural spine to either side, the posterior face of the arch is indented by a small facet.

Judging by the relatively deeper subcentral keel, lower and more medially placed postzygapophyseal crests, and lower, more triangular neural crest, seven vertebral specimens come from the more anterior part of the trunk region. Several of these also have a more prominent, although still faint, vertical groove extending from the subcentral foramen down the lateral face of the subcentral keel. MCZ 3509 (Fig. 9-3M, N) preserves an intact, bicipital transverse process on the left side. In extant Amphiuma spp. bicipital transverse processes are restricted to the first two trunk vertebrae. MCZ 3509 lacks the foramen for exit of the second spinal nerve that opens in the anterior part of the first trunk vertebra in some extant individuals of Amphiuma spp. (Edwards, 1976; pers. obs., 1999). MCZ 3508 (Fig. 9-3O, P) and MCZ 3632 (unfigured) also appear to be from the anteriormost part of the trunk region because each specimen preserves the broken base of a bicipital transverse process. MCZ 3508 is pathological—the anterior cotyle is distorted and the anterior part of the midventral keel is twisted to the left. A non-pathological, but notable, feature in this specimen is a prominent elliptical pit that opens ventrally along the posterior part of the midventral keel. A similar pit occurs in two extant Amphiuma spp. skeletons available to me: in the fourth trunk vertebra of A. means (FMNH 196143) and the fifth and sixth trunk vertebrae of A. tridactylum (UALVP 14364).

The eight inferred posterior trunk vertebrae are transitional into the caudal region (see below) in having the midventral keel further reduced, the neural crest and, often, the postzygapophyseal crests relatively lower, and the posterior end of each neural spine shifted more laterally. MCZ 3629 (Fig. 9-3Q, R) is typical of most specimens from this region in retaining weak basapophyses, an elongate and low neural crest, and posteriorly short neural spines. UALVP 43835 (Fig. 9-3S–U) evidently is from the posterior limit of the trunk region: the anterior basapophyses are absent, the neural crest is restricted to the anterior half of the neural arch, and the neural spines are posteriorly elongate, with the posterior end of each displaced far laterally.

Caudal Vertebrae (Fig. 9-3V–X)—Caudals have not previously been described or figured for Proamphiuma cretacea. The two specimens at hand include one (MCZ 3630) listed by Edwards (1976:308) from Estes' (1969) topotypic series and UALVP 43840. These specimens are associated with trunk vertebrae of Proamphiuma by provenance, size, and overall structure and are identified as caudals based on the presence of paired hypapophyses, instead of a subcentral keel, and a spinal foramen piercing the wall of the neural arch. Edwards (1976) also listed another three caudals for the genus: two of these (MCZ 3627 and 3635) are neither from the caudal region nor referrable to Proamphiuma; the third specimen (MCZ 3628) is likely a caudal, but it cannot confidently be referred to any salamander genus.

The more nearly complete caudal is UALVP 43840 (Fig. 9-3V–X). This specimen is missing the transverse process and the ventral edge of the hypapophysis on the left side and all four zygapophyseal processes. The centrum is amphicoelous and about 3.0 mm in ventral midline length. The anterior and posterior cotyles are subcircular in outline, deeply concave, slightly infilled with calcified cartilage, and the notochordal pit opens in the center of the cotyle. The intact hypapophysis on the right side is a shallow, mediolaterally narrow flange that extends between the anterior and posterior cotyles and is free distally. A unicipital transverse process projects lateroventrally from about the midpoint of the centrum on the right side. The base of the process is pierced by a vertebrarterial canal. The dorsal alar process resembles that on the trunk vertebrae, but the anterior and posterior alar processes form a broad and laterally pointed, triangular plate. Basapophyses are lacking. The spinal foramen pierces the wall of the neural arch midway between the posterior cotyle and base of the transverse process. The neural and postzygapophyseal crests and neural spines resemble those on posterior trunk vertebrae. Based on comparisons with extant Amphiuma spp. the combination of shallow and flange-like hypapophyses, prominent transverse process with wing-like anterior and posterior alar processes, and low and widely divergent neural spines argue for UALVP 43840 having come from the anteriormost part of the caudal series. This interpretation is important because in extant Amphiuma spp. intravertebral exit of spinal nerves is confined to more posterior caudals (Edwards, 1976).

MCZ 3630 (unfigured) lacks the distal parts of the paired hypapophyses, both transverse processes, and much of the neural arch. Although the distal ends of the hypapophyses are broken, when intact these processes would have differed from those on

UALVP 43840 in being deeper and in projecting ventroposteriorly and slightly laterally. These features suggest that MCZ 3630 occupied a more posterior position in the caudal series.

Dentary (Fig. 9-4A–C)—UALVP 14316 is an incomplete left dentary first reported and referred to Proamphiuma by Naylor (1978). This specimen is about 6.5 mm long and lacks the symphyseal end and posterior part of the area for attachment of the postdentary bones. No teeth are preserved, but the posterior ten or 11 tooth positions are present. Comparisons with dentaries of living amphiumids (Fig. 9-4D–F) suggest that UALVP 14316 is missing only the first three or four tooth positions, for an estimated count of 13–15 loci, and the bone was relatively shorter when complete. A row of four external nutritive foramina are present, the posteriormost of which lies at about the level of the fourth locus from the posterior end and directly opposite from the internal opening for the mandibular canal. UALVP 14316 differs from other described Lancian salamander dentaries (Naylor, 1978) and resembles those of extant Amphiuma spp. and A. jepseni (Estes, 1969:figs. 3a, b, 5) in the following combination of features: bone robust, relatively elongate, and weakly tapered anteriorly in lingual or labial view; lingual surface broadly convex lingually and perforated by prominent external mental foramina; dorsal edge twists lingually towards the posterior end in dorsal view; dental parapet relatively tall and, judging by the preserved walls of the pedicels, evidently bore highly pleurodont and relatively large, widely spaced teeth; dorsal edge behind tooth row developed into a low dorsal process that, in life, contributed to the coronoid process of the postdentary bones; and subdental shelf developed as a horizontal shelf anteriorly, with posterolingual edge notched to receive anterior end of angular, and absent more posteriorly. These features, plus the provenance and moderate size of UALVP 14316 support its association with vertebrae described above for Proamphiuma.

Remarks

In absolute and relative terms, Proamphiuma is one of the most poorly represented salamanders at the Bug Creek Anthills (Estes et al., 1969; Bryant, 1989; this study). Proamphiuma is known from just two collections—one in the MCZ (Estes, 1969, 1981;

Estes et al., 1969) and one in the UALVP (Naylor, 1978; this study)—and atlantal counts indicate that at least seven individuals are represented. Although sufficient numbers of vertebrae are available to document the vertebral morphology of the genus, the dentary UALVP 14316 remains the only skull element known for Proamphiuma. Given that many institutions besides the MCZ and UALVP have collected from the Bug Creek Anthills and that Cenozoic amphiumids have robust and distinctive skull elements, odds are favorable that additional skull bones will eventually be recognized for Proamphiuma.

There are no reliable occurrences of Proamphiuma from outside of the holotype locality. Holman's (1977:394) statement that Proamphiuma "is known from the late Palaeocene of Wyoming" is incorrect and refers, instead, to Amphiuma jepseni. Naylor (1978:507; pers. comm. from J. G. Armstrong) reported Proamphiuma from the late Campanian–early Maastrichtian (Edmontonian) Fruitland Formation of New Mexico, yet no mention of the genus appears in Armstrong-Ziegler's (1980) descriptive paper or in faunal lists (Armstrong-Ziegler, 1978; Hunt and Lucas, 1992, 1993) of lower vertebrates from the unit. Fox (1976:8) recorded Proamphiuma in a preliminary faunal list for the middle Campanian (Judithian) Dinosaur Park Formation (= upper Oldman Formation of Fox), Alberta, based on specimens in the collection of the UALVP, but I have not seen any specimens in this collection that are referrable to the genus. Denton and O'Neill (1998:492) suggested that fragmentary elements from the Marshalltown Formation (Campanian) of New Jersey may pertain to Proamphiuma, but this record cannot be substantiated until the specimens in question are described and figured.

The 43 specimens at hand for Proamphiuma are small, yet solidly ossified and the vertebral specimens have well developed crests and processes. Despite their small size, these specimens thus appear to be from relatively mature individuals. When scaled against skeletons from extant amphiumids and assuming similar vertebral counts, the dentary and largest vertebrae at hand for Proamphiuma suggest a total body length in the range of 30 cm. This is approximately the maximum size of extant Amphiuma pholeter (Means, 1996). By contrast extant A. means and A. tridactylum are considerably larger, each with record total body lengths of just over 100 cm (Conant and Collins, 1991). Extant species of Amphiuma are nocturnal, secretive burrowers that inhabit shallow, sluggish waters (Baker, 1945; Salthe, 1973b, c; Means, 1996). By analogy Proamphiuma probably pursued a similar lifestyle.

DISCUSSION

Taxonomic Status of Proamphiuma

Vertebrae and the dentary reported above are characteristic for amphiumids and comparisons with extant amphiumids suggest that the 43 specimens from the Bug Creek Anthills pertain to a single taxon—namely Proamphiuma cretacea. Rieppel and Grande's (1998) contention that the name P. cretacea is a nomen dubium within the Amphiumidae is weakened by three factors: (1) they did not examine any specimens of P. cretacea firsthand, but instead relied on Estes' (1969, 1981) published accounts of topotypic vertebra then assigned to the species; (2) they examined vertebrae from just two (Amphiuma means and A. tridactylum) of the three living species of Amphiuma; and (3) as is clear from their comments on page 707, they explicitly considered just one (centrum constricted) of the seven features given in Estes' (1969, 1981) diagnoses for P. cretacea. My firsthand comparisons of all known specimens of P. cretacea and representative specimens from all three extant Amphiuma spp. confirm that some vertebral characters listed by Estes (1969, 1981) are not diagnostically reliable at the generic level, yet many differences remain between Proamphiuma and Amphiuma.

Estes (1969, 1981) believed that Proamphiuma differed from extant Amphiuma in seven vertebral characters: subcentral keel and postzygapophyseal crests (i.e., "muscle crests" of Estes), basapophyses, and neural crest (= "neural spine" of Estes) less prominent; neural arch on atlas directed more nearly posteriorly; and trunk vertebrae narrower and more constricted medially. I consider the first four characters diagnostically reliable (see below), but the last three are not appropriate for differentiating amphiumid genera. The angle at which the atlantal neural arch is inclined posteriorly, as measured along the dorsal edge of the neural crest in lateral view, is more variable within Proamphiuma than Estes (1969, 1981) suspected and overlaps substantially with extant species of Amphiuma. Among atlantes now available for Proamphiuma (Fig. 9-2A, D, H, L) the angle described by the dorsal edge of the arch ranges from about 13° to 28° (n=5) and is steepest on the two largest specimens (UALVP 40045 and 43813), suggesting that the arch becomes steeper with growth. In specimens available to me the atlantal neural arch is similarly steep in A. means (28°-31°; n=2) and A. tridactylum

(33°; n=1), but essentially horizontal in the one individual of A. pholeter (Fig. 9-1A, I, and Q, respectively). The shape and proportions of trunk vertebrae differ among amphiumids only at the specific level. Trunk vertebrae of P. cretacea, A. pholeter, and, judging by Estes' figures (1969:fig. 3c–f) of the best preserved vertebra from the holotype of A. jepseni, differ from trunk vertebrae of A. means and A. tridactylum in being less constricted or waisted medially in dorsal outline (contra Estes, 1969) and relatively more elongate (Figs. 9-1, 9-3).

Known elements of Proamphiuma differ from those of extant Amphiuma spp. as follows (see Figs. 9-1 to 9-4): (1) postzygapophyseal crests on postatlantal vertebrae relatively lower; (2) subcentral keel on trunk vertebrae relatively shallower; (3) anterior basapophyses relatively shorter, with anterior end typically in line with or behind rim of anterior cotyle (versus anterior end of basapophyses projecting past cotyle); (4) neural crest on postatlantal vertebrae relatively lower; (5) neural crest on postatlantal vertebrae extends anteriorly to leading edge of roof (versus anterior end of crest approximately in line with posterior edge of prezygapophyseal facets; (6) leading edge of neural crest on trunk vertebrae inclined posterodorsally in lateral view (versus inclined more dorsoposteriorly); (7) neural crest on inferred middle trunk vertebrae broadly rounded anteriorly and dorsal edge horizontal in lateral profile (versus neural crest on all trunk vertebrae resembles a posteriorly tilted square, with anterior and dorsal edges meeting at a sharp, nearly right-angled junction); (8) anterior caudals pierced by spinal foramen (versus spinal foramen absent from first two caudals, present in ninth and all subsequent caudals, with intervening transitional zone of two to seven caudals; Edwards, 1976); (9) ventral rims of posterior and anterior cotyles on atlas approximately in line in lateral view (versus posterior cotyle expanded ventrally, with ventral rim well below level of anterior cotyles); (10) postzygapophyseal processes on atlas shallow and indistinct (versus prominent and project ventrally); (11) internal opening of mandibular canal and posteriormost external nutritive foramen opposite one another in dentary (versus internal opening of mandibular canal lies well behind level of posteriormost external nutritive foramen); and (12) internal opening of mandibular canal in dentary lies anterior to level of posterior end of tooth row (versus opening in line with or behind level of posterior end of tooth row). Considering that postzygapophyseal crests are autapomorphic for amphiumids, the relatively lower crest in Proamphiuma probably represents the primitive amphiumid condition. Outgroup comparisons with the basal urodeles Hynobius and Cryptobranchus suggest that, relative to extant Amphiuma spp., Proamphiuma exhibits the primitive state for another seven characters (2–6, 9, 11) and the derived state for characters 8 and 10. Polarities for states of the remaining two characters are equivocal: the characteristic profiles of the neural crest (character 7) in Amphiuma and Proamphiuma are not seen in Hynobius or Cryptobranchus; whereas for character 12 Hynobius exhibits the Proamphiuma condition and Cryptobranchus exhibits the Amphiuma condition.

The late Paleocene Amphiuma jepseni cannot be compared as satisfactorily with Proamphiuma and extant species of Amphiuma, because I have not examined the three reported specimens of A. jepseni and many relevant characters cannot be determined from published descriptions (Estes, 1969, 1975, 1981) for the species. No atlantes or caudal vertebrae have been reported for A. jepseni, the three dentaries are too fragmentary and obscured by matrix (Estes, 1969:fig. 3a, b, 5) to show the position of the lingual opening for the mandibular canal, and the sole trunk vertebra figured by Estes (1969:fig. 3c–f) is broken anteriorly in such a manner that neither the length nor profile of the neural crest can be determined with confidence. Judging by Estes' (1969, 1981) descriptions and figures, trunk vertebrae of A. jepseni resemble those of extant congeners and differ from Proamphiuma in having a more prominent neural crest, postzygapophyseal crests, subcentral keel, and basapophyses. At present these are the only character states supporting membership of A. jepseni within Amphiuma. The skull of A. jepseni is relatively short and broad, and my reconstruction of the dentary UALVP 14316 suggests this was also the condition for Proamphiuma. Given that extant Amphiuma spp. are unusual among living salamanders in having a narrow and elongate skull, the relatively shorter and broader skull in A. jepseni and inferred for Proamphiuma is probably a primitive resemblance.

In summary, Proamphiuma primitively differs from Amphiuma in four characters describing the lesser development of vertebral crests and processes; these differences are subtle, but distinct. Proamphiuma differs further from the three extant species of Amphiuma (conditions unknown for A. jepseni) in two derived character states (one each from the atlas and caudal vertebrae) that may be autapomorphic within the family, four plesiomorphies (two from the trunk vertebrae and one each from the atlas and dentary), and two character states (one each from the trunk vertebrae and dentary) of uncertain polarities. I believe this suite of differences is sufficiently extensive to warrant the continued recognition of P. cretacea as a diagnosable and valid amphiumid taxon (contra Rieppel and Grande, 1998).

Relationships Within the Amphiumidae

The only cladistic study of relationships among amphiumids is Karlin and Means' (1994) electrophoretic analysis of 24 loci for the three extant species of Amphiuma. A more comprehensive analysis of relationships among the five recognized amphiumid species is premature until specimens described by Estes (1969, 1975, 1981) for A. jepseni are critically re-examined and ideally, broad agreement is reached on the immediate outgroups of the Amphiumidae. Nevertheless, sufficient information now exists to propose the following nested set of relationships within the family: Proamphiuma (A. jepseni (A. pholeter (A. means + A. tridactylum))). This proposed pattern can be tested in the future by a formal cladistic analysis.

Vertebrae of Proamphiuma exhibit the full complement of basapophyses, crests, and processes that are characteristic for amphiumids (Estes, 1969, 1981; Naylor, 1978), including the unique postzygapophyseal crests that are associated with the modified dorsalis trunci epaxial trunk musculature in extant amphiumids. Weaker development of these vertebral structures in Proamphiuma, compared to Amphiuma, implies that the associated vertebral musculature was present, but less pronounced (Estes, 1969, 1981; Naylor, 1978). The atlas in Proamphiuma and extant Amphiuma spp. also resemble one another in the structure of the neural arch, odontoid process, and anterior cotyles, a combination that implies a similar pattern of atlanto-cranial articulation and associated musculature (Naylor, 1978); see Erdman and Cundall (1984) for information on the atlanto-cranial complex in living amphiumids. Proamphiuma exhibits two more characteristic amphiumid vertebral features that have not previously been identified for the genus: (1) an elongate trunk can be inferred from the presence of unicipital transverse processes on all but the anteriormost trunk vertebrae and (2) deeply concave anterior cotyles on the atlas indicate that the complementary occipital condyles on the skull were stalked (i.e., posteriorly elongate). In extant amphiumids these conditions seem to be associated with burrowing and feeding, respectively. Elongation of the body is a common trend in fish, amphibians, and reptiles and facilitates movement through crevices and similarly confined spaces (Gans, 1975). Extant amphiumids have increased the number of precaudals to about 65–70 vertebrae (Baker, 1945; Rieppel and Grande, 1998; pers. obs., 1999) and are accomplished burrowers (Baker, 1945; Knepton, 1954; Salthe, 1973b, c). Manipulation of skeletons from extant amphiumids shows that stalked occipital condyles and deep atlantal anterior cotyles allow the skull to rotate dorsoventrally in a wide arc about the atlanto-cranial joint. Erdman and Cundall's (1984) functional study of feeding in A. tridactylum demonstrated that rapid anterodorsal displacement of the joint aids in snapping the mouth closed during the latter part of the feeding strike.

Proamphiuma and Amphiuma are the only two amphiumid genera that I recognize and, by default, are sister-taxa. Given that Proamphiuma shares no apomorphies with any amphiumid taxon, other than those character states that are primitive for the family, for the purpose of deciphering the evolutionary history of the Amphiumidae it is more informative to view Proamphiuma as the basalmost member of the family. In terms of its provenance and known morphology Proamphiuma is a good structural ancestor for Amphiuma, if not directly ancestral to the latter (Estes, 1969, 1981; Naylor, 1978). Proamphiuma also provides a minimum date of latest Cretaceous for the origin of the Amphiumidae and its occurrence in present day Montana is consistent with the view (Naylor, 1978; Milner, 1983; Duellman and Trueb, 1986) that amphiumids are endemic to North America.

The four species of Amphiuma are united by four vertebral synapomorphies presumably related to enhanced development and performance of the associated trunk muscles: neural and postzygapophyseal crests relatively high, subcentral keel relatively deep, and anterior basapophyses relatively more elongate, extending past rim of anterior cotyle. The three extant species are united by the shared presence of an elongate, narrow snout and corresponding cranial modifications—e.g., dentary anteriorly elongate; maxilla, vomer, and their respective tooth rows posteriorly elongate; and parasphenoid narrow. The tapered snout and elongate jaws in extant Amphiuma spp. aid in borrowing through loose substrate, moving through narrow burrows, and, in combination with the posteriorly elongate mouth opening, permit the consumption of larger, more diverse, and more active prey (Erdman and Cundall, 1984). These observations imply that the short-snouted A. jepseni and Proamphiuma, if I have correctly interpreted the form of the snout in the latter based on the dentary UALVP 14316, were less active burrowers, perhaps resembling A. pholeter in favoring mucky bottom sediments (Means, 1996), and preyed upon smaller, less active prey.

The extant species of Amphiuma form a morphocline in which limbs become relatively shorter and the number of toes reduced from three in A. tridactylum, to two in A. means, to one in A. pholeter (Neill, 1964), yet Karlin and Means' (1994) electrophoretic analysis identified the first two species as each other's closest relatives. Two putative trunk vertebral synapomorphies also support a sister-pair relationship between A. tridactylum and A. means: (1) anterior alar process more rectangular in ventral or dorsal outline and uniformly broad anteriorly along length of transverse process (alar process primitively triangular in outline, broadest medially, and narrowing laterally along transverse process) and (2) neural arch relatively wide and strongly constricted medially in dorsal view (arch primitively narrower and less constricted medially). The implications of this arrangement are two-fold. First, limb length and toe counts were reduced independently in A. means and A. pholeter. Second, rather than being typical or representative amphiumids as phylogenetic analyses (Larson and Dimmick, 1993; Hay et al., 1995) and functional studies (Erdman and Cundall, 1984; Reilly and Lauder, 1992) routinely assume, A. tridactylum and A. means appear to be the most "advanced" members of the family. As such, A. pholeter arguably is a better choice for a representative (i.e., "primitive") living member of the genus and family.

The phylogeny I have proposed here and the limited fossil record for amphiumids imply that the characteristic atlanto-cranial joint and elongate trunk and the unique vertebromuscular complex of the family were established by the latest Cretaceous. Amphiuma jepseni provides a minimum date of post-late Paleocene for elongation of the snout and associated cranial modifications seen in living amphiumids. The sequence in which other hallmark amphiumid attributes (e.g., limbs reduced; number of toes reduced; premaxillae fused, with vomerine process and pars dorsalis posteriorly elongate) arose and the levels at which these are apomorphic cannot be deciphered from the fossil record. Such findings must await the discovery of additional amphiumid fossils from appropriate horizons.

CONCLUSIONS

Examination of all known specimens of the latest Cretaceous amphiumid Proamphiuma cretacea and representative specimens of the three extant species of Amphiuma yields the following results:

(1) Proamphiuma cretacea is restricted to the late Maastrichtian (Lancian) Bug Creek Anthills, in the Hell Creek Formation of Montana. Four of the 17 topotypic vertebrae originally listed for P. cretacea cannot be referred to the taxon. Additional specimens reported here from the holotype locality include atlantes, trunk vertebrae, and a caudal that triple the number of available vertebral specimens and the only skull element (a dentary) yet identified for the taxon.

(2) Proamphiuma cretacea is a diagnosable amphiumid taxon, the geologically oldest member of the family, and the type and only species in the genus. Proamphiuma differs primitively from the Cenozoic Amphiuma in four character states describing lesser development of vertebral processes and crests, and differs further from the three extant species of Amphiuma (conditions unknown based on published reports of the late Paleocene A. jepseni) in a set of apomorphies, plesiomorphies, and character states of uncertain polarities from the vertebrae and dentary.

(3) The following relationships are hypothesized among the five valid amphiumid species: Proamphiuma cretacea (Amphiuma jepseni (A. pholeter (A. means + A. tridactylum). Proamphiuma is a good structural ancestor for, if not the actual ancestor of, Amphiuma. This phylogeny and fossil evidence implies that the characteristic atlanto-cranial joint and elongate trunk and the unique vertebromuscular complex of amphiumids arose before elongation of the snout and associated cranial modifications typical of living amphiumids. The fossil record is too limited to indicate the sequence in which other important amphiumid features arose and the levels at which these are apomorphic.

FIGURE 9-1. Vertebrae of extant species of Amphiuma Garden; Recent, southeastern USA. A. means Garden, type species (**A–H**): **A–E**, atlas, FMNH 196143, in (**A**) left lateral, (**B**) dorsal, (**C**) ventral, (**D**) anterior, and (**E**) posterior views; **F–H**, middle trunk vertebra, UALVP 14507, in (**F**) right lateral, (**G**) dorsal, and (**H**) ventral views. A. tridactylum Cuvier, UALVP 14364 (**I–P**): **I, J**, atlas, in (**I**) right lateral and (**J**) anterior views; **K–M**, middle trunk vertebra, in (**K**) right lateral, (**L**) dorsal, and (**M**) ventral views; **N–P**, first cloacal vertebra, in (**N**) left lateral, (**O**) dorsal, and (**P**) ventral views. A. pholeter Neill, UALVP 14487 (**Q–V**): **Q–S**, atlas, in (**Q**) left lateral, (**R**) dorsal, and (**S**) anterior views;**T–V**, middle trunk vertebra in (**T**) left lateral, (**U**) dorsal, and (**V**) ventral views. Specimens at different scales: top (**A–E**), upper middle (**F–H**,) lower middle (**I–P**), and bottom (**Q–V**) scale bars = 1 mm.

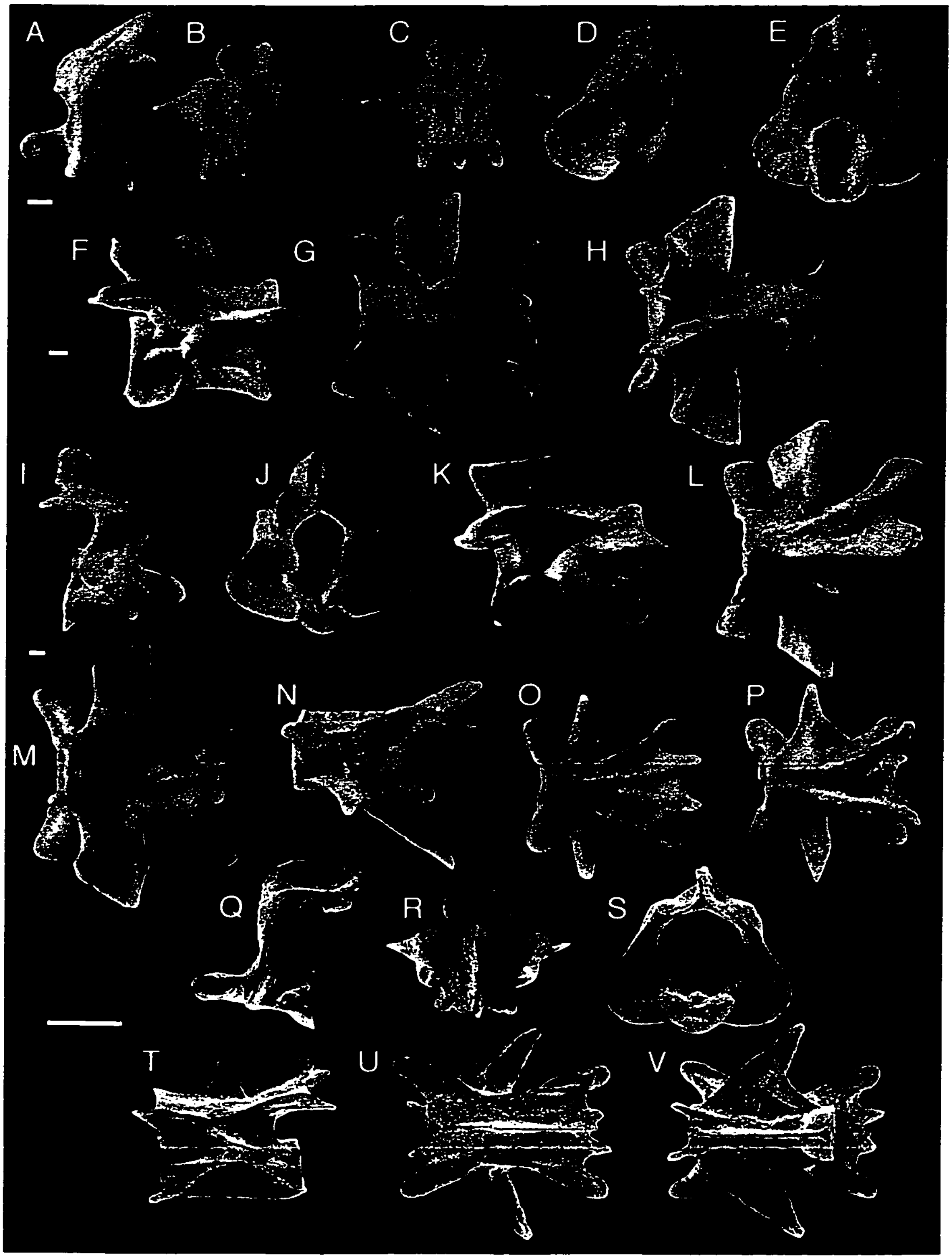
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FIGURE 9-2. Atlantes of Proamphiuma cretacea Estes; late Maastrichtian (Lancian) Bug Creek Anthills, Hell Creek Formation, Montana. **A–C**, MCZ 3505, atlas with roof of neural arch fractured, in (A) right lateral (B) dorsal, and (C) anterior views; **D–G**, UALVP 43813, atlas missing lateroposterior edges of arch, in (D) right lateral (E) dorsal, (F) ventral, and (G) anterior views; **H–K**, UALVP 43814, atlas missing left side of odontoid process and right posterior edge of neural arch, in (H) left lateral, (I) dorsal, (J) anterior, and (K) posterior views; **L, M**, UALVP 43815, small atlas missing left edge of odontoid process and posterior part of neural arch on left side, in (L) right lateral and (M) anterior views; **N**, UALVP 43816, atlantal centrum showing hair passing through right spinal foramen, in dorsal view. Specimens at same scale: scale bar = 1 mm.

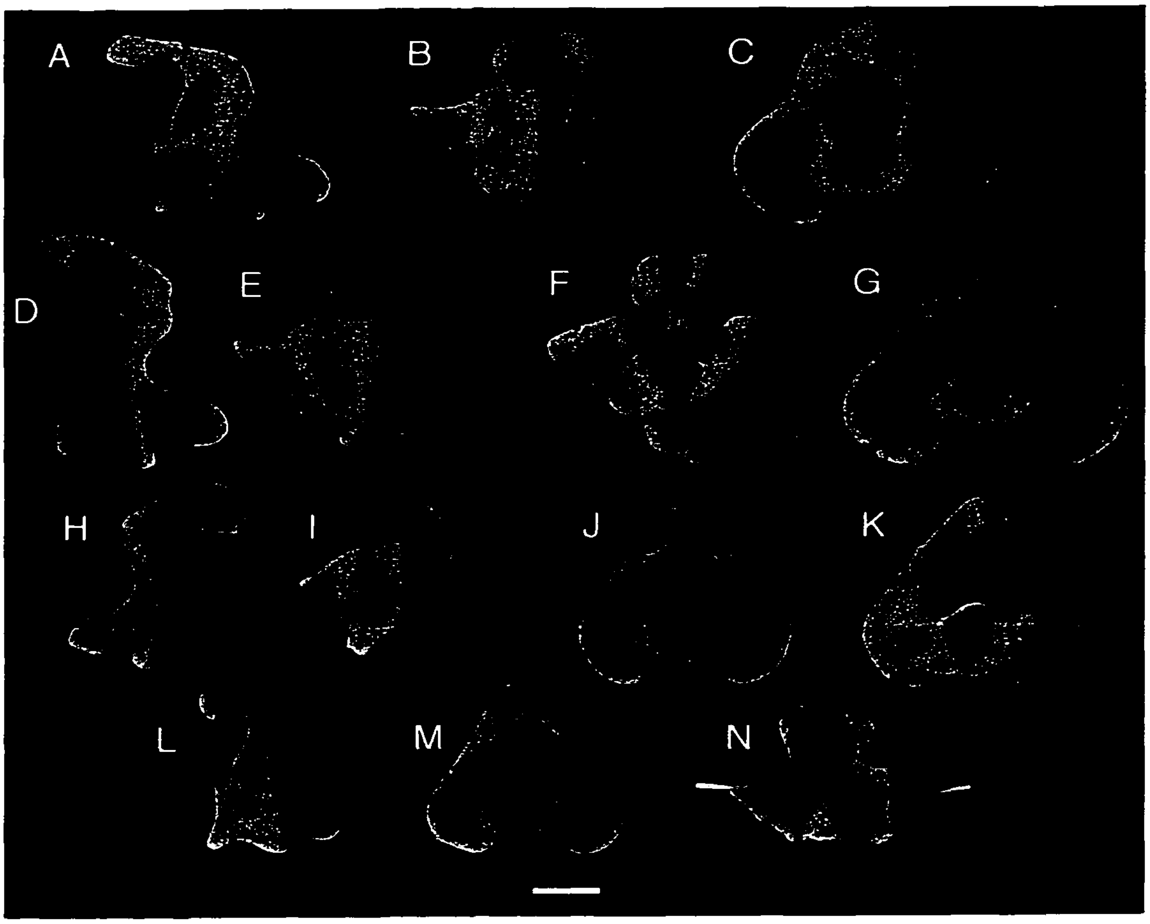
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FIGURE 9-3. Postatlantal vertebrae of Proamphiuma cretacea Estes; late Maastrichtian (Lancian) Bug Creek Anthills, Hell Creek Formation, Montana. Middle trunk vertebrae (A–L): **A**, **B**, MCZ 3504, holotype, in (**A**) right lateral and (**B**) dorsal views; **C–E**, UALVP 43818, in (**C**) right lateral, (**D**) dorsal, and (**E**) ventral views; **F–H**, UALVP 43830, in **F**, ventral, **G**, anterior, and **H**, posterior views; **I**, **J**, UALVP 43831, in **I**, right lateral and **J**, dorsal views; **K**, **L**, UALVP 43839, in (**K**) left lateral and (**L**) dorsal views. Anterior trunk vertebrae (M–P): **M**, **N**, MCZ 3509, in (**M**) left lateral and (**N**) dorsal views; **O**, **P**, MCZ 3508, in (**O**) right lateral and (**P**) ventral views. Posterior trunk vertebrae (Q–U): **Q**, **R**, MCZ 3629, in (**Q**) left lateral and (**R**) dorsal views; **S–U**, UALVP 43835, in (**S**) right lateral, (**T**) dorsal, and (**U**) ventral views. Anterior caudal vertebra (V–X): UALVP 43840, in (**V**) right lateral view, with arrow pointing to spinal foramen, and (**W**) dorsal and (**X**) ventral views. Specimens at same scale: scale bar = 1 mm.

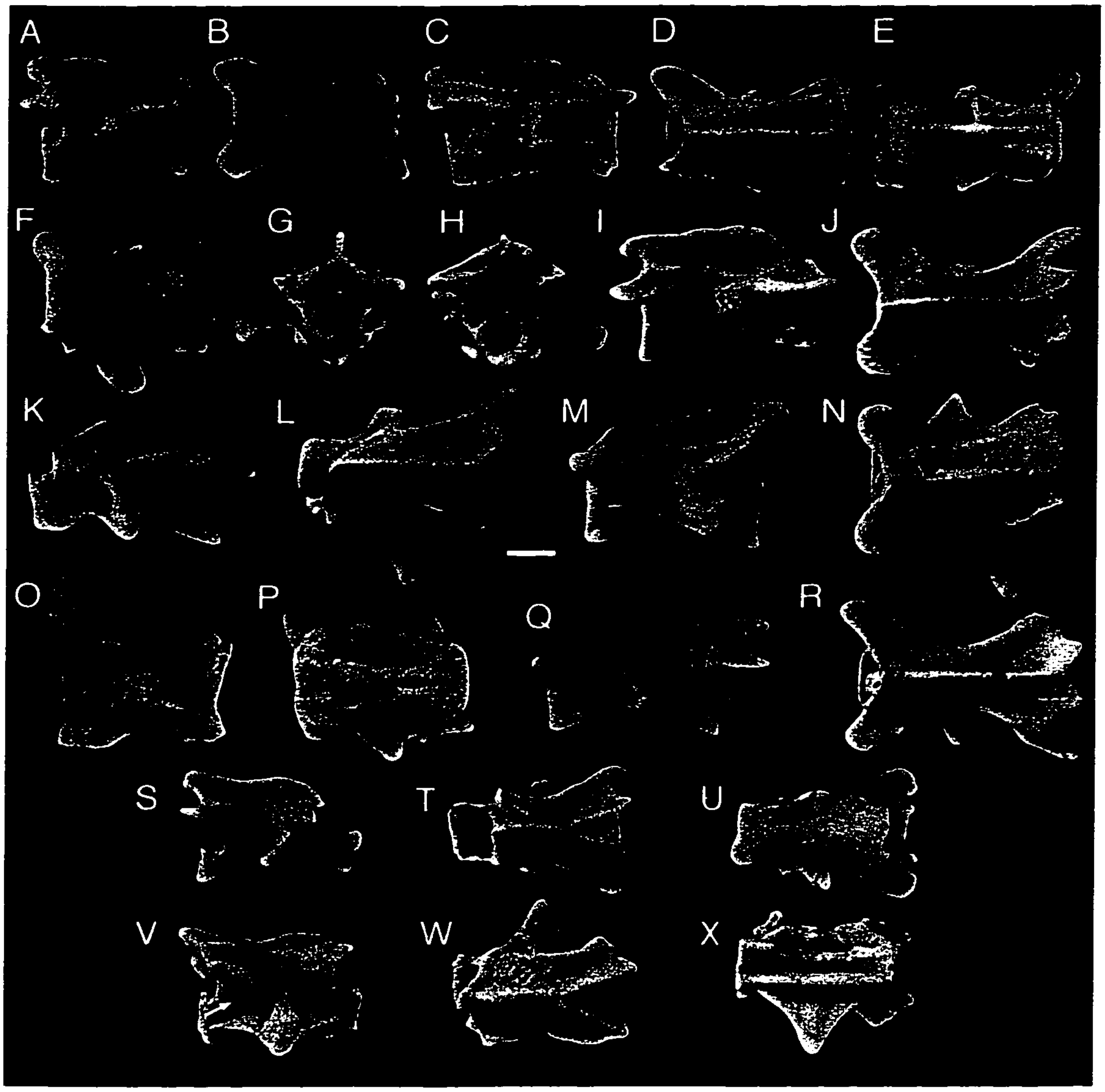
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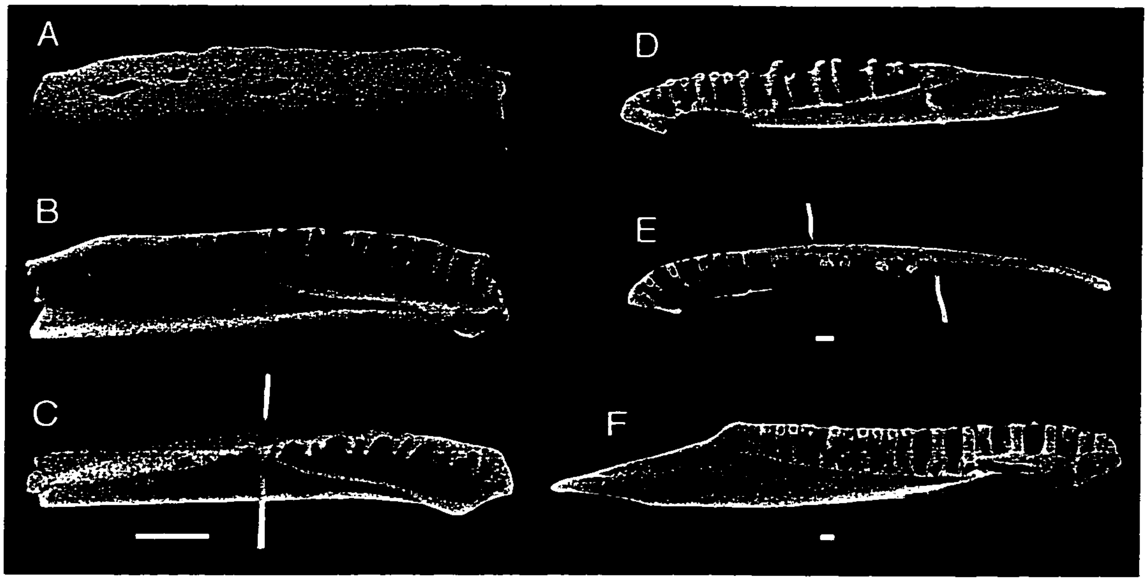
FIGURE 9-4. Dentaries of amphiumids; late Maastrichtian (Lancian) and Recent, USA. Proamphiuma cretacea Estes (A–C); late Maastrichtian (Lancian) Bug Creek Anthills, Hell Creek Formation, Montana: UALVP 14316, left dentary, in (A) labial and (B) lingual views and (C) occlusal view showing hair passing transversely through mandibular canal between lingual opening for canal and posteriormost external nutritive foramen. Extant species of Amphiuma Garden (D–F); unrecorded localities, southeastern USA: **D**, **E**, Amphiuma means Garden, type species, FMNH 98657, right dentary, in (D) lingual and (E) occlusal views, showing wire passing obliquely (mesiolabially–distolingually) through mandibular canal between lingual opening for canal and posteriormost external nutritive foramen; **F**, A. tridactylum Cuvier, UALVP 14364, left dentary, in lingual view. Specimens at different scales: left (A–C), top right (D and E), and bottom right (F) scale bars = 1 mm.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CHAPTER 10 — REVISION OF HABROSAURUS GILMORE AND RELATIONSHIPS AMONG SIRENID SALAMANDERS

INTRODUCTION

The Sirenidae Gray are paedomorphic, aquatic salamanders from the Late Cretaceous and Cenozoic of North America. Living sirenids range from 250 to 950 mm in maximum total length and are readily identified by their elongate body, gill slits, external gills, reduced forelimbs, and lack of a pelvic girdle and hindlimbs (Duellman and Trueb, 1986). The higher level affinities of sirenids have proven difficult to resolve, largely because the family exhibits a conflicting suite of paedomorphic character states, symplesiomorphies, and apomorphies. Sirenids are widely regarded as crown-clade salamanders (i.e., urodeles sensu Milner, 1988; see also Evans and Milner, 1996) and variously have been interpreted as the sister-taxon of all other urodeles (Hecht and Edwards, 1977:fig. 6a; Milner, 1983; Duellman and Trueb, 1986; Sever, 1991; Hedges and Maxson, 1993; Larson and Dimmick, 1993; Hay et al., 1995), one of the most advanced families of urodeles (Hecht and Edwards, 1977:figs. 5, 6b; Naylor, 1978; Estes, 1981; R. Cloutier, unpublished analysis cited by Trueb, 1993:fig. 6.9), or intermediate urodeles (Edwards, 1976; Larson, 1991). The belief that sirenids constitute an order of amphibians distinct from salamanders (Cope, 1889; Goin and Goin, 1962) was effectively discredited by Estes (1965).

Three sirenid genera are commonly recognized: Siren Linnaeus (six species, Eocene–Recent); Pseudobranchus Gray (four species, Pliocene–Recent); and Habrosaurus Gilmore (two species, Campanian–Paleocene) (Goin and Auffenberg, 1955, 1957, 1958; Estes, 1964, 1965, 1981; Martoff, 1972, 1973a, b; 1974a, b, Holman, 1977; Moler and Kezer, 1993; this study). For reasons discussed below I exclude the Gondwanan Cretaceous salamanders Kababisha Evans et al. and Noterpeton Rage et al. from the Sirenidae. The four extant sirenid species are limited to the central and southeastern USA and northeasternmost Mexico (Martoff, 1972, 1974b), whereas fossils are known in the central and southeastern USA and the Western Interior, from Texas north into southern

Alberta and Saskatchewan (e.g., Estes, 1981; Holman and Voorhies, 1985; Holman, 1995).

The fossil genus Habrosaurus has long been regarded as monotypic. Gilmore (1928) described the type species H. dilatus as a new taxon of indeterminate lizard, characterized by peculiar teeth with expanded and flattened crowns, based on four incomplete dentaries from the type area of the late Maastrichtian (Lancian) Lance Formation, Niobrara County, Wyoming. Three decades later, Goin and Auffenberg (1958) described the new sirenid genus and species Adelphesiren olivae for two incomplete trunk vertebrae, also from the type Lance Formation. Estes (1964) reported on a series of isolated sirenid skull and postcranial elements from various localities in the type Lance Formation that allowed him to reinterpret dentaries of Habrosaurus as belonging to a sirenid salamander, associate dentaries of Habrosaurus and trunk vertebrae of Adelphesiren—thereby placing the latter name as a junior synonym of the former—and describe additional elements (upper jaws, palatal bones, atlantes, caudal vertebrae, and ceratobranchials) for H. dilatus. He subsequently provided a cranial reconstruction (Estes, 1965:figs. 3, 4a) and rediagnosed and briefly redescribed the genus (Estes, 1981:94–95). Although Habrosaurus since has been reported from another 15 Campanian to Paleocene formations in North America (see generic account, below), our knowledge of the genus rests almost exclusively on the isolated skull bones and vertebrae described and illustrated by Estes (1964) for the type species from the Lance Formation. Below I report on additional examples of these elements from the Upper Cretaceous Lance, Hell Creek, Frenchman, and Dinosaur Park formations and Paleocene Lebo Formation that (1) provide new information about Habrosaurus and the type species, (2) permit the description of a second species, and (3) yield insights into relationships and evolutionary trends among the three sirenid genera.

Here I restrict the Sirenidae to Habrosaurus, Pseudobranchus, and Siren (contra Evans et al., 1996) and follow Naylor (1978) and Estes (1981) in allying sirenids with salamandrids within a restricted Salamandroidea Noble. For comparative purposes I examined the following taxa and specimens of extant sirenids (Figs. 10-1, 10-2): S. intermedia Le Conte: UALVP 14486, cleared and stained individual; UALVP 40053, trunk vertebra; S. lacertina Linnaeus: UALVP 14404, skeleton; UALVP 40052, trunk vertebra; and P. striatus (Le Conte): UALVP 40054, atlas; UALVP 40055, trunk vertebra.

SYSTEMATIC PALEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order CAUDATA Scopoli, 1777
Crown-order URODELA Dumèril, 1806
Suborder SALAMANDROIDEA Noble, 1931 (sensu Estes, 1981)
Family SIRENIDAE Gray, 1825

Remarks—Monophyly of the Sirenidae has never been questioned, yet none of the seven autapomorphies listed by Duellman and Trueb (1986:495) reliably unite all three sirenid genera. Four apomorphies (muscle adductor mandibulae internus superficialis originates from side of skull; glomeruli well developed in anterior part of kidney; 46–48 macrochromosomes and no microchromosomes; and interventricular septum present) involve characters that cannot be determined for Habrosaurus. This is also the case for another putative autapomorphy not listed by Duellman and Trueb (1986:495), but identified as such in their figure 17-1, namely the lack of a pelvic girdle and hindlimbs. The interventricular septum cannot even be regarded as autapomorphic among caudates for Siren and Pseudobranchus, because Putnam and Dunn (1978) reported this structure in the extant proteid Necturus Rafinesque. The final three putative sirenid autapomorphies identified by Duellman and Trueb (1986)—teeth arranged in patches on palatal bones; premaxillary teeth replaced by horny beak; and nasal ossifies from median anlagen to articulate laterally with pars dorsalis on premaxilla—are restricted to Siren (Fig. 10-1A–C) and Pseudobranchus (Duellman and Trueb, 1986:fig. 13-3), with Habrosaurus retaining the primitive state for each of the relevant characters (see account for Habrosaurus, below). I have not identified any reliable autapomorphies for the Sirenidae, but the following combination of derived character states is unique among caudates to all three sirenid genera and provisionally supports monophyly of the family: teeth non-pedicellate; palatine teeth arranged in multiple, parallel rows; spinal nerve foramen pierces posterior half of each postatlantal vertebra; trunk and anterior caudal vertebrae have triradiate arrangement of alar processes associated with transverse process, prominent interzygapophyseal ridges, and Y-shaped configuration of dorsal crests, with median neural crest restricted to anterior half of arch and paired, prominent aliform processes diverging posterolaterally onto postzygapophyses; transverse processes bicipitate on anterior trunk vertebrae and unicipitate on more posterior vertebrae; and ribs restricted to anterior part of trunk series and articulating with bicipital transverse processes on vertebrae in this region. Other diagnostic, but evidently primitive, vertebral features for sirenids include amphicoelous post-atlantal vertebrae and paired anterior basapophyses on trunk vertebrae. Although I have not been able to examine dentaries of Pseudobranchus, dentaries of Siren and Habrosaurus exhibit three character states that appear to be derived among caudates and, depending on the condition in Pseudobranchus, may also support monophyly of the Sirenidae: ventral margin and area behind occlusal margin sharply deflected ventrally; notch in dorsal edge immediately behind occlusal margin; and narrow groove extends along labial surface below and parallel to more posterior part of occlusal margin.

Extant Siren and Pseudobranchus are reliably separated by differences in cranial structure, numbers of toes and gill slits, and coloration (Cope, 1889; Martof, 1972). Trunk vertebral characters have also been used to separate the two genera (Goin and Auffenberg, 1955; Estes, 1981; Meylan, 1995) and are the sole basis for recognizing the four fossil species of Siren and two fossil species of Pseudobranchus (Goin and Auffenberg, 1955, 1957, 1958, Holman, 1977; Estes, 1981). This practise needs to be re-evaluated because such identifications rely on subtle and, in some cases, taxonomically questionable differences in vertebral structure for which the range of variation in living species has not been adequately documented (see Lynch, 1965; Estes, 1981). The familial identity of the purported amphiumid Paleoamphiuma tetradactylum Rieppel and Grande (Eocene, Wyoming) also deserves reconsideration, because published figures of trunk vertebrae (Rieppel and Grande, 1998:figs. 4, 5) in the holotype skeleton show the Y-shaped arrangement of dorsal crests typical for sirenids; further study of this skeleton will be the focus of a collaborative study by Drs Rieppel and Grande and myself.

Sirenids are not reliably known from outside of North America. Brunner's (1956) report of an indeterminate species of Siren from the Pleistocene of Germany is founded on a parasphenoid (Brunner, 1956:abb. 7, fig. 3) unlike that in extant sirenids and, instead, is probably from a teleost (Estes, 1981). Yadagiri (1986) described supposed sirenid dentaries from the Early Jurassic of India, but the figured specimens (Yadagiri, 1986:pl. Ii, j) are poorly preserved fragments that are neither diagnostically sirenid (Evans et al., 1996) nor urodelan (Milner, 1993) in structure. Evans et al. (1996) recently proposed that the Gondwanan urodeles Kababisha (two species; Cenomanian, Sudan) and the monotypic Noterpeton (Maastrichtian, Bolivia) are sirenids, rendering the name Noterpetontidae Rage et al. a junior subjective synonym of Sirenidae. Many of the resemblances listed by Evans et al. (1996) between Kababisha and unequivocal sirenids are not unique to sirenids, are of uncertain polarities or homologies, or, at best, appear to only approach the condition in sirenids. The same is true for sirenid-like features in trunk vertebrae described by Rage et al. (1993) for Noterpeton. Other features—notably the procoelous-like vertebrae, lack of the premaxillary pars dorsalis, and the unique symphyseal dentary tooth in Kababisha and the procoelous vertebrae of Noterpeton (jaws are undescribed for Noterpeton)—differentiate these genera from all other caudates. For these reasons I view Kababisha and Noterpeton as distinctive and, possibly, closely related salamanders that convergently resemble sirenids in some aspects of vertebral structure. Rage (1997) expressed similar doubts over the higher level affinities of these enigmatic genera.

Genus HABROSAURUS Gilmore, 1928

Adelphesiren Goin and Auffenberg, 1958:453–456, figs. 188, 189.

Type Species—Habrosaurus dilatus Gilmore.

Included Species—Habrosaurus dilatus and H. prodilatus, sp. nov.

Distribution—Middle Campanian (Judithian) to middle (Torrejonian) Paleocene, North American Western Interior. See "Remarks" below.

Revised Diagnosis—Genus of Sirenidae differing from Siren and Pseudobranchus in three character states that are autapomorphic among caudates: crowns on marginal and palatal teeth mesiodistally expanded and bear a mesiodistally aligned crest; wear facet variably developed on crowns of marginal and palatal teeth; and atlas having articular surface continuous across anterior face of odontoid process and paired anterior cotyles. Differs further from Siren and Pseudobranchus in one character state of uncertain polarity—basapophyses free from anterior alar process—and in the following primitive character states: skull relatively broader; pars dorsalis on premaxilla arises near medial edge of bone and, evidently, separated paired nasals; maxilla unreduced; vomer and palatine unfused, with latter larger and more elongate posteriorly; parasphenoid does not project anteriorly between paired vomers and premaxillae; premaxilla, maxilla, and dentary retain teeth; single row of vomerine teeth parallels anterior and lateral margins of bone; odontoid process on atlas arises between paired anterior cotyles and tapers to blunt distal end; anterior alar process on trunk vertebrae less pronounced; and neural crest on trunk vertebrae relatively lower.

Remarks

Diagnostic Features of Habrosaurus and its Species—Most of the elements described by Estes (1964) for Habrosaurus, then known only by the type species, were correctly identified and associated. The holotype and referred dentaries and the referred post-atlantal vertebrae, including the holotype of Adelphesiren olivae, are diagnostic for sirenids. Dentaries of Habrosaurus can be associated with premaxillae, maxillae, vomers, and palatines based on the unique teeth, whereas the association of trunk vertebrae with the unusual atlantes is supported by the complementary form of the cotyles, size, and frequency of occurrence. The identity of the bone that Estes (1964:74) described as the first ceratobranchial is uncertain. Judging by the published description and drawing (Estes, 1964:fig. 36f), the bone differs from the ceratobranchial of extant Siren (cf., Wilder, 1891:pl. 39, fig. 7) in being stouter and in having the shaft more sinuous and the anterior and posterior ends markedly wider than the shaft. Estes (1964:74) stated that some of the Lancian specimens resemble the ceratobranchial of extant Siren in having a slightly developed laterodorsal ridge, but on the only figured specimen (AMNH 8117) this ridge is developed into a prominent, procurved process that is not seen, to my knowledge, on ceratobranchials of any extant salamanders (cf., Duellman and Trueb, 1986:fig. 13-7). I have not identified any other characteristic sirenid elements that could be attributed to Habrosaurus in collections available to me.

Habrosaurus is a distinctive salamander. Previous diagnoses for the genus relied on characters of the jaws and dentition (Gilmore, 1928; Estes, 1964, 1981) and postatlantal vertebrae (Goin and Auffenberg, 1958; Estes, 1964, 1981); many of these remain valid differences. Also important are characters describing the proportions of the skull, the structure and contacts of the premaxilla, palatine, and vomer (see Estes, 1965), and previously overlooked palatal and atlantal characters. Habrosaurus differs from Siren and Pseudobranchus as follows: (1) skull relatively broader, as evidenced by the broadly convex outline of the premaxilla and dentary; (2) pars dorsalis on premaxilla arises near medial edge of bone and, evidently, extended between the paired nasals (versus pars dorsalis arises from median or lateral part of bone and articulates along lateral edge of nasal); (3) maxilla unreduced (versus maxilla reduced to a tiny bone in Siren and lost in Pseudobranchus; Duellman and Trueb, 1986); (4) vomer and palatine unfused, with the latter posteriorly elongate and larger (versus bones fuse ontogenetically and vomerine component larger); (5) anterior end of parasphenoid lies behind premaxillae and vomers (versus anterior end of parasphenoid projects between paired vomers and premaxillae); (6) premaxilla, maxilla, and dentary retain teeth (versus teeth absent, with horny beak covering occlusal surfaces of dentary and premaxilla); (7) vomerine teeth arranged in a single row, curving parallel to anterior and lateral margins of bone (versus multiple rows of teeth extending lateroposteriorly across bone); (8) tooth crowns mesiodistally expanded, with mesiodistal crest (versus crowns conical and lacking crest); (9) wear facet variably developed on tooth crowns (versus no facet); (10) articular surface on atlas for contact with skull continuous across anterior face of odontoid process and paired anterior cotyles (versus articular facets paired, with facet on either side extending medially across anterior face of cotyle and anterodorsally onto ventrolateral face of odontoid process); (11) odontoid process on atlas arises between paired anterior cotyles and tapers to blunt distal end (versus process arises between dorsal halves of anterior cotyles and somewhat bifurcate distally, with lateroanterior edge of each half curled ventrally); (12) free anterior basapophyses on trunk vertebrae (versus all but distal end of basapophysis confluent with anterior alar process); (13) anterior alar process on trunk vertebrae less pronounced (contra Estes, 1964), arising beside anterior cotyle and extending posterolaterally as a triangular plate to the transverse process (versus arises beside anterior cotyle, projects lateroanteriorly beyond cotyle, and continues posterolaterally as a broad, wing-like flange to transverse process); and (14) neural crest on trunk vertebrae relatively lower, similar in height to paired aliform processes (versus neural crest taller than aliform processes). I have not been able to examine dentaries of *Pseudobranchus*, but dentaries of *Habrosaurus* differ from those of *Siren* in having the area for attachment of the postdentary bones accounting for about a third of the total dentary length (versus over half in *Siren*) and in having a markedly deeper, more pronounced labial groove.

Of the above characters, three (8–10) appear to be unique among salamanders to *Habrosaurus* and, thus, may be considered derived for the genus. A continuous articular surface across the anterior face of the atlas is also seen among caudates in *Kababisha*; however, the condition in the African genus is due to loss of the odontoid process and medial confluence of the anterior cotyles (Evans et al., 1996:text-figs. 1E, 4E, 5A, 6B, G), and is not homologous with the condition in *Habrosaurus*. Homologies of the anterior basapophyses (character 12) in *Habrosaurus*, *Siren*, and *Pseudobranchus* are uncertain. Estes (1964:79) suggested that basapophyses in the last two genera were either incorporated into the anterior alar process or replaced by an anterior extension of the process; in either case, Estes (1964) implicitly regarded the basapophyses in *Habrosaurus* as homologous to those of other salamanders and, by implication, primitive relative to the condition in extant sirenids. Based on his belief that the muscle projecting from the anterior alar process in extant *Siren* is not homologous with the anterior basapophyseal muscles in non-sirenids, Naylor (1978:570–571) regarded the so-called basapophyses in sirenids as not homologous with "true" basapophyses of other salamanders and suggested the prominent basapophyseal-like structures in *Habrosaurus* were secondarily derived from the anterior alar process. Regardless of the homologies and relative apomorphies of the anterior basapophyses in sirenids, these structures differ in a diagnostically informative manner between *Habrosaurus* on one hand and *Siren* and *Pseudobranchus* on the other. For the remaining characters, states seen in *Habrosaurus* resemble those of non-sirenid salamanders and, for this reason, are probably primitive relative to *Siren* and *Pseudobranchus*. Characters 1, 2, and 5 rely on marginal jaws and vomers available for *H*. *dilatus* and on Estes' (1965:figs. 3, 4a) cranial reconstruction for the species, and similarly can be inferred from jaws available for the new Judithian species. The retention of maxillary teeth in the new Judithian congener is inferred from the fact that the holotype and referred premaxilla bear well-developed teeth. Other characters relating to the maxilla, palatal bones, and trunk vertebrae are known only for the type species of *Habrosaurus*; I assume states for these characters are identical in the Judithian species, because in other salamanders these elements generally are similar among congeners.

Estes (1964, 1981) believed that Habrosaurus differed further from other sirenids in having simple, triangular-shaped haemal spines on inferred posterior caudals, rather than the more elaborate spines seen in Siren and Pseudobranchus. The validity of this claim is difficult to judge because although the presumed posterior caudal figured by Estes (cf., Estes, 1964:fig. 37b versus Fig. 10-2H, I) for Habrosaurus has a simple haemal spine, in both this regard and its well-developed neural crest the specimen more closely resembles anterior caudals of extant Siren. Estes (1964:79–80) stated that trunk vertebrae of Habrosaurus and Pseudobranchus resemble one another and differ from Siren as follows: posterior interzygapophyseal ridge curves anteroventrally to meet dorsal lamina of transverse process midway along centrum, well posterior to base of prezygapophysis (versus posterior interzygapophyseal ridge essentially straight and anteriorly contacts dorsal lamina at base of prezygapophysis); shallow median ridge present between aliform processes; and zygapophyses project more laterally. Specimens available to me indicate that these characters are more variable within and among Habrosaurus and Siren than Estes (1964; see also Goin and Auffenberg, 1955) believed and, thus, are not reliable for differentiating the two genera.

I recognize two species of Habrosaurus based on the following characters of the marginal teeth (see Fig. 10-3): relative length and build (i.e., gracile or robust); amount of constriction between pedicel and crown; structure of crown; spacing of crowns on adjacent teeth; and size and position of wear facet on crown. Differences between the two congeners are distinctive, yet subtle, and can be related to different feeding strategies. These morphological differences are not size-related, because they are evident in comparable-sized jaws from both congeners.

Distribution of Habrosaurus—Habrosaurus has been reported in faunal lists and occasional descriptive accounts for 16 Campanian–Paleocene formations. Diagnostic specimens available to me or adequately described, figured, or both in publications confirm reports of Habrosaurus in the following seven units in the Western Interior: middle Campanian (Judithian) Dinosaur Park Formation (= upper Oldman Formation of some authors), Alberta (Fox, 1976) and Judith River Formation, Montana (Sahni, 1972); late Maastrichtian (Lancian) Frenchman Formation, Saskatchewan (Fox, 1989; Tokaryk, 1997), Lance Formation, Wyoming (Gilmore, 1928; Goin and Auffenberg, 1958; Estes, 1964, 1981; Breithaupt, 1982), and Hell Creek Formation, Montana (Estes et al., 1969; Bryant, 1989); lower Paleocene part (Puercan) of the Tornillo Formation, New Mexico (Standhardt, 1986); and middle Paleocene (Torrejonian) Lebo Formation, Montana. The Lebo Formation has yielded the only skeleton—as yet undescribed and unfigured—reported for Habrosaurus (Sullivan, 1991). Specimens at hand from the Dinosaur Park, Lance, Hell Creek, Frenchman, and Lebo formations are identifiable to species. Dentaries (AMNH 8477, 8478) reported by Sahni (1972) from the Judith River Formation and the atlantal centrum (LSUMG V-927) figured by Standhardt (1986:fig. 32) from the upper Javelina Member of the Tornillo Formation can be identified only to genus.

Other occurrences for Habrosaurus are unconfirmed. Fox (1972, 1976) recorded Habrosaurus in preliminary faunal lists for the early Campanian (Aquilan) Milk River Formation, Alberta, based on specimens in the collection of the UALVP, but I have not seen any diagnostic sirenid specimens in this collection. The youngest reported occurrence for the genus, that of H. dilatus from the upper Paleocene part (Tiffanian) of the Fort Union Formation, Park County, Wyoming, is unproven because Estes (1981:94) did not figure or adequately describe voucher specimens. This is also true for reports of the type species from the middle Campanian (Judithian) "Mesaverde" Formation, Wyoming (Breithaupt, 1985) and Kaiparowits Formation, Utah (Eaton et al., 1999), late Maastrichtian (Lancian) part of the Ferris Formation, Wyoming (Lillegraven and Eberle, 1999), lower Paleocene (Puercan) Tullock Formation, Montana (Bryant, 1989), and middle Paleocene (Torrejonian) Tongue River Formation, Montana (Estes, 1976, 1981) of Montana. Reports of H. dilatus from the lower and middle Paleocene (Puercan and Torrejonian) Nacimiento Formation of New Mexico (Sullivan and Lucas, 1986; Williamson and Lucas, 1993) are suspect, because the figured voucher dentary (UCMP 89714; Williamson and Lucas, 1993:fig.9A) lacks the teeth and the shape of the bone is not diagnostic for Habrosaurus. There is one possible occurrence from outside of the Western Interior: Denton and O'Neill (1998:492) mentioned an atlas and cranial bones of "cf. Habrosaurus" (erroneously identified by them as a "sirenian"—i.e., an order of aquatic mammals) from the Campanian basal Marshalltown Formation of New Jersey, but this biogeographically intriguing record cannot be confirmed until the relevant specimens are described and figured.

HABROSAURUS DILATUS Gilmore, 1928

(Figs. 10-3A–F, 10-4 to 10-8)

Adelphesiren olivae Goin and Auffenberg, 1958:454–456, figs. 188, 189.

Holotype—USNM 10749, left dentary missing symphyseal and posterior ends, and preserving four intact teeth and bases of six more teeth (Gilmore, 1928: fig. 106, pl. 26, fig. 9; Estes, 1964:pl. 3, top).

Holotype Horizon and Locality—Late Maastrichtian (Lancian) Lance Formation; unrecorded locality in type area of formation, Niobrara County, Wyoming, USA. The type area of the Lance Formation covers approximately 175 square miles (Clemens, 1963).

Referred Specimens—Lance Formation, multiple localities, Wyoming: unspecified locality(ies) in type area: USNM 10813, 10815, 10816 (Gilmore, 1928:pl. 26, fig. 7), 17018, dentaries; CM 6467, 6448, holotype and referred trunk vertebrae, respectively, of Adelphesiren olivae (Goin and Auffenberg, 1958:figs. 188, 189); Bushy Tailed Blowout: UALVP 43910–43913, premaxilla; UALVP 43857, maxilla; UALVP 1614, 43873, 43874, 43915–43918, dentaries; UALVP 43914, vomer; UALVP 43919, atlas; UALVP 43895–43899, trunk vertebrae; UALVP 43901, caudal vertebra. Hell Creek Formation, Bug Creek Anthills, Montana: UALVP 43849–43854, premaxillae; UALVP 43855, 43856, maxillae; 43858–43871, dentaries; UALVP 43872, lot of seven fragmentary dentaries; UALVP 43875, 43876, vomers; UALVP 43877, palatine; UALVP 40046–40048, 43878–43882, atlantes; UALVP 40049, 40050, 43883–43894, trunk vertebrae; UALVP 43900, caudal vertebra. Frenchman Formation, Wounded Knee, Saskatchewan: UALVP 43921–43926, premaxillae; UALVP 43927, maxilla; UALVP 43930–43933, dentaries; UALVP 43928, 43929, vomers, UALVP 43934, atlas. Lebo Formation, unknown locality, Montana: USNM 25871, palatine.

The above list does not included referred jaws, palatal bones, and vertebrae reported by Estes (1964) from various localities in the type Lance Formation. I have excluded one (USNM 10817; unfigured) of the three referred dentaries listed by Gilmore (1928:162 and caption for pl. 26) from the Lance Formation, because the structure of the bone (relatively elongate and gracile; ventral edge descends posteriorly at shallow angle;

labial face indented by broad and shallow trough) and the preserved tooth bases indicates USNM 10817 pertains to the batrachosauroidid salamander Opisthotriton Auffenberg.

Distribution—Late Maastrichtian–middle Paleocene, North American Western Interior: Lance Formation, Wyoming, Hell Creek Formation, Montana, and Frenchman Formation, Saskatchewan, all late Maastrichtian or Lancian in age; and Lebo Formation (middle Paleocene or Torrejonian), Montana.

Revised Diagnosis—Species of Habrosaurus with marginal teeth differing from those on comparable-sized jaws of the new Judithian species described below as follows: teeth relatively stouter and about ninety percent as long; neck between pedicel and crown more constricted; crowns expanded labiolingually and more bulbous; crowns on adjacent teeth nearly contacting one another; and prominent wear facets on more anterior teeth, often with crowns ground flat in larger individuals.

Description

None of the jaws, palatal bones, and vertebrae listed above for Habrosaurus dilatus are complete. Specimens from the Lance, Hell Creek, and Lebo formations are comparable in preservation to those reported and figured by Estes (1964), whereas specimens from the Frenchman Formation typically are more fragmentary and abraded. Unless noted otherwise, descriptions below are composites.

Premaxilla (Estes, 1964:fig. 36c–e; here:Fig. 10-4A–G)—The most nearly complete of the 16 specimens at hand is UALVP 43849 (Fig. 10-4A–D), a right premaxilla missing all but one of the teeth and the distal ends of the pars dorsalis and vomerine process, from the Bug Creek Anthills. This and other specimens at hand show that the bone is more robust than in extant sirenids. Indistinct suture marks on the flattened, medial face of the pars palatinum and pars dentalis indicate that the premaxillae were weakly sutured across these surfaces in life. The premaxilla is smooth and broadly convex externally, indicating that the snout was blunt in outline. Although no premaxilla yet reported has an intact pars dorsalis, three specimens (UALVP 43849, 43854, and 43911) preserve a substantial part of the proximal region of the process. The pars dorsalis arises from the medial part of the premaxilla as a mediolaterally wide, labiolingually flattened, and, evidently, elongate process that extends posteriorly at about 30° from the horizontal in a shallow, dorsally convex curve. As preserved, the distal part of the process slightly expands medially in UALVP 43849 and 43911 (unfigured), but not in UALVP 43854 (cf., Fig. 10-4A, B versus E). The medial edge of the pars dorsalis was free of bony contacts proximally, but medial expansion of the process in UALVP 43849 and 43911 suggests that processes on opposite premaxillae probably contacted one another more distally in some individuals. The more distal part of the pars dorsalis on UALVP 43854 has a shallow, labiolateral trough, presumably for articulation with the nasal.

In lingual view, a narrow groove extends posteriorly along the pars dorsalis in most specimens. A slot in the lateral half of the base of the pars dorsalis (Fig. 10-4C, D) participates in articulation between the premaxilla and vomer (see account for latter element, below). The pars palatinum is a labiolingually narrow, horizontal shelf that medially bears a small, triangular-shaped, and posteriorly projecting vomerine process. This process is broken on most specimens at hand, but is preserved intact on UALVP 43925 (unfigured) and nearly so on UALVP 43910 (Fig. 10-4G). The pars palatinum narrows laterally into the maxillary process, the lateral face of which is vertical and bears weak scars for contact with the maxilla. The pars dentalis is moderately deep and becomes shallower laterally.

Maxilla (Estes, 1964:fig. 35a–c; here:Fig. 10-4H–J)—In contrast to the more nearly complete maxillae figured by Estes (1964), the four specimens available to me preserve only about the anterior half to two-thirds of the bone. UALVP 43855 (Fig. 10-4H–J), a right maxilla from the Bug Creek Anthills, is the best preserved specimen and the basis for my description here. The main body of the bone is broken transversely at the level of the posterior edge of the nasal process and preserves the anterior six loci, including one intact tooth. In labial surface is smooth and the pars facialis is low. The distal part of the nasal process is missing, but the preserved base suggests the process was triangular in outline, in contrast to the more squarish outline seen on maxillae figured by Estes (1964:fig. 35a, b). The lingual face and posterior edge of the nasal process are roughened, evidently for contact with a more dorsal bone. A narrow and dorsally convex ridge extends anteriorly along the dorsal edge of the pars facialis, above the second and third loci from the anterior end of the tooth row. The anterior end of the pars palatinum is expanded lingually and swollen, and the anterior face is indented by a shallow concavity for contact with the maxillary process on the premaxilla. To either side of and above the concavity, several indistinct ridges wrap around the anterior end of the maxilla; Estes (1964) suggested these ridges served as attachment points for ligaments connecting the maxilla and premaxilla. As on the premaxilla, the pars dentalis is shallow. More nearly complete specimens reported by Estes (1964) show that the posterior end of pars palatinum is slightly expanded lingually and the tooth row terminates well in front of the posterior end of the bone.

Dentary (Estes, 1964:fig. 34 and pl. 3, top; here:Fig. 10-5)—Of the 36 referred specimens at hand, sufficient overlap exists between the five figured specimens to adequately document the structure of the dentary. The bone is moderately elongate, robust in construction, and broadly curved in occlusal or ventral outline. The area behind the tooth row for attachment of the postdentary bones—none of which have been identified—accounts for about a third of the total length of the dentary. The dorsal edge along the tooth row is straight in labial or lingual outline and, judging by the condition in extant Siren (Fig. 10-1D), probably tilted slightly labially in life. Immediately behind the tooth row the dorsal edge of the bone is developed into a distally blunt, posterodorsally directed process set off ventrally from the remainder of the bone by a V-shaped facet for articulation with a postdentary bone. Behind this notch, the dorsal edge descends posteroventrally to the broadly rounded posterior end of the bone. The ventral edge of the bone is essentially horizontal along the anteriormost part of the bone, to about the level of the second or third locus from the anterior end, then descends at a pronounced angle of about 25° to 35° relative to the dorsal margin of the bone.

The labial face of the dentary is smooth, except for a narrow groove that extends anteriorly from the notch behind the tooth row and parallels the occlusal margin to about the level of the sixth to eight locus from the posterior end of the tooth row. The groove is deepest posteriorly, considerably more so than in dentaries of extant sirenids, and becomes shallower anteriorly. Estes (1964:78) stated this groove carried "nutrient structures." Comparisons with extant Siren and Norris' (1913:274 and fig. 44)) description of cranial nerves in S. lacertina suggest the labial groove in the dentary of Habrosaurus probably carried the ramulus mandibularis externus branch of the ramus mandibularis cranial verve V and, perhaps, blood vessels. Estes (1964) noted that in some larger dentaries of Habrosaurus dilatus the posterior part of the groove is enclosed or roofed labially by bone. A hair pushed through the groove in one such specimen, UALVP 43917 (Fig. 10-5C), demonstrates that the enclosed posterior part of the groove is not infilled with bone, but remains open as a canal.

The symphysis is expanded posteriorly into a labiolingually narrow plate, with the symphyseal face flattened and roughened for articulation with the opposite dentary. In lingual view the dental parapet is low and becomes shallower posteriorly along the jaw. The subdental shelf is lingually narrow and confined to the anterior part of the bone below the first four to six loci. From the posterior end of this shelf, an indistinct ridge extends posteriorly below the tooth row. Comparisons with extant sirenids suggest this ridge probably was the site of attachment for the coronoid, although no such element has been identified for Habrosaurus. The Meckelian groove originates at the posterior end of the subdental shelf and deepens posteriorly. The inner face of the Meckelian groove and lingual surface of the more posterior part of the dentary bear indistinct, elongate grooves and ridges for articulation with postdentary bones.

Marginal Teeth (Figs. 10-3, 10-4A–D, G–H, 10-5A, B, D–G)—The marginal teeth are non-pedicellate, relatively closely spaced, and moderately pleurodont in attachment—i.e., attached along basal half to third of shaft to the lingual wall of the jaw (Fig. 10-3A). Teeth become smaller in size, less pleurodont in attachment, and the crowns less expanded towards the distal end of the tooth row. Each tooth is robust in build and somewhat wedge-shaped in mesial or distal view, with a lingually expanded base and distally tapered shaft. Midway along its height, the shaft may be slightly swollen in a barrel-like fashion. The junction between the shaft and crown is demarcated by a constricted neck. The crown is spatulate or bulbous in form, being expanded labiolingually and mesiodistally to the extent that the mesial and distal edges of crowns on adjacent teeth approach (Fig. 10-3A) and may contact or overlap (Fig. 10-5D, E) one another. In pristine teeth (Fig. 10-3B, C) the crown is broadly convex and a low, blunt, median crest extends mesiodistally across the occlusal surface. Most crowns show evidence of wear in the form of a bevelled facet. Some teeth exhibit modest wear, with a small facet lying lingual to the median crest and facing lingually and slightly occlusally. This is the condition on the sole intact tooth located midway along the maxillary tooth row on UALVP 43855 and more posterior dentary teeth, such as on UALVP 43865 (Fig.

10-3A) and 43918 (Fig. 10-3D). On more extensively worn teeth the wear facet broadens labially, to the extent that the entire occlusolingual face of the crown, including the median crest, is ground flat and, on a few teeth, the pulp cavity is exposed. Such prominent wear facets occur on teeth near the anterior end of large dentaries (e.g., UALVP 43867; Fig. 10-3E) and on large premaxillae (e.g., UALVP 43910: Fig. 10-3F). Manipulation of the last two specimens, which are from comparable-sized individuals, shows that the prominent occlusolingual wear facets were formed by the anteroventrally directed premaxillary teeth meeting at an acute angle with and grinding against the more nearly vertical dentary teeth. Occlusolingual wear facets developed on more posterior dentary and maxillary teeth imply that teeth in this region were tilted slightly outwards.

In premaxillae at hand with an intact tooth row, four specimens have four loci and five specimens have five loci. These values accord well with premaxillary tooth counts of three to five reported by Estes (1964), although it is unclear whether his counts included teeth plus empty tooth slots or just teeth. None of the maxillae or dentaries available to me have an intact tooth row; Estes (1964) reported counts of eight to 12 and ten to 16 teeth, respectively, for these elements. Estes' (1964) suggestion that tooth counts decrease as element size increases is corroborated by premaxillae available to me and seems to hold true for the dentaries. Most teeth have a prominent replacement foramen lingually at the base and occasional specimens have one or a few empty replacement slots. The dentary UALVP 43865 preserves two in situ replacement crowns, one each at the second and seventh loci—this is the first direct evidence for tooth replacement in Habrosaurus.

Vomer (Estes, 1964:fig. 36a–b; here:Fig. 10-6A–F)—The vomer is a moderate-sized, shallow, and plate-like bone that is slightly longer than wide. The anterior and lateral margins are broadly convex in dorsal or ventral outline. Of the five available specimens, only UALVP 43914 (Fig. 10-6A, B) preserves the medial and posterior margins intact. In this specimen the medial margin accounts for about the anterior half of the bone and is anteroposteriorly straight. The bone is swollen ventrally adjacent to the medial edge of the tooth row, and the medial face is vertical and flattened medially for contact across the midline with the opposite vomer. The remainder of the medial margin trends posterolaterally, is thin, and shows no evidence of bony contact(s). The posterolateral end of the bone is narrow and truncate, with the posterior face swollen ventrally and flattened anteriorly for contact posteriorly with the palatine. A short and broad premaxillary process, best preserved on UALVP 43876 (Fig. 10-6D–E), projects anterodorsally from the anterior margin of the vomer. The anterior margin of the process is thin and broadly rounded, whereas the medial edge is indented by a shallow, scoop-shaped facet. In life the anterior end of the premaxillary process fit into the lingual slot between the pars palatinum and pars dorsalis on the premaxilla; in turn, the medial facet in the premaxillary process on the vomer received the posteriorly projecting vomerine process from the premaxilla (Estes, 1964). In dorsal view the medial half of the dorsal surface of the vomer is indented by an elongate, shallow trough. Estes (1964:73) suggested this "median channel" held the floor of the nasal capsule, but it is equally probable that anterolateral edge of the parasphenoid overlapped the vomer in this region.

The vomer ventrally bears a single row of teeth that extends in a broadly convex arc parallel to the anterior and lateral margins of the bone. Teeth decrease in size posteriorly and are attached labially along the basal quarter of their height to a narrow, low ridge that becomes concomitantly shallower posteriorly. Except for being less pleurodont and having the crowns slightly less expanded, vomerine teeth otherwise resemble those on the marginal jaws. The two most medial teeth on UALVP 43914 have shallow occlusolingual wear facets (Fig. 10-6C). The only specimen with an intact tooth row, UALVP 43914, has eight loci consisting of two complete and four broken teeth and spaces for two more teeth. Estes (1964) reported nine teeth in vomers available to him.

Palatine (Estes, 1964:fig. 35d–f; here:Fig. 10-6G–I)—None of the palatines listed by Estes (1964) were intact and the same is true for the two specimens available to me. UALVP 43877 (Fig. 10-6G, H) is broken along three margins and preserves 16 intact teeth and the bases for four more teeth. USNM 25871 (Fig. 10-6I, J), the more nearly complete specimen, is broken on all sides and preserves 40 teeth and the broken bases of two more. USNM 25871 is from a larger individual, comparable in size to those represented by the largest figured premaxilla and dentary. Judging by the more nearly complete specimens figured by Estes (1964), UALVP 43877 is from the right side and USNM 25871 is from the left. The bone is a shallow plate, with the inferred lateral and medial edges warped dorsally to produce a broadly convex occlusal surface. Neither specimen is sufficiently intact to show the anteriorly pointed, somewhat oval outline inferred by Estes (1964; see also Estes, 1965:fig. 3), although the size of USNM 25871 corroborates Estes' (1964, 1965) belief that the palatine was substantially larger than the vomer.

Palatine teeth resemble those on the vomer and marginal jaws in being non-pedicellate and some details of crown structure, yet differ in attachment, arrangement, and form.
Teeth are fused at their base to the palatine and are arranged in parallel, broadly concave to nearly straight rows that extend anteromedially to posterolaterally across the bone (Fig. 10-6I, white line). UALVP 43877 and USNM 25871 preserve sections of six and eight tooth rows, respectively. Palatine teeth are stout, labiolingually compressed, and mesiodistally expanded. Within a given tooth row, the long axes of the row and its teeth are not in perfect alignment; instead, teeth are orientated with the anterior end pointing slightly more laterally and the posterior end pointing slightly more medially. In medioanterior or lateroposterior view the crown is slightly wider than the base and there is no constriction or other demarcation between the crown and shaft. On unworn teeth the crown is blunt and bears a low crest extending along the long axis of the crown and slightly offset medioposteriorly from the midline. Teeth become smaller and the crowns more pointed towards the anterior and posterior ends of the plate. USNM 25871 shows that tooth wear is most pronounced laterally on the plate, to the extent that crowns on the lateralmost teeth are ground flat. UALVP 43877 preserves a tooth at the anterolateral corner with a lingual replacement pit in the base (Fig. 10-6H, arrow). This is the first evidence for palatine tooth replacement in Habrosaurus. The lateral position of this replacement pit and increase in tooth wear laterally across the plate suggest that palatine tooth rows are replaced in waves, with new teeth forming lingually and moving peripherally (i.e., lingually) to replace older teeth as the latter are resorbed. This pattern is seen in extant Siren (Fig. 10-1B, arrows) and is considered primitive for urodeles (Regal, 1966).

Atlas (Estes, 1964:fig. 37a; here:Fig. 10-7)—A size series of ten atlantal centra is available. The smallest and largest specimens each are broken laterally, but when complete the largest (UALVP 43881; Fig. 10-7K-O) would have been about three times larger than the smallest (UALVP 40047; unfigured). The centrum is relatively short and broad, ranging in midline length (including odontoid process) from about 2.4 mm to an estimated 6.2 mm (n=10) and intercotylar width from about 3.4 mm to an estimated 11.7

mm (n=10). The ratio of midline length:intercotylar width varies from 0.5–0.8 (n=10) and the centrum tends to become relatively shorter with growth. The paired anterior cotyles lie below the neural canal and are confluent medially with the median odontoid process. In anterior view each anterior cotyle is dorsoventrally depressed, with the lateral end broadly rounded in anterior outline and projecting slightly beyond the lateral wall of the centrum. The odontoid process arises between the anterior cotyles and is a robust projection with a shallowly concave dorsal surface. Evans et al. (1996:88) stated that the odontoid process is absent and the anterior cotyles are confluent with one another in Habrosaurus—this is incorrect. Atlantes previously figured for Habrosaurus (Estes, 1964:fig. 37a; Standhardt, 1986:fig. 32) have an odontoid process, albeit weakly developed, that separates the anterior cotyles. In such specimens (see also Fig. 10-7A–E, I–O) the odontoid process is anteriorly short and broadly convex in dorsal or ventral outline; in anterior view the process is relatively deep and the lower edge extends well below the level of the ventral rim of the anterior cotyles. Specimens now at hand show that these features develop ontogenetically in H. dilatus, although there is considerable variation in the expression of their development. In small atlantes, such as UALVP 43879 (Fig. 10-7F–H), the odontoid process is more prominently developed as an anteriorly elongate and squarish projection, with a truncate leading edge. The process is also shallower and the ventral surface lies just slightly below the level of the ventral rim of the anterior cotyles. The atlas consistently lacks discrete articular facets on the anterior cotyles and odontoid process. Instead, a continuous articular facet extends medially across the anterior face of the left cotyle, wraps around the lateral and anterior faces of the odontoid process, and extends laterally across the right anterior cotyle. The articular surface on the anterior cotyles is flat to shallowly convex and tilted slightly dorsally, whereas on the odontoid process the articular surface is shallowly convex and tilted slightly ventrally. The dorsomedian edge of the odontoid process is indented by a "V"- or "U"-shaped notch that becomes more prominent with growth, but never bisects the articular surface. In the largest specimen (UALVP 43881), the dorsal surface of the notch bears a rectangular bony protuberance (Fig. 10-7K, M) of unknown identity and function.

The posterior cotyle is concave and the inner wall is coated with a thin film of calcified cartilage. In small atlantes the cotyle is circular in posterior outline and shallowly concave, whereas in large atlantes the cotyle is deeper and more oval in outline, with the narrower end produced ventrally. The notochordal pit is closed in all specimens, except in the largest (UALVP 43881; Fig. 10-7N) where a small pit opens in the dorsal quarter of the cotyle. Sagittal breakage through the centrum of this specimen shows that the notochordal pit is closed anteriorly and did not extend into the odontoid process.

A relatively narrow and shallow subcentral keel extends along the ventral midline of the centrum, from the base of the odontoid process to the ventral rim of the posterior cotyle. To either side of the keel, the centrum is penetrated by several subcentral foramina. With growth the subcentral keel becomes relatively deeper and wider and the number of foramina increases, resulting in a perforated ventral surface. A dorsoventrally compressed and laterally narrow flange extends along the ventrolateral edge of the centrum, between the posterior face of the anterior cotyle and the rim of the posterior cotyle. This flange forms the ventral boundary of a fossa along the lateral wall of the centrum. Several pits and foramina penetrate the centrum in this region; the largest foramen opens just in front of the rim of the posterior cotyle. No basapophyses are present.

No atlantes yet reported for Habrosaurus have an intact neural arch, which suggests that the arch is a delicate structure. Five specimens (UALVP 40048, 43879, 43880, 43919, and 43934) at hand preserve the broken base of the arch on one or both sides. Judging by the broken bases, the wall of the neural arch is anteroposteriorly short and mediolaterally thin. The foramen for exit of the first spinal nerve is enclosed by bone. The foramen extends through the anterior part of the base of the neural arch and opens laterally in the posterodorsal surface of the anterior cotyle (Fig. 10-7A). Behind the spinal foramen, a short transverse process projects lateroposteriorly from the base of the wall. The distal end of the process is pointed and shows no evidence of having articulated with a rib. The base of the transverse process gives rise to two struts: one is a laterally narrow flange that extends anteroventrally to below the lateral opening of the spinal foramen, then expands laterally to join with the laterodorsal or lateral edge of the posterior surface of the anterior cotyle; and the second is an indistinct ridge that runs up the lateral surface of the wall of the arch for a short distance before grading into the bone. Compared to extant sirenids, atlantes of H. dilatus more closely resemble those of Siren in having a prominent transverse process and a shorter ridge extending from the transverse process up the wall of the arch, whereas the inferred delicate build of the arch in H.

dilatus is more reminiscent of the condition in Pseudobranchus.

Trunk Vertebra (Estes, 1964:fig. 37c; here:Fig. 10-8A–L)—As with specimens reported by Estes (1964), none of the 19 trunk vertebrae at hand are complete. Estes (1965:fig. 1C) provided a photograph of a trunk vertebra (UCMP 54212) with reconstructed transverse processes and postzygapophyses. Trunk vertebrae at hand range in midventral length from about 4.3 to 13.6 mm (n=13); some specimens available to Estes (1964) were larger still, with centra lengths of 19 mm (Estes, 1964:74). Variation along the trunk series in extant sirenids involves subtle differences in overall build of the centrum, the form of processes and crests, and orientation of the transverse processes (Cope, 1889:pl. 43; Estes, 1964; Naylor, 1978; pers. obs., 1999). As little of this variation is evident in trunk vertebrae at hand for Habrosaurus dilatus, I have not been able to infer the relative position of individual specimens along the trunk series. Estes (1964:77) mentioned, but did not figure, vertebrae with bicipital transverse processes that, by comparison with extant sirenids, probably came from the anteriormost six or so positions along the trunk region. In the few specimens available to me with an intact transverse process the process is unicipitate, indicating that these specimens are from more posterior positions along the trunk region.

In overall build, the trunk vertebrae are robust and blocky elements. The centrum is amphicoelous. Both cotyles are deeply concave and the inner surface is coated with a thin film of calcified cartilage. The notochordal pit is open in some specimens and closed in others, regardless of overall size. Where open, the notochordal pit is moderate in size and lies in the dorsal half of the cotyle. The cotyles are roughly circular in outline, with the posterior cotyle occasionally more oval and having the narrower end directed ventrally. The centrum is excavated on either side of the midline. The subcentral keel is narrow and deep, but does not project below the level of the ventral rim of the cotyles. The ventral edge of the keel is straight, sinuous, or ventrally concave in lateral outline. A shallow groove for blood vessels may extend vertically up the lateral face of the keel to the subcentral foramen. The latter is a large opening at about the midpoint of the centrum, just above and to either side of the base of the subcentral keel. Smaller subcentral foramina may perforate the bone in this region. The paired anterior basapophyses are free of the anterior alar process and are prominently developed as elongate, flat, sword-like structures that arise just dorsoanterior to the major subcentral foramen and extend forward and ventrolaterally to the ventrolateral rim of the anterior cotyle. On the few specimens preserving an intact basapophysis, the anterior end of the process is acute or broadly rounded in outline and projects past the cotylar rim. In anterior view, several small pits open in the anterior face of the centrum: a series of small pits opens in the anterior face of the prezygapophyseal process and, more ventrally, one pit may open between the basapophysis and anterior rim of the cotyle. Estes (1964) suggested these pits were attachment sites for ligaments, presumably associated with subvertebralis muscles.

In specimens with an intact transverse process, the process is unicipitate, moderately elongate, and projects laterally and slightly posteriorly from about the midpoint of the centrum; Estes (1964:fig. 37a) figured a specimen in which the intact transverse process extends slightly ventrally. The distal tip of the transverse process is pointed, lacks a facet for contact with a rib, and lies approximately in line with the lateral edges of the zygapophyses. As in extant sirenids, three alar processes are associated with the transverse process. The largest of these, the anterior alar process, is a triangular-shaped flange in ventral outline that arises along the entire ventroanterior length of the transverse process, then extends anteriorly and narrows laterally to the rim of the anterior cotyle. In the few specimens that preserve a reasonably intact anterior alar process, the outer margin is straight to shallowly concave medially in dorsal or ventral outline; however, the margin is decidingly convex in a specimen figured by Estes (1964:fig. 37c). The posterior alar process is a smaller triangular flange that arises along the basal third to half of the ventroposterior edge of the transverse process and narrows medially as it extends posteriorly to the posterior cotylar rim. The dorsal alar process is an indistinct, low ridge that arises anterodorsally along the proximal half or less of the transverse process, then extends anteriorly and rapidly narrows medially to join with the anterior interzygapophyseal ridge. The latter continues anteriorly and slightly dorsally as a laterally narrow ridge to the base of the prezygapophyseal process. The posterior interzygapophyseal ridge extends posterodorsally, often in a dorsally convex arc, from the base of the dorsal alar process to the base of the postzygapophysis. This complex of interzygapophyseal ridges and the trio of alar processes demarcate two deep fossae in the lateral wall of the vertebra: an elongate fossa anterior to the transverse process and a shorter fossa behind the process. A prominent vertebrarterial canal extends through the base of the transverse process, connecting the two fossae. Just behind the base of the transverse process, a moderate sized spinal foramen (Fig. 10-8I, arrow) opens in the lateral wall of the neural arch.

The neural canal is slightly broader than tall, with the roof forming a broad, dorsally convex arc in anterior view. In dorsal outline the neural arch is slightly longer than wide and shallowly constricted medially. The zygapophyseal processes are stout, slightly longer than wide, broadly rounded distally, and often splayed laterally. The prezygapophyseal facet is generally elliptical in outline, whereas the postzygapophyseal facet tends to be more oval, with the posterior end wider. The pre- and postzygapophyseal facets either lie in the horizontal plane or the former may face slightly dorsomedially and the latter ventrolaterally. The neural crest and paired aliform processes are relatively low and arranged in the characteristic "Y"-shaped pattern: the neural crest is confined to the anterior third to half of the arch and the aliform processes diverge posterolaterally and extend onto the postzygapophseal processes. In lateral profile the neural crest is low and in the shape of a drumlin or triangle, with the apex located more anteriorly. The dorsal edge of the crest is smooth, except in UALVP 43895 where a prominent pit of unknown function opens at the apex. The neural crest narrows and becomes lower posteriorly. Aliform processes increase in height posteriorly and the posterior face of each bears a prominent, posteriorly directed facet for contact with the epaxial musculature. A low, median ridge is variably present between the aliform processes. On some specimens, particularly larger ones, the dorsal surface of the neural arch is roughened or wrinkled in texture.

Caudal Vertebra (Estes, 1964:fig. 37b; here:Fig. 10-8M–R)—The two caudal vertebrae, UALVP 43900 (Fig. 10-8M–O) and 34901 (Fig. 10-8P–R), are about 6.9 mm in midventral length and more nearly complete than the specimen (AMNH 8115) figured by Estes (1964:fig. 37b). Both specimens are similar in size, proportions, and structure to trunk vertebrae described above. The posterior half of the wall of the neural arch is perforated by a spinal foramen (Fig. 10-8M, arrow). Identification of UALVP 43900 and 43901 as caudals is supported by the posteriorly shortened aliform processes and concomitantly elongated neural crest, absence of basapophyses, and presence of a pair of ventroposteriorly directed haemal spines. A large foramen extends transversely through both haemal spines in UALVP 43901, but only through the left haemal spine in UALVP

43900. By comparison with extant Siren, the laterally uncompressed centrum and arch and the presence of distally free haemal spines indicate that both vertebrae are from the anterior part of the caudal series. Both specimens differ from caudals of extant Siren in having the zygapophyseal facets lying horizontally, rather than having the pre- and postzygapophyseal facets facing more medially and laterally, respectively. The relatively longer haemal spines, taller and dorsoposteriorly directed aliform processes, and lower neural crest on UALVP 43901 are consistent with this specimen having occupied a more posterior position along the caudal series than UALVP 43900.

Remarks

Compared to the Judithian species described below, marginal teeth of the type species are more robust and have bulbous crowns with a more prominent wear facet. Vomerine and palatal teeth are similarly robust, have wear facets, and the palatal teeth are arranged in closely spaced, parallel rows to form a crushing pavement. In light of these attributes, Estes' (1964:162) suggestion that H. dilatus favored a durophagous diet, possibly consisting largely of molluscs and hard-bodied arthropods, is a reasonable interpretation.

Specimens listed above confirm the presence of Habrosaurus dilatus in four formations (three Lancian and one Torrejonian) in the North American Western Interior. Other Lancian–Torrejonian records from the Western Interior (Estes, 1976; Standhardt, 1986; Sullivan and Lucas, 1986; Bryant, 1989; Williamson and Lucas, 1993; Lillegraven and Eberle, 1999) are unconfirmed, but the species is probably represented in at least some of the units in question. The youngest verifiable occurrence of H. dilatus is in the middle Paleocene (Torrejonian) Lebo Formation, Montana, and is founded on a fragmentary palatine (USNM 25871) reported here and, possibly, an undescribed skeleton (AMNH 2675) mentioned by Sullivan (1991). I have not been able to substantiate a younger occurrence, in the upper Paleocene (Tiffanian) Fort Union Formation in Park County, Wyoming (Estes, 1981:94), because no voucher specimens were described or figured. H. dilatus is not reliably known from pre-Lancian horizons. Where identifiable to species, specimens from older horizons pertain to the new Judithian species described below.

HABROSAURUS PRODILATUS, sp. nov.

(Figs. 10-3G–J, 10-9)

Holotype—UALVP 43906, incomplete right premaxilla missing distal end of vomerine process and most of pars dorsalis, and preserving three intact teeth, one nearly complete tooth, and broken bases of three teeth (Fig. 10-3G–I, 10-9A, B).

Holotype Horizon and Locality—Middle Campanian (Judithian), Dinosaur Park Formation; Irvine, Alberta, Canada.

Etymology—Latin "pro," = before, combined with Latin, "dilatus," = spread or expanded, specific epithet of the type species; in reference to the earlier age and possible ancestral status of the new congener.

Referred Specimens—All specimens are from the holotype horizon and locality: UALVP 43902–43905, premaxillae; UALVP 43907–43909, dentaries; UALVP 40051, atlantal centrum.

Distribution—Known only from the holotype locality.

Diagnosis—Species of Habrosaurus with marginal teeth differing from those on comparable-sized jaws of H. dilatus as follows: teeth more gracile and about ten percent longer; neck between pedicel and crown less constricted; crowns compressed labiolingually and more chisel-like; crowns more widely spaced; and wear facets, where present, less extensive and restricted to distal tip of crown.

Description

Premaxillae, dentaries, and atlas are all incomplete. Specimens are associated by their characteristic sirenid structure and provenance, while jaws are associated further on the strength of their diagnostic teeth. The nine specimens resemble homologous bones of the type species, except the jaws differ in details of their dentition.

Premaxilla (Fig. 10-9A–E)—The five specimens collectively document most of the structure of the premaxilla, except for the distal part of the pars dorsalis and vomerine process. The two most nearly complete specimens, UALVP 43906 (holotype; Fig. 10-9A, B) and 43904 (Fig. 10-9C–E), resemble referred, Lancian premaxillae of

Habrosaurus dilatus as follows: bone moderately robust in build; labial surface smooth and broadly convex externally; weak scars on medial face of pars palatinum and pars dentalis for sutured contact with opposite premaxilla; pars dorsalis moderately broad and flat, arising near medial edge, extending posterodorsally, and having slot in base of lingual face for receipt of complementary process from vomer; pars palatinum a lingually narrow shelf, becoming narrower lingually; maxillary process weakly developed and lateral end truncate for contact with maxilla; and pars dentalis moderately deep. Judging by the preserved base of the vomerine process on UALVP 43905 (not figured), the process resembled that in H. dilatus. No specimen preserves the elongate groove on the inner face of the pars dorsalis seen in some premaxillae of the type species.

Dentary (Fig. 10-9F–K)—The three dentaries are less nearly complete than those listed above for Habrosaurus dilatus and provide no information about the structure of the bone behind the tooth row. The most nearly complete specimen, UALVP 43907 (Fig. 10-9F, G), is from the left side and preserves about the anterior half of the bone. UALVP 43908 (Fig. 10-9H, I) is the symphyseal end of a right dentary and UALVP 43909 (Fig. 10-9J, K) is a fragment preserving the posterior part of the tooth row and adjacent bone from a large, left dentary. Collectively the three specimens show that the dentary resembles that of the type species in being moderately robust in build and broadly curved labially and in having the occlusal edge straight in lateral profile, ventral edge of bone and Meckelian groove deflected ventroposteriorly, subdental shelf weakly developed anterior to Meckelian groove, and symphysis developed lingually as a thin plate. The narrow groove extending along the labial surface below and parallel to the posterior part of the dorsal edge is not evident in UALVP 43907, but the groove is roofed labially by bone and open anteriorly on UALVP 43909 (Fig. 10-9J, arrow).

Marginal Teeth (Fig. 10-3G–J)—Marginal teeth are known only for the premaxilla and dentary of Habrosaurus prodilatus. Teeth on these bones resemble those in the type species in being moderately pleurodont and non-pedicellate and in having a prominent lingual replacement pit at the base, the shaft lingually broadest at its base and tapering distally, and the crown slightly expanded mesiodistally (cf., Fig. 10-3A–F versus G–J). In lingual view the shaft is relatively narrower and less swollen, with the mesial and distal sides nearly straight to slightly convex and tapering distally to a weakly constricted neck. The crown is labiolingually compressed and resembles a chisel (Fig.

10-3G–I). A low, median crest extends mesiodistally along the apex of the crown and, to either side, the labial and lingual faces of the crown are steeply inclined and flat. The crown is only slightly expanded mesiodistally and crowns on adjacent teeth remain well separated from one another. About half of the intact premaxillary teeth each have a weakly developed wear facet in the form of a shallowly bevelled surface that extends mesiodistally across the tip of the crown (Fig. 10-3J). This wear facet is lacking on the remaining intact premaxillary teeth and the dentary teeth. The premaxillae UALVP 43904 and 43906 each have an intact tooth row with, respectively, six and seven loci. No dentary has an intact tooth row; the specimen with the most nearly complete tooth row, UALVP 43907, preserves the first 11 loci and, by comparison with dentaries of the type species, may be missing no more than the posteriormost six loci.

Atlas (Fig. 10-9L, M)—UALVP 40051 is a dorsoventrally crushed atlantal centrum, about 2.4 mm in midline length and 2.8 mm in intercotylar width. Each anterior cotyle is broader than high in anterior outline, with the articular surface slightly convex and facing anterolaterally and slightly dorsally. The odontoid process is short, wide, and broadly rounded distally in dorsal or ventral outline and deep in anterior view. The articular surface for contact with the skull is continuous across the anterior cotyles and odontoid process. The posterior cotyle is subcircular in posterior outline, deeply excavated, and a notochordal pit opens in the dorsal half of the cotyle. The base of the neural arch is present on the right side and encloses a spinal foramen; the floor of the canal connecting the medial and lateral openings of the spinal foramen is exposed on the left side of the centrum.

Remarks

Because I regard tooth characters as important for differentiating species of Habrosaurus I have chosen the specimen with the best preserved teeth, in this case the premaxilla UALVP 43906, as the holotype for the new species.

Habrosaurus prodilatus currently is known only from the Irvine locality in the Dinosaur Park Formation of southwestern Alberta, where it is represented by a handful of jaws and one atlantal centrum. The lack of additional specimens at the richly fossiliferous Irvine locality and other similarly productive microsites in the same unit further to the west in Dinosaur Provincial Park suggests that H. prodilatus was a rare component of the Judithian salamander assemblage in present day southern Alberta. Although Habrosaurus has been reported (as H. dilatus) in two other Judithian units further to the south, neither record can be attributed with confidence to H. prodilatus. Fragmentary dentaries (AMNH 8477, 8478) reported by Sahni (1972) from the Judith River Formation, Montana, cannot be identified more precisely than Habrosaurus sp. because both specimens lack the diagnostically critical teeth. The record from the "Mesaverde" Formation of Wyoming is presented in a faunal list (Breithaupt, 1985) and is founded on undescribed and unfigured specimens.

RELATIONSHIPS AND EVOLUTIONARY TRENDS WITHIN THE SIRENIDAE

A sister-pair relationship between the Cenozoic genera Siren and Pseudobranchus is supported by an extensive list of apomorphies: marginal teeth lost and replaced by horny beak; pars dorsalis arises from lateral edge of premaxilla and extends lateral to nasal; parasphenoid extends anteriorly between paired vomers and premaxillae; odontoid process on atlas shallow, weakly bifurcate distally, and slightly recurved; skull narrow; maxilla greatly reduced in Siren and absent in Pseudobranchus; vomer and palatine fuse ontogenetically; vomerine teeth arranged in multiple rows; expanded, wing-like anterior alar process on trunk vertebrae; and dorsally expanded neural crest on trunk vertebrae. The first four of these character states are autapomorphic among salamanders to Siren and Pseudobranchus. In retaining the inferred primitive state for each of the characters listed above, Habrosaurus can justifiably be regarded as the sister-taxon to Siren and Pseudobranchus. Although Estes (1964, 1965, 1981) implied that Habrosaurus was ancestral to modern sirenids, a direct ancestor-descendent relationship is unlikely considering the specialized dentition (Naylor, 1978) and continuous articular surface on the atlas (present study) of Habrosaurus. In other morphological respects, Habrosaurus is probably representative of the basal sirenid morphotype.

As the earliest and inferred most basal sirenid, Habrosaurus also provides a minimum date of middle Campanian for the origins of the Sirenidae and more inclusive Salamandroidea. The earliest accepted salamandrid fossils are vertebrae from the late Paleocene of Walbeck, Germany, and Cernay, France (Estes et al., 1967; Estes, 1981;

Milner, 1993). Astibia et al.'s (1990) report of an indeterminate salamandrid genus and species at Laño (late Campanian or early Maastrichtian), Spain, has been challenged by Duffaud and Rage (1999). who contended that salamandrid-like vertebrae and humerus from the locality are not convincingly diagnostic for the family.

Except for having discrete basapophyses, post-atlantal vertebrae of Habrosaurus otherwise have the full complement of processes and crests seen in extant sirenids. While this structural complex suggests that the characteristic vertebromuscular pattern described for extant Siren by Auffenberg (1959) and Naylor (1978) was established by the Late Cretaceous, the narrower anterior and posterior alar processes on the transverse processes and the lower dorsal crests on the neural arch in Habrosaurus imply that the associated muscles were less extensively developed. Inferred more posterior trunk vertebrae of Habrosaurus also resemble those of extant sirenids in having unicipital transverse processes that did not articulate distally with ribs. Given that such processes are commonly associated with elongation of the trunk in aquatic salamanders, Habrosaurus probably further resembled extant sirenids in being aquatic and in having an elongate body. The undescribed Paleocene skeleton of Habrosaurus mentioned by Sullivan (1991) may prove informative for providing additional information about the anatomy of the genus.

Two divergent feeding mechanisms can be postulated for the Sirenidae (Estes, 1964, 1965)—shearing and crushing. While the characteristic crushing dentition of Habrosaurus dilatus implies that the species was specialized for durophagous feeding (Estes, 1964; Naylor, 1978), the older H. prodilatus shows less extreme modifications in this direction and, thus, is instructive for tracing dental evolution in the genus. Two attributes appear to have been important pre-adaptations for developing a crushing dentition: (1) displacement of the jaw-skull joint below the occlusal margin of the dentary, inferred for Habrosaurus from the ventral deflection of the ventral margin of the dentary and area for attachment of the postdentary bones, ensures that the upper and lower jaws meet along their entire lengths at essentially the same time and that equal force is applied along the jaw margins during occlusion (Estes, 1964) and (2) non-pedicellate teeth ensure that the crown remains stable relative to the shaft during biting. Judging by the structure of teeth retained on the coronoid, vomer, and palate in extant sirenids (Means, 1972:fig. 2; here:Fig. 10-1B) and of marginal and palatal teeth in other salamanders, I propose that marginal teeth in sirenids primitively were non-pedicellate, elongate, and pointed monocuspids used to grab and hold prey. Marginal teeth in H. prodilatus are more derived, relative to the inferred, primitive sirenid condition, in that the crown is labiolingually compressed and a crest extends mesiodistally across the apex of the crown. Although these chisel-like teeth seem well adapted for shearing, and probably did so, the presence of faint mesiodistal wear facets across the tips of some crowns indicates that the upper and lower teeth were also beginning to occlude against one another, rather than simply shearing past one another. The more specialized marginal teeth of H. dilatus can be readily derived from the chisel-like teeth of H. prodilatus by expanding the crowns mesiodistally and labiolingually to increase the area of occlusion and by having the teeth become relatively stouter to withstand stresses generated during the crushing bite. Wear facets on teeth of H. dilatus are more extensive, to the extent that the crown may be ground away, and have shifted slightly lingually to lie on the occlusolingual face of the crown. This complex of features implies refinement of the crushing bite and, in turn, suggests a more elaborate pattern of jaw mechanics than demanded by the "gape and suck" strategy regarded by Reilly and Lauder (1992) as typical for aquatic salamanders. Although wear facets in H. dilatus evidently were generated by the upper and lower teeth grinding against one another, I have not seen any striations on wear facets that indicate the relative movement of the upper and lower jaws during occlusion. It is not clear whether wear facets on palatal teeth were generated by contact with teeth on the dentaries, implying considerable movement on the part of the dentaries, or by contact with hard food items. The shearing bite in Siren and Pseudobranchus is attained in a different manner: marginal teeth are lost and replaced by a horny beak with a sharp occlusal edge (Estes, 1964).

The implications of the above observations are three-fold. First, the specialized crushing dentition of Habrosaurus dilatus is derived within the genus from a chisel-like dentition similar to that in H. prodilatus. I regard the latter condition as primitive for the genus, but derived relative to other sirenids. Second, evidence of a rudimentary crushing bite in H. prodilatus implies that the species had already shifted into a more durophagous diet and, thus, documents a transitional stage leading to the attainment of the specialized crushing dentition of H. dilatus. Should an older congener ever be identified, I predict it would have chisel-like marginal teeth used solely for shearing. Third, based on its geological age, geographical range, crown structure, and inferred pattern of occlusion H. prodilatus is a good structural ancestor for, if not directly ancestral to, H. dilatus.

The three sirenid genera also differ in two atlantal characters: the atlas of Habrosaurus is more derived in having a single articular surface across the anterior face of the atlas, whereas the atlas in Siren and Pseudobranchus is more derived in having the odontoid process displaced dorsally, with the lateroanterior edges slightly bifurcate distally and curled lateroventrally. These apomorphies are associated with the atlanto-cranial joint, but I am at a loss to explain the functional advantage of either derived character state.

CONCLUSIONS

The major findings of my study are as follows:

(1) Unequivocal sirenids are limited to North America, with Habrosaurus being the geologically oldest of the three named genera. Habrosaurus has been reported from 15 early Campanian (Aquilan) to upper Paleocene (Tiffanian) units in the Western Interior and one Campanian formation in New Jersey, but the genus is reliably known from just seven middle Campanian (Judithian) to middle Paleocene (Torrejonian) units in the Western Interior.

(2) Habrosaurus is unique among salamanders in having: crowns of marginal and palatal teeth mesiodistally expanded and bearing a mesiodistally aligned crest; wear facets variably developed on crowns of marginal and palatal teeth; and articular surface on atlas for contact with skull continuous across odontoid process and paired anterior cotyles. The genus further differs from the Cenozoic sirenids Siren and Pseudobranchus in numerous cranial and vertebral plesiomorphies and one trunk character state of uncertain polarity.

(3) Two species of Habrosaurus are recognized based on the structure and wear patterns of the marginal teeth. H. dilatus Gilmore is known by premaxillae, maxillae, dentaries, vomers, palatines, atlantes, and trunk and caudal vertebrae from the late Maastrichtian (Lancian) of Saskatchewan, Montana, and Wyoming and middle Paleocene (Torrejonian) of Montana. Ceratobranchials previously referred to the species are not diagnostic for sirenids. H. prodilatus, sp. nov. is known by premaxillae and dentaries from the middle Campanian (Judithian) of Alberta.

(4) Habrosaurus is identified as the most basal sirenid, but dental and atlantal autapomorphies argue against the genus being ancestral to either of the Cenozoic genera. Instead, Siren and Pseudobranchus are postulated to be sister-taxa on the strength of numerous derived character states, including four autapomorphies (marginal teeth lost and replaced with horny beak; pars dorsalis arises laterally on premaxilla and articulates along medial edge of nasal; parasphenoid projects anteriorly between paired vomers and premaxillae; and modified odontoid process). Loss of the pelvic girdle and hindlimbs is also unique among caudates to Siren and Pseudobranchus, but the condition in Habrosaurus remains unknown.

(5) The primitive marginal and palatal dentition in sirenids probably consisted of non-pedicellate, elongate, and monocuspid teeth. The chisel-like marginal teeth with weak wear facets in H. prodilatus and the bulbous, expanded teeth with prominent wear facets in H. dilatus are postulated to be derived and form a transformation series within the family. Most sirenids emphasize a shearing bite, either through the use of chisel-like marginal teeth (H. prodilatus) or by replacing marginal teeth with a horny beak (Siren and Pseudobranchus). H. dilatus is unique among sirenids and unusual among caudates as a whole in having a crushing dentition.

FIGURE 10-1. Skull of Siren lacertina Linnaeus, type species, UALVP 14404; extant, southeastern USA. **A**, skull and mandibles in approximate articulation, in dorsal view; **B**, anterior part of skull, in ventral view, with approximate size and position of rudimentary maxillae indicated by dotted lines and arrow pointing to row of four lingual replacement tooth crowns; **C**, anterior part of skull, in anterodorsal view, highlighting structure and contacts of premaxilla (white outline) and nasal (black outline) on right side of skull (left in figure); **D**, skull and mandibles in approximate articulation, in right lateral view, showing orientation of dentary and ventral displacement of skull-jaw joint below level of occlusal edge of dentary; **E**, right mandible, in labial view; **F**, left dentary, in lingual view. Outlines of maxillae (**B**) based on drawings by Parker (1882:pl.38, figs. 5, 6) for S. lacertina and cleared and stained specimen (UALVP 14486) of S. intermedia; the maxillae are located too far medially in drawings by Carroll and Holmes (1980:fig. 11) and Trueb (1993:fig. 6-11). Figures at different scales: scale bars: top (**B**, **C**), middle (**A**, **B**), and bottom (**E**, **F**) scale bars = 1 mm.

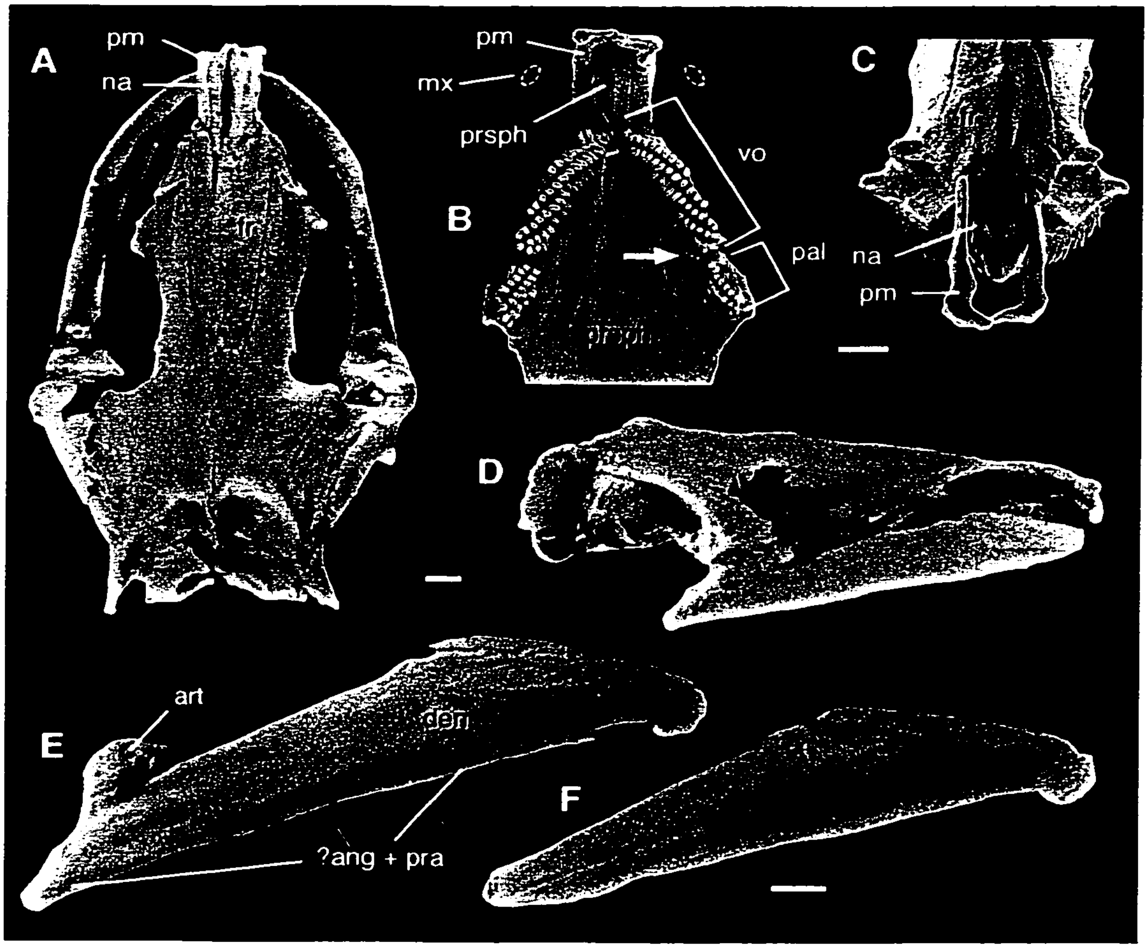
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FIGURE 10-2. Vertebrae of Siren Linnaeus and Pseudobranchus Gray; extant, southeastern USA. Siren lacertina Linnaeus, type species, UALVP 14404 (A–I): **A–D**, atlas, in (**A**) anterior, (**B**) left lateral, (**C**) dorsal, and (**D**) ventral views; **E–G**, mid-trunk vertebra, in (**E**) left lateral, (**F**) dorsal, and (**G**) ventral views; **H**, **I**, anterior caudal vertebra, in (**H**) left lateral and (**I**) dorsal views. Siren intermedia Le Conte, UALVP 40053, middle trunk vertebra (**J–L**), in (**J**) left lateral, (**K**) dorsal, and (**L**) ventral views. Pseudobranchus striatus (Le Conte) (**M–R**): **M–O**, atlas, UALVP 40054, in (**M**) anterior, (**N**) left lateral, and (**O**) dorsal views; **P–R**, trunk vertebra, UALVP 40055, in (**P**) left lateral, (**Q**) dorsal, and (**R**) ventral views. Specimens at different scales: top (**A–I**), middle (**J–L**), and bottom (**M–R**) scale bars = 1 mm.

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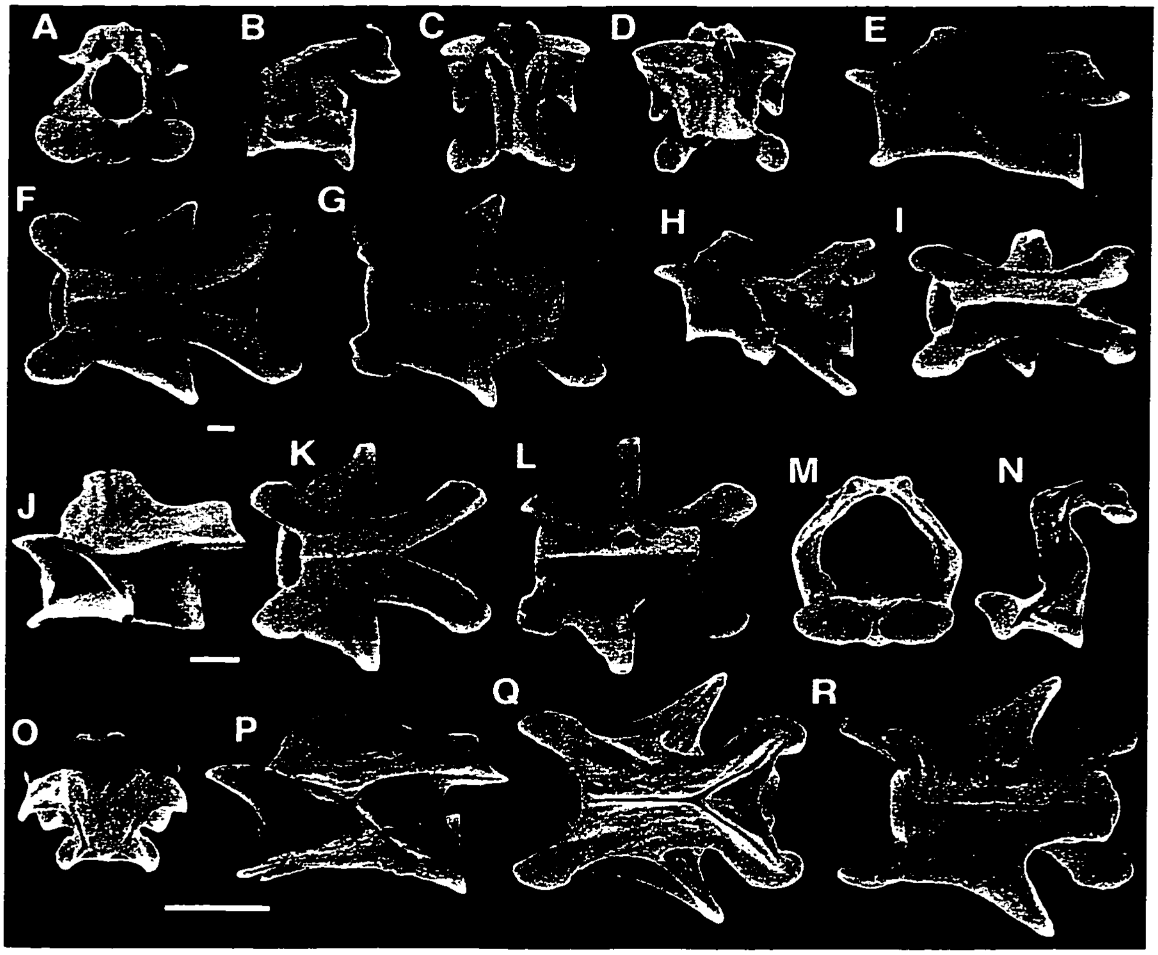

FIGURE 10-3. Marginal teeth of *Habrosaurus* Gilmore; middle Campanian (Judithian) and late Maastrichtian (Lancian), North American Western Interior. *H. dilatus* Gilmore, type species (**A–F**); late Maastrichtian (Lancian), Montana and Wyoming: **A**, UALVP 43865, right dentary, closeup of three representative teeth with moderately worn crowns, in lingual view; **B**, **C**, UALVP 43853, left premaxilla, closeups of tooth with unworn crown in (**B**) oblique (laterolabial and slightly occlusal) and (**C**) oblique (mediolingual and slightly occlusal) views; **D**, UALVP 43918, left dentary, closeup of tooth with shallow lingual wear facet on crown, in lingual view; **E**, UALVP 43867, left dentary, closeup of tooth with crown ground flat, in oblique (lingual and slightly mesio-occlusal) view; **F**, UALVP 43910, left premaxilla, closeup of medial three teeth, with an extensive lingual wear facet, in oblique (laterolingual and occlusal) view. Provenances: UALVP 43865, 43867, 43918, Hell Creek Formation, Montana; UALVP 43910, 43918, Lance Formation, Wyoming. *H. prodilatus*, sp. nov. (**G–J**); Irvine, middle Campanian (Judithian), Dinosaur Park Formation, Alberta: **G–I**, UALVP 43906, holotype right premaxilla, closeups of medial two teeth with unworn crowns in (**G**) lingual, (**H**) occlusal, with labial surface pointing to top of page, and (**I**) oblique (linguomedial and occlusal) views; **J**, UALVP 43902, right premaxilla, closeup of medial three teeth, each with a shallow wear facet across tip of crown, in oblique (occlusomedial and slightly lingual) view. Premaxillary teeth (**B**, **C**, **F**, **G**, **I**, and **J**) inverted, with crown(s) pointing to top of page. Specimens at different scales: top left scale bar (**A**) = 1 mm; top right scale bar (**B–E**) = 0.5 mm; middle right scale bar (**F**) = 1 mm; and bottom scale bar (**G–J**) = 0.5 mm.

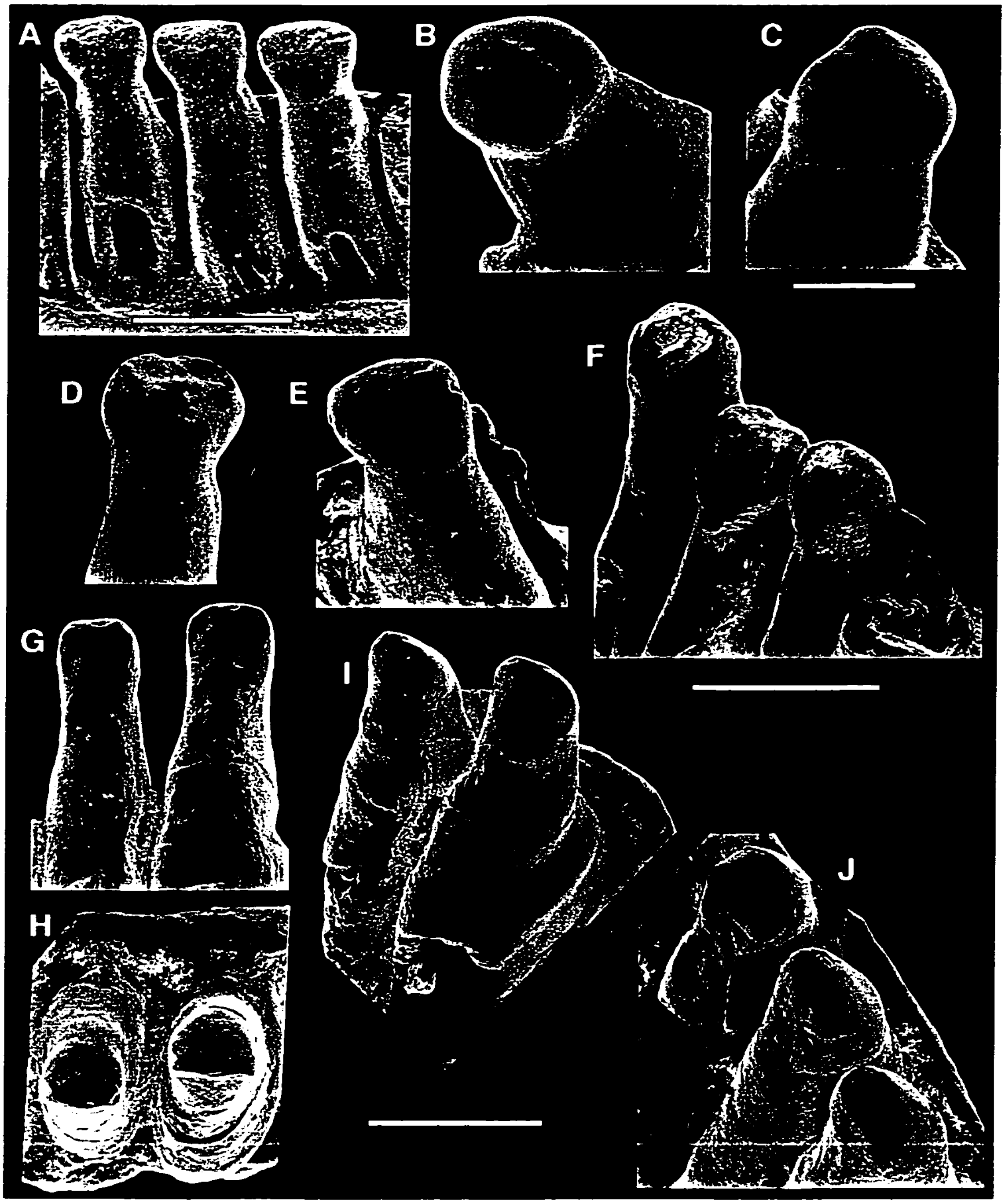
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FIGURE 10-4. Premaxillae and maxilla of Habrosaurus dilatus Gilmore; late Maastrichtian (Lancian), Montana and Wyoming. Premaxillae (A–G): **A–D**, UALVP 43849, incomplete right premaxilla, in (**A**) occlusal, (**B**) dorsal, (**C**) lingual, and (**D**) lateral and slightly lingual views; **E**, **F**, UALVP 43854, incomplete left premaxilla, in (**E**) dorsal and (**F**) lateral and slightly anterodorsal views; **G**, UALVP 43910, incomplete left premaxilla, in occlusal view. Maxilla (**H–J**): UALVP 43855, incomplete right maxilla lacking posterior end, in (**H**) labial and slightly anterior, (**I**) lingual, and (**J**) occlusal views. Provenances: UALVP 43849, 43854, 43855, Hell Creek Formation, Montana; UALVP 43910, Lance Formation, Wyoming. Specimens at same scale: scale bar = 1 mm.

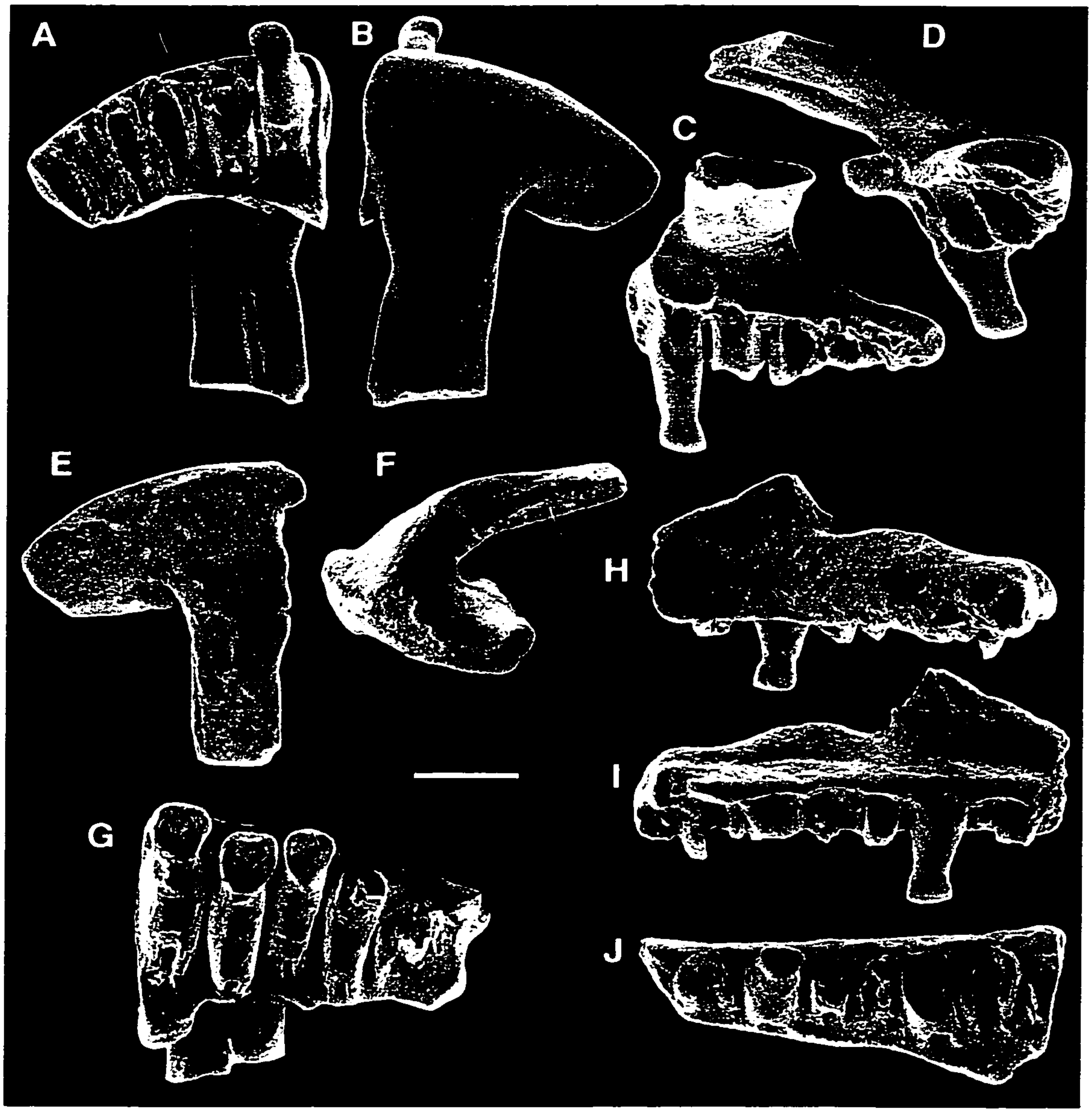
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FIGURE 10-5. Dentaries of Habrosaurus dilatus Gilmore; late Maastrichtian (Lancian), Montana and Wyoming. **A**, **B**, UALVP 43918, incomplete left dentary, in (**A**) labial and (**B**) lingual views; **C**, UALVP 43917, incomplete left dentary, in labial view, with hair extending through canal roofed labially by bone; **D**, **E**, UALVP 43859, incomplete right dentary, in (**D**) labial and (**E**) lingual views; **F**, **G**, UALVP 43865, incomplete right dentary, (**F**) in lingual view, with arrows pointing to in situ replacement tooth crowns at second and seventh preserved loci, and (**G**) closeup of more posterior replacement tooth crown in oblique (postero-occlusal and slightly lingual) view; **H**–**J**, UALVP 43867, incomplete right dentary, in (**H**) labial, (**I**) lingual and slightly ventral, and (**J**) occlusal views. Provenances: UALVP 43859, 43865, 43867, Hell Creek Formation, Montana; UALVP 43917, 43918, Lance Formation, Wyoming. Figures at different scales: bottom center scale bar (**A**–**F**, **H**–**I**) = 1 mm; bottom right scale bar (**G**) = 0.5 mm.

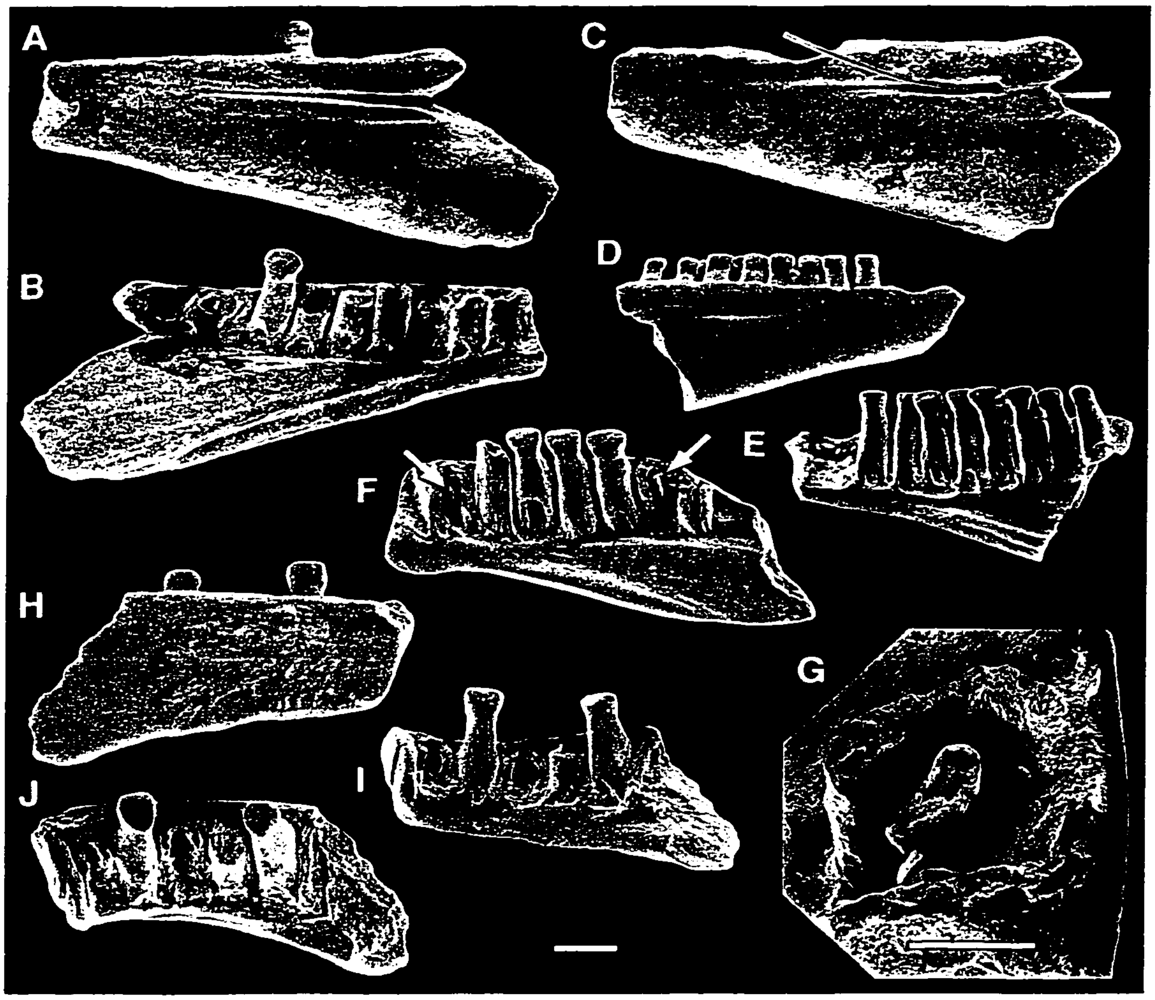
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FIGURE 10-6. Vomers and palatines of Habrosaurus dilatus Gilmore; late Maastrichtian (Lancian) and middle Paleocene (Torrejonian), Montana and Wyoming. Vomers (**A–F**): **A–C**, UALVP 43914, nearly complete right vomer, in (**A**) occlusal and (**B**) dorsal views and (**C**) closeup of medial two teeth in oblique (linguolateral and slightly occlusal) view; **D–F**, UALVP 43876, incomplete left vomer, in (**D**) occlusal, (**E**) medioanterior and slightly ventral, (**F**) lateral and slightly anterior and ventral views. Palatines (**G–J**): **G**, **H**, UALVP 43877, incomplete right palatine, in (**G**) occlusal and (**H**) lateroanterior views, with arrow pointing to lingual replacement pit in base of tooth; **I**, **J**, USNM 25871, incomplete left palatine, in (**I**) occlusal view, with white line tracing path of a tooth row, and (**J**) anterior and slightly occlusal view. Provenances: UALVP 43876, 43877, Hell Creek Formation (Lancian), Montana; UALVP 43914, Lance Formation (Lancian), Wyoming; USNM 25871, Lebo Formation (Torrejonian), Montana. Figures at different scales: middle left scale bar (**C**) = 0.5 mm; bottom left (**A**, **B**, **D–H**) and right (**I**, **J**) scale bars = 1 mm.

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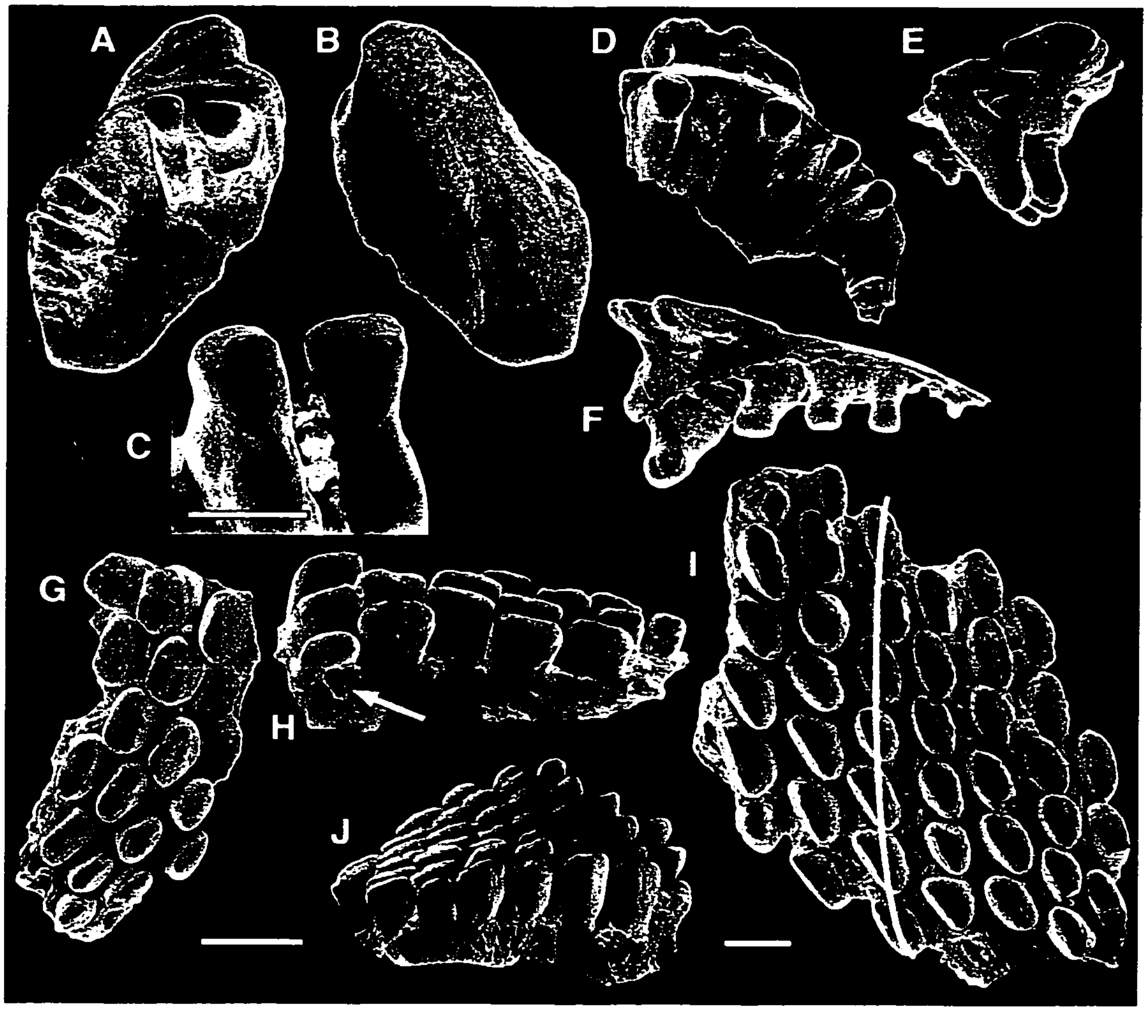

FIGURE 10-7. Atlantes of Habrosaurus dilatus Gilmore; Bug Creek Anthills, late Maastrichtian (Lancian), Hell Creek Formation, Montana. **A–E**, UALVP 43880, centrum preserving base of arch on both sides, in (**A**) dorsal view, with hair extending through spinal foramen on right side, and in (**B**) ventral, (**C**) anterior, (**D**) posterior, and (**E**) left lateral views; **F–H**, UALVP 43879, centrum preserving base of arch on both sides, in (**F**) dorsal, (**G**) ventral, and (**H**) anterior views; **I**, **J**, UALVP 40048, centrum preserving base of arch on both sides, in (**I**) dorsal and (**J**) ventral views; **K–T**, UALVP 43881, centrum missing much of right side of bone including anterior right cotyle, in (**K**) dorsal, (**L**) ventral, (**M**) anterior, (**N**) posterior, and (**O**) left lateral views. Specimens at same scale: scale bar = 1 mm.


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FIGURE 10-8. Trunk and caudal vertebrae of Habrosaurus dilatus Gilmore; late Maastrichtian (Lancian), Montana and Wyoming. Trunk vertebrae (**A–L**): **A–E**, UALVP 43893, in (**A**) left lateral, (**B**) dorsal, (**C**) ventral, (**D**) anterior, and (**E**) posterior views; **F–H**, UALVP 43891, trunk vertebra, in (**F**) right lateral, (**G**) dorsal, and (**H**) ventral views; **I**, **J**, UALVP 43886, trunk vertebra, in (**I**) right lateral and (**J**) ventral views; **K**, **L**, UALVP 43895, in (**K**) anterior and (**L**) dorsal views. Caudal vertebrae (**M–R**): **M–O**, UALVP 43900, in (**M**) right lateral, (**N**) dorsal, and (**O**) ventral views; **P–R**, UALVP 43901, in (**P**) left lateral, (**Q**) right lateral; and (**R**) ventral views. Provenances: UALVP 43886, 43891, 43893, 43900, Hell Creek Formation, Montana; UALVP 43895, 43901, Lance Formation, Wyoming. Arrows (**I**, **M**) point to spinal nerve foramen. Specimens at same scale: scale bar = 1 mm.

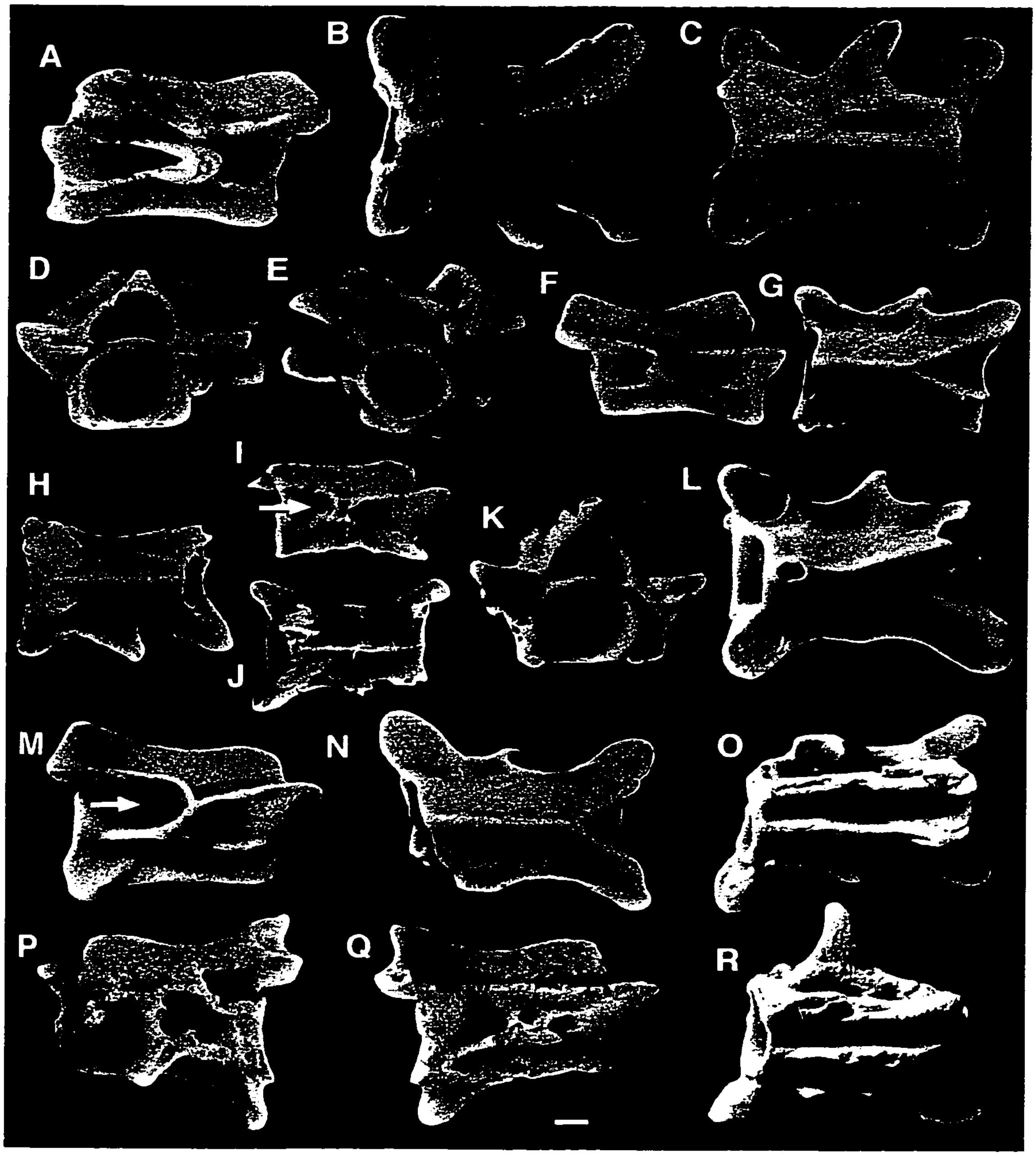
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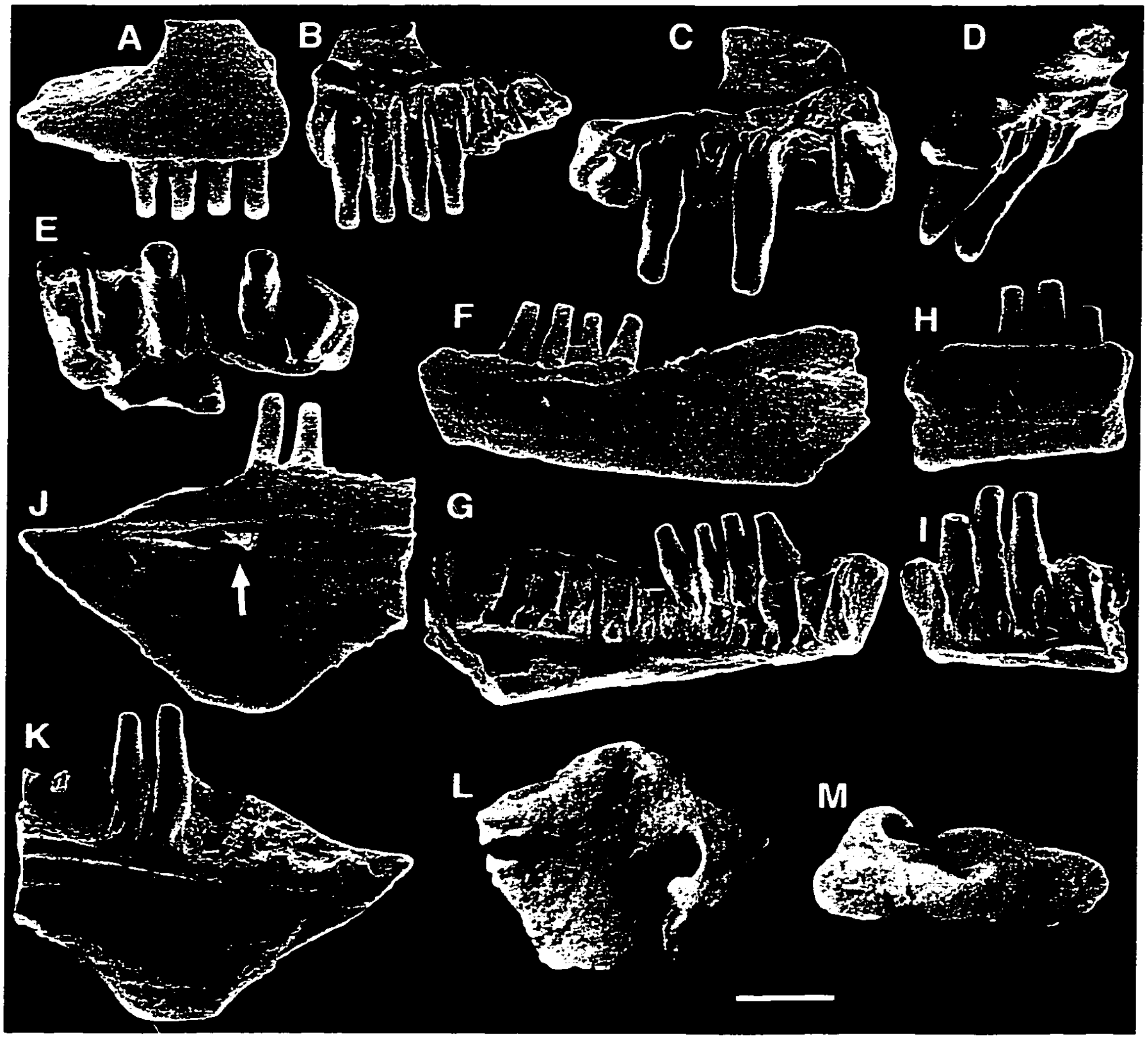
FIGURE 10-9. Premaxillae, dentaries, and atlas of Habrosaurus prodilatus, sp. nov; Irvine, middle Campanian (Judithian), Dinosaur Park Formation, Alberta. Premaxillae (A–E): **A–B**, UALVP 43906, holotype, incomplete right premaxilla, in (**A**) labial and (**B**) lingual views; **C–E**, UALVP 43904, incomplete left premaxilla, in (**C**) lingual, (**D**) lateral, and (**E**) occlusal views. Dentaries (**F–K**): **F**, **G**, UALVP 43907, incomplete left dentary, in (**F**) labial and (**G**) lingual views; **H**, **I**, UALVP 43908, anterior end of right dentary, in (**H**) labial and (**I**) lingual views; **J**, **K**, UALVP 43909, fragmentary left dentary, in (**J**) labial view, with arrow pointing to anterior opening of labially enclosed canal, and (**K**) lingual views. Atlantal centrum (**L**, **M**): UALVP 40051, in (**L**) anterior and (**M**) dorsal views. Specimens at same scale: scale bar = 1 mm.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CHAPTER 11 — NEW VERTEBRAE AND TAXA OF BATRACHOSAUROIDID AND SCAPHERPETONTID SALAMANDERS FROM THE CAMPANIAN AND MAASTRICHTIAN OF THE NORTH AMERICAN WESTERN INTERIOR

INTRODUCTION

The Batrachosauroididae Auffenberg and Scapherpetontidae Auffenberg and Goin are Early Cretaceous to Tertiary, paedomorphic salamanders that superficially resemble one another, but are not closely related (e.g., Estes, 1969a, 1981; Naylor, 1983; Duellman and Trueb, 1986). Among living salamanders, batrachosauroidids and scapherpetontids are probably most comparable to proteids in overall form and lifestyle. Batrachosauroidids and scapherpetontids are well represented in North America, particularly in the Campanian and Maastrichtian of the Western Interior where four monotypic genera have been recognized: the batrachosauroidids Opisthotriton Auffenberg and Prodesmodon Estes, and the scapherpetontids Scapherpeton Cope and Lisserpeton Estes (e.g., Cope, 1876a; Auffenberg and Goin, 1959; Auffenberg, 1961; Estes, 1964, 1965, 1969a, 1981; Naylor, 1979, 1981:table 1). The holotype of each genus is a distinctive trunk vertebra and additional vertebrae from various positions along the column have been referred with a fair degree of confidence to each taxon (e.g., Auffenberg, 1961; Estes, 1964, 1965, 1969a, 1981; Naylor, 1979). Cranial and appendicular elements have also been described for each taxon (e.g., Auffenberg, 1961; Estes, 1964, 1965, 1969a, 1981; Naylor, 1979), but generally with less confidence owing to the difficulty of associating isolated elements from different parts of the skeleton.

Our understanding of these genera relies largely on descriptive accounts published from the late 1950s to early 1980s on Cretaceous and Paleocene specimens (e.g., Auffenberg and Goin, 1959; Auffenberg, 1961; Estes, 1964, 1965, 1969a, 1975, 1976; 1981; Naylor, 1979, 1981:table 1). Since then new fossils, characters, and taxa have been identified, both in North America and elsewhere (e.g., Nessov, 1981; Sullivan, 1991; Evans and Milner, 1996; Denton and O'Neill, 1998), and the four previously recognized genera need to be reconsidered in light of these discoveries. The purposes of this chapter are two-fold. First, to identify, diagnose, and describe batrachosauroidid and scapherpetontid taxa from the Campanian and Maastrichtian of the North American Western Interior. In addition to the four previously named monotypic genera, I recognize four new taxa: two new batrachosauroidid genera and species; a new scapherpetontid genus and species; and a new species of the scapherpetontid Piceoerpeton Meszoely. The existence of two of these new taxa was first hinted at by Naylor (1983) on the strength of a single atlas for each. Second, I review the fossil record for both families and comment on relationships within each.

My focus throughout this chapter is on vertebrae because these are diagnostic at the familial and generic level and isolated examples can be associated with confidence. In my opinion, many previous associations of vertebral and cranial remains are not well established and deserve to be critically evaluated. This task will require larger samples of cranial specimens than are at my disposal. I follow Estes (1981) in allying batrachosauroidids and proteids within the Proteoidea (Cope) and in allying scapherpetontids with ambystomatids, dicamptodontids (i.e., dicamptodontines + Rhyacotrition) within the Ambystomatoidea Noble.

SYSTEMATIC PALEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order CAUDATA Scopoli, 1777
Crown-order URODELA Dumèril, 1806
Suborder PROTEOIDEA (Cope, 1889) (sensu Estes, 1981)
Family BATRACHOSAUROIDIDAE Auffenberg, 1958

Remarks—The Batrachosauroididae are known by isolated elements and skeletons from the early Campanian to Pliocene of North America and the Berriasian, Campanian, and late Paleocene–middle Eocene of western Europe (e.g., Estes, 1981; Naylor, 1981:table 1; Milner, 1993a; Cifelli et al., 1999; Evans and McGowan, unpublished). Records from the Turonian and Coniacian of Middle Asia (Nessov, 1981, 1988, 1997) are unproven (see below). Atlantes are diagnostic for the family in the following combination of characters: odontoid process reduced to an anteriorly short, horizontal shelf or ridge that spans between the medial edges of the anterior cotyles and lacks articular surfaces for contact with skull; anterior cotyles subcircular or slightly compressed laterally in anterior outline; articular surface of anterior cotyles deeply concave; thick layer of calcified cartilage coating inner walls of the posterior cotyle; and neural arch moderate in height and robust in construction. Contrary to Estes' (1981:29) revised familial diagnosis, the odontoid process is present on batrachosauroidid atlantes, but the process is reduced markedly in anterior length and thickness compared to the primitive caudate condition. Where known, post-atlantal vertebrae are characteristic in being amphicoelous or opisthocoelous and in having the cotyles at least partially infilled with a thick layer of calcified cartilage, the subcentral keel thin and moderately deep, the transverse processes bicipitate (at least anteriorly), the neural crest a low ridge, and the neural spine low, moderately elongate posteriorly, forked on more posterior vertebrae, and typically finished distally in bone. Trunk vertebrae lack spinal foramina. Denton and O'Neill's (1998) report of spinal foramina in caudals of Parrisia is not convincing (see their figure 7B), but these foramina are evident in a caudal referred below to Opisthotriton. Vertebral characters useful for differentiating among batrachosauroidid genera include those that describe the relative position of the odontoid process, outline and relative size of the anterior cotyles, position of the posterior cotyle relative to the anterior cotyles, presence or absence of the notochordal pit, form and structure of the neural arch roof, and structure of the postzygapophyses on the atlas and the structure of the centrum, neural arch, and associated crests and processes on the trunk vertebrae.

Six previously named genera may confidently be included in the Batrachosauroididae: the type genus Batrachosauroides Taylor and Hesse, early Eocene–middle Miocene, southern and western USA; Opisthotriton Auffenberg, early Campanian–late Palaeocene and Prodesmodon Estes, middle Campanian–late Maastrichtian, both North American Western Interior; Peratosauroides Naylor, Pliocene, California; Parrisia Denton and O'Neill, Campanian, New Jersey; and Palaeoproteus Herre, late Paleocene–middle Eocene, France and Germany (e.g., Herre, 1935; Taylor and Hesse, 1943; Auffenberg, 1961; Estes, 1964, 1969a, 1975, 1976, 1981; Estes et al., 1967; Naylor, 1979, 1981:table 1; Denton and O'Neill, 1998). Below I present revised diagnoses and expanded descriptions for Opisthotriton and Prodesmodon, and name two new monotypic genera, one represented by a unique atlas from the late Maastrichtian of

Wyoming and the second represented by distinctive atlantes and a trunk vertebra from the early Campanian of Alberta. Other reported occurrences for the family are discussed in the second part of this chapter.

Genus OPISTHOTRITON Auffenberg, 1961

Type Species—Opisthotriton kayi Auffenberg; early Campanian–late Paleocene (Aquilan–Tiffanian), North American Western Interior.

Distribution—As for the type species.

Diagnosis—As for the type and only recognized species (see "Remarks," below).

Remarks—Opisthotriton has been reported from numerous localities of early Campanian to late Paleocene and, possibly, early Eocene age in the Western Interior (e.g., Estes, 1981; Naylor, 1981) and two species have formally been named. The type species O. kayi was named on a characteristic trunk vertebra (Auffenberg, 1961) from the late Maastrichtian of Wyoming. Abundant Campanian–Paleocene vertebral, limb, and skull elements and two incomplete upper Paleocene skeletons also have been referred to the species (e.g., Auffenberg, 1961; Estes, 1964, 1969a, 1975, 1976, 1981; Naylor, 1979, 1981). Other undescribed skeletons (late Paleocene, Alberta) in the collection of the UALVP have tentatively been referred to the type species (Naylor, 1981)—one of these, UALVP 16274 (Fig. 11-1), is the most nearly complete skeleton known for the genus. A second congener, O. gidleyi Sullivan, was named on a skull from the middle Paleocene (Torrejonian) Lebo Formation, Montana, and held to differ from O. kayi "in having a vertical quadrate and teeth extending posteriorly on the dentary" (Sullivan, 1991:294). The taxonomic validity of these characters is questionable. More importantly, judging from Sullivan's published description and drawing (1991:294–295, fig. 3), the holotype skull and only specimen of O. gidleyi is so incomplete and crushed that it cannot meaningfully be compared to any referred cranial material of O. kayi: the quadrates appear to be largely absent, crushing of the skull has almost certainly distorted the position of what remains of these bones, and the posterior extent of the dentary tooth row cannot be determined with confidence. I thus regard the name O. gidleyi as a nomen dubium. Isolated elements of a "small species of Opisthotriton" mentioned by Parris and Grandstaff (1989:35A) from the Campanian of New Jersey have more recently been described by Denton and O'Neill (1998) as pertaining to the monotypic batrachosauroidid Parrisia.

Vertebral resemblances initially argued for placing Opisthotriton first in the Salamandridae (Auffenberg, 1961) and then in the Plethodontididae (Estes, 1964; Wake, 1966). Membership in the Batrachosauroididae now is widely accepted based on a suite of cranial and vertebral characters (Estes, 1969a, 1975, 1981; Naylor, 1979, 1981; Duellman and Trueb, 1986).

OPISTHOTRITON KAYI Auffenberg, 1961

(Figs. 11-1 to 11-4)

Opisthotriton gidleyi Sullivan, 1991:294–296, fig.3.

Holotype—CMNH 6488, nearly complete middle trunk vertebra lacking right postzygapophysis and distal end of neural spine (Auffenberg, 1961:fig.1)

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Lance Formation; unrecorded locality in type area of formation, Niobrara County, Wyoming, USA.

Referred Specimens—Deadhorse Coulee Member, Milk River Formation, MR-9, Alberta: UALVP 40068, "morph II" atlas; Dinosaur Park Formation, Irvine, Alberta: UALVP 12096, 40067, "morph II" atlantes; Hell Creek Formation, Bug Creek Anthills, Montana: UALVP 40056–40061, "morph I" atlantes; UALVP 40062, lot of eight "morph I" morph" atlantes; UALVP 40063, 40064, "morph II" atlantes; UALVP 40065, lot of four "morph II" atlantes; UALVP 40069, 40070, 40072, 40073, trunk vertebrae; UALVP 40074, caudal vertebra; Lance Formation, Bushy Tailed Blowout, Wyoming: UALVP 40066, USNM 482351, "morph II" atlantes; UALVP 40071, trunk vertebra.

Except for UALVP 12096, none of the specimens listed above previously have been referred to Opisthotriton kayi. Other diagnostic, referred specimens include isolated vertebrae and skull elements from Lancian-Torrejonian horizons in Wyoming and Montana and skeletons from the Tiffanian of Alberta, Montana, and Wyoming (see "Remarks, below).

Distribution—Campanian to Paleocene, North American Western Interior: early Campanian (Aquilan): Deadhorse Coulee Member, Milk River Formation, Alberta;

middle Campanian (Judithian): Dinosaur Park Formation, Alberta; late Maastrichtian (Lancian): Hell Creek Formation, Montana, and Lance Formation, Wyoming; middle Paleocene (Torrejonian): Tongue River and Lebo formations, Montana; late Paleocene (Tiffanian): Fort Union Formation, Wyoming, and Paskapoo and Porcupine Hills formations, Alberta.

Revised Diagnosis—Species of batrachosauroidid unique among batrachosauroidids for which trunk vertebrae are known in having subcentral keel on more anterior trunk vertebrae deep, extending well below ventral rim of cotyles. Most closely resembles Parrisia and differs from other taxa in having trunk vertebrae weakly opisthocoelous, with anterior cotyle almost completely infilled with calcified cartilage, anterior face flattened, and depression for notochordal pit typically present, but differs further from Parrisia and resembles other taxa in having anterior and posterior cotyles approximately in line and neural spine(s) finished in cartilage. Differs further from Batrachosauroides, Peratosauroides, and Palaeoproteus, and resembles Parrisia, Prodesmodon, and Verdigriserpeton in having prominent posterior basapophyses on trunk vertebrae; differs further from first two taxa and resembles others in having transverse processes not strongly divergent. Two atlantal morphs recognized, both differing from atlantes of other batrachosauroidids as follows: from Palaeoproteus in having postzygapophyses not extending past posterior edge of neural arch; from Parrisia in lacking protuberances above anterior cotyles; from Prodesmodon in lacking bony ball on anterior end of neural crest; from Batrachosauroides and Peratosauroides in having neural canal larger relative to size of anterior cotyles; from Peratosauroides, Esteserpeton, and Verdigriserpeton in having posterior cotyle typically in line with anterior cotyles; from Peratosauroides and Esteserpeton in having neural crest narrowing posteriorly; from Esteserpeton in having neural crest relatively taller and narrower; and from Verdigriserpeton in having more robust neural arch and in lacking paired anterior projections on anterior end of neural arch.

Description

Vertebrae of Opisthotriton have previously been described from both isolated specimens (Auffenberg, 1961; Estes, 1964, 1969a, 1976, 1981; Naylor, 1979, 1981) and articulated, incomplete vertebral columns (Estes, 1976). My descriptions below focus on isolated, well-preserved uppermost Cretaceous atlantes, trunk vertebrae, and a caudal that provide new information about these elements. Although not described here, the Paleocene skeleton UALVP 16274 (Fig. 11-1) preserves a nearly complete vertebral column that is useful for associating and identifying the relative position of isolated vertebrae. Where appropriate, reference is made to this informative skeleton.

Atlas (Figs. 11-1 to 11-3)—The centrum is relatively short and broad, ranging in midline length from about 1.4–3.7 mm and intercotylar width from about 2.7–7.4 mm. The paired anterior cotyles are deeply concave, subcircular in anterior outline, and extend up about the ventral two-fifths to one-half of the neural arch. The anterior cotyles are vertical, with the lateral margins projecting slightly posteriorly. The odontoid process arises at about the level of the midpoint of the anterior cotyles or slightly below. The process is a shallow, horizontal shelf, with a flat or shallowly concave dorsal surface, and varies from an indistinct ridge or bar to an anteriorly short process with a convex or truncate anterior margin. In some specimens exhibiting the latter condition, the leading face of the odontoid process bears a small median facet. No other articular surfaces are evident on the odontoid process, suggesting minimal contact anteriorly with the skull.

The posterior cotyle is subcircular in outline and deeply concave. A prominent layer of calcified cartilage covers the anterior part of the inner walls and extends posteriorly along the roof of the cotyle. The ventral margin of the cotyle lies approximately in line with or slightly below the ventral edges of the anterior cotyles and the dorsal margin of the posterior cotyle is well dorsal to the level of the odontoid process. The ventral face of the centrum may be perforated by one or more foramina of various sizes. No subcentral keel or basapophyses are present. An indistinct ridge may extend along the ventrolateral edge of the centrum, from the posterior surface of the anterior cotyle to the rim of the posterior cotyle. More dorsally, the lateral wall of the centrum is perforated by several foramina of various sizes. The spinal foramen extends transversely through the base of the wall of the neural arch and opens externally in the posterior face of the anterior cotyle. A short lateral projection may be developed behind the external opening for the spinal foramen.

The neural canal is a laterally compressed oval, with the ventral part pinched between the paired anterior cotyles. The neural arch is moderately tall, relatively robust in build, and dorsally bears a prominent, ridge-like neural crest that tapers posteriorly and is paralleled on either side by a posteriorly elongate trough. In lateral aspect, the anterior end of the neural crest typically projects slightly in front of the anterior edge of the wall of the arch. The postzygapophyseal processes are moderate in size and relatively short. The pedicel of the process is offset from the arch by a constricted base and projects ventrolaterally. The postzygapophyseal facet is oval in outline, with the broader end directed posteriorly, and the articular face is flattened to shallowly concave.

Campanian and Maastrichtian specimens at hand can be divided into two distinctive morphs, which I call informally call "morph I" and "morph II." Although these morphs have not previously been recognized, examples of both have been referred to Opisthotriton by previous workers. For example, Estes (1976:fig. 4A, B) figured a morph I atlas from the Tongue River Formation and Naylor (1979:fig. 5D–F) figured a morph II atlas from the Dinosaur Park Formation. A size series of morph I atlantes is available from the Bug Creek Anthills (Fig. 11-2). Morph II atlantes are less common in collections of the UALVP; nevertheless, a putative size series can be assembled with specimens from Aquilan, Judithian, and Lancian localities (Fig. 11-3). Morph I atlantes differ from morph II atlantes as follows: largest specimens are about 30 percent larger in intercotylar width; notochordal pit open (versus pit closed); neural arch more elongate posteriorly, with length of roof of neural arch in the horizontal plane about twice that of centrum (versus arch about one and a half times as long as centrum); roof of neural arch more tapered posteriorly; anterior part of neural crest relatively wider and lower on large atlantes, with leading edge variably notched (versus crest relatively narrower and inflated dorsally on large atlantes and leading edge lacks notch); neural crest grades into roof of arch at about level of postzygapophyseal processes (versus crest extends posteriorly almost to posterior end of arch); and dorsal surface of neural arch to either side of crest indented by a narrow, deep groove (versus a broad, shallow trough). Morph I atlantes also tend to have a more deeply forked neural spine and relatively more gracile postzygapophyseal processes, but these differences are not consistent. Estes (1975, 1976, 1981) stated that the odontoid tended to be most pronounced in some Paleocene atlantes of Opisthotriton. Samples available to me confirm that the odontoid process is variably developed, but this variation occurs in both morphs, regardless of absolute size or geological age of specimens.

Trunk Vertebrae (Fig. 11-1, 11-4)—The pair of skeletons described by Estes (1975) and the undescribed skeleton UALVP 16274 indicate that vertebral structure varies posteriorly in a predictable manner along the trunk series in Opisthotriton kayi as follows: anterior cotyle on first trunk vertebra better ossified than in subsequent vertebrae; subcentral keel indistinct on first trunk vertebra, becoming successively deeper and then shallower along remainder of series; posterior basapophyses indistinct on first trunk vertebra and present on subsequent vertebrae, being elongate on more anterior vertebrae and shorter on more posterior vertebrae; transverse processes shorten, become stouter, and change from bicipitate to unicipitate; anterior alar process on transverse process changes from narrow, indistinct ridge to triangular flange; neural crest and spine low on first trunk vertebra, both become higher along more anterior part of series, then lower again on more posterior vertebrae; neural spine changes from single to divergently forked; pterygopophyseal processes absent on first trunk vertebra (contra Estes, 1964), present on second to about tenth vertebra, absent more posteriorly.

Trunk characters are most pronounced on vertebrae from about the second to tenth positions along the series. The best preserved and largest specimen at hand from this region is UALVP 40071 (Fig. 11-4A–E): the specimen lacks the distal ends of the transverse processes on both sides, the distal part of the left basapophysis, the leading edge of the subcentral keel, and the distal tip of the left neural spine. The centrum is about 6.6 mm long. The anterior cotyle is subcircular in outline and is almost fully infilled with a thick layer of calcified cartilage that protrudes anteriorly to form a thick, rounded rim around the anterior margin of the cotyle. The anterior face of the calcified cartilage is slightly concave and bears an open pit in the center. The posterior cotyle is larger and slightly compressed laterally in outline, deeply concave internally, and the walls in the anterior half are coated with a thinner, but still prominent, layer of calcified cartilage. The subcentral keel is a thin, plate-like structure that extends between the anterior and posterior cotyles and projects well below the level of the cotyles. When intact, the ventral edge of the keel would have been essentially straight; Estes (1964) noted that the ventral edge of the keel may also be convex, concave, or sinuous. Two tiny subcentral foramina are present to either side of the keel. The posterior basapophysis is a robust prong that arises from about the midpoint of the centrum to extend posteroventrally and project slightly laterally away from the centrum. The distal part of the basapophysis is connected to the centrum via a thick web of bone; the tip of the basapophysis is approximately in line with the rim of the posterior cotyle posteriorly and with the edge of the subcentral keel ventrally. A shallow ridge, presumably for muscular attachment, extends along the lateral face of the basapophysis. The preserved bases of the transverse processes indicate that these were bicipitate when intact, with the dorsal and ventral processes appressed to one another. The lower process gives rise anteriorly and posteriorly to a small, triangular alar process, each of which extends horizontally to the adjacent wall of the centrum. A narrow vertebrarterial canal passes through the base of the transverse process. The anterior entrance to this canal is divided into two foramina on both sides and, on the left side, a foramen in the ventral base of the posterior alar process appears to open dorsoanteriorly into the canal.

The neural canal is narrow and low in anterior view. The neural arch is elongate and constricted medially midway along its length in dorsal view and, in lateral aspect, rises towards the posterior end. The pre- and postzygapophyseal processes are moderately elongate and splay outwards at about a 30° angle. The prezygapophyseal facet is squarish in outline, with the leading edge tilted dorsally and the articular face shallowly convex. The postzygapophyseal facet is more nearly elliptical, the lateral edge is tilted ventrally, and the articular face is shallowly concave. A low and dorsally convex ridge—termed the "'pterygopophyseal-like' structures" by Estes (1964:83)—extends along the dorsal surface of the postzygapophyseal process, becomes higher and broader distally, and terminates in a blunt end near the lateroposterior corner of the postzygapophyseal process. The neural crest is a low, but prominent blade that rises posterodorsally at about 30° from the horizontal. Although broken distally on the right side, the neural spine clearly terminated in two blunt and weakly bifurcate prongs, suggesting that UALVP 40071 occupied a more posterior position along the anterior part of the trunk series. The ventral face of the neural spine bears two deep, elongate facets that are separated by a median keel.

Two vertebrae at hand came from more anterior positions along the trunk series. UALVP 40069 (Fig. 11-4F–I) is nearly complete and can be identified as a first trunk vertebra based on the following combination of features: blocky build; centrum relatively short; subcentral keel low, an indistinct ridge posteriorly, and swollen, but flattened anteriorly; posterior basapophyses short, indistinct ridges; transverse processes short; and neural crest nearly horizontal. The anterior cotyle is infilled with calcified cartilage and retains only a shallow depression in the center of the anterior face. UALVP 40069 differs further from more posterior vertebrae in having the prezygapophyseal processes more massive than the postzygapophyseal processes and the leading edge of the neural crest is swollen, with a flattened face that tilts backwards. Although lacking the posterior part of the neural arch, UALVP 40070 (Fig. 11-4J) appears to be from an intermediate position along the anterior part of the column based on features that are intermediate between those of UALVP 40069 and 40071: centrum moderately elongate; subcentral keel a shallow plate; posterior basapophyses moderately developed; and calcified cartilage in anterior cotyle indented by a shallow pit. UALVP 40070 is notable for preserving intact transverse processes on the right side: these are elongate and weakly bicipitate, with the dorsal and ventral processes connected to one another by a thin web of bone, and the distal end of each is finished in a concave facet for articulation with the complementary rib head.

The remaining two figured trunk vertebrae are from the middle or posterior part of the series, as evidenced by such features as the shallower subcentral keel, more closely appressed bicipital transverse processes, enlarged anterior alar process, and flatter neural arch bearing a lower neural crest and more divergent, pointed neural spines. In the better preserved specimen, UALVP 40072 (Fig. 11-4K, L), the alar process can be seen to be a triangular plate that extends laterally along most of length of the transverse process, the posterior basapophysis is greatly reduced in size relative to UALVP 40071 and remains appressed along its entire length to the centrum, and the anterior end of the subcentral keel projects slightly below the level of the ventral rim of the anterior cotyle. In UALVP 40073 (Fig. 11-4M) the neural crest is reduced further to a low ridge, the neural spines project posteriorly at a lower angle, and the subcentral keel does not extend below the level of either cotyle; these features imply that this vertebra occupied an even more posterior position along the column.

Caudal Vertebra (Fig. 11-4N-R)—Caudal vertebrae have only been reported once before for Opisthotriton: Estes (1976:fig. 4G, H) figured an anterior and posterior caudal, respectively, from the middle Palaeocene Tongue River Formation, but did not describe either specimen. UALVP 40074 compares favorably with the specimen (PU 17039e) figured by Estes (1976:fig. 4G) and similarly can be identified as an anterior caudal based the following combination of features: centrum and neural arch laterally compressed; basapophyses absent; preserved bases of haemal arch present; base of reduced and evidently unicipital transverse present on left side, with remnants of associated struts preserved on both sides. The pre- and postzygapophyses appear to be smaller and more steeply angled on UALVP 40074, suggesting a more posterior position along the caudal series than PU 17039e. UALVP 40074 preserves a nearly complete neural arch. The neural crest is moderately high, blade-like, and extends posterodorsally at a more pronounced angle, compared to inferred posterior trunk vertebrae described above, and terminates in a bluntly pointed neural spine. On the posterior part of the neural arch, to either side of the crest, is developed a deep groove that deepens anteriorly to end in one (right) or two (left) deep pits that penetrate the bone slightly behind the level of the base of the transverse process. A small opening is present in the posterior half of the wall of the neural arch on both sides; a hair can be pushed through the opening in the right side into the neural canal (Fig. 11-4N), demonstrating that this opening is a foramen, not a blind pit or the posterior opening of the vertebrarterial canal. Based on its position, this opening is interpreted as a spinal foramen. UALVP 40074 can provisionally be referred to Opisthotriton, rather than Prodesmodon, based on its larger size, incomplete infilling of the anterior cotyle with calcified cartilage, and higher neural arch.

Remarks

Auffenberg (1961) founded the type species Opisthotriton kayi on a small collection of trunk vertebrae (including the holotype specimen), two incomplete atlantes, a maxilla, and the anterior end of a dentary from the type area of the Lance Formation in Wyoming. Estes (1964) provided an expanded diagnosis and description for the species based on a larger collection of better preserved atlantes, trunk vertebrae, premaxillae, maxillae, dentaries, vomers, and a pterygopalatine from the Lance Formation and transferred the maxilla that Auffenberg (1961) had described to Scapherpeton tectum. Subsequent publications documented new occurrences and provided further information on these and other bones of the species (e.g., Estes, 1969a, 1975, 1976, 1981; Estes et al., 1969a; Naylor, 1979, 1981). The two incomplete skeletons reported by Estes (1969a, 1975, 1981) from the late Paleocene (Tiffanian) of Wyoming have been important for supporting Estes' (1964, 1976, 1981) associations of isolated elements.

Several authors have noted minor variation in the structure of referred atlantes (Estes, 1975, 1976, 1981) and vomers (Naylor, 1981) of Opisthotriton kayi. Yet aside from Naylor's (1981:10) suggestion that subtle differences among vomers may indicate the presence of two congeners in the earliest Paleocene of Montana, previous associations of isolated elements and skeletons of O. kayi have not been seriously questioned. Isolated atlantes reported above indicate that differences in these elements are more pronounced than was previously believed. Two morphs are identified that differ in absolute size, the presence or absence of the notochordal pit, and the form and structure of the neural arch. Size series available for each morph demonstrate that these differences are not ontogenetic. The two morphs exhibit an interesting stratigraphic distribution: both morphs are known from Lancian–Tiffanian localities, while morph II atlantes are also known from older Judithian and Aquilan localities. Given that the Judithian and Aquilan records are based on just two and one specimens, respectively, the lack of morph I atlantes in collections from these horizons may well be a sampling artifact. Although the degree of difference between the two morphs is consistent with each belonging to different species or genera, three factors prevent retaining one morph in O. kayi and transferring the second to another taxon. First, neither atlantal morph can be associated with more confidence than the other to the holotype trunk vertebra of O. kayi. Second, samples available to me of isolated, referred trunk vertebrae of O. kayi do not reveal the presence of two distinctive morphs that potentially could be associated with either of the atlantal morphs. Third, both atlantal morphs are present in Palaeocene skeletons having trunk vertebrae that appear all but identical to the holotype trunk vertebra of O. kayi: the atlantal morph I occurs a described skeleton (PU 14643; see Estes, 1975:fig. 2C) and the atlantal morph II occurs in an undescribed skeleton (UALVP 16274; here:Fig. 11-1). Until these matters can be satisfactorily addressed, I conservatively retain both atlantal morphs within O. kayi.

Opisthotriton has been recorded from over 20 formations in the North American Western Interior (e.g., Estes, 1981; Naylor, 1981). Specimens available to me and published accounts indicate that the genus, as currently understood and accepted here, is reliably known from the following nine units: early Campanian (Aquilan) Deadhorse Coulee Member in the Milk River Formation and middle Campanian (Judithian) Dinosaur

Park Formation, both in Alberta (Fox, 1976; Naylor, 1979:fig. 5D–F), the late Maastrichtian (Lancian) Hell Creek Formation of Montana and Lance Formation of Wyoming (Auffenberg, 1961; Estes, 1964, 1969a, 1981; Estes et al., 1969; Breithaupt, 1982; L. Bryant, 1989), the middle Paleocene (Torrejonian) Tongue River Formation (Estes, 1976) and Lebo Formation (Sullivan, 1991), both in Montana, and the upper Paleocene (Tiffanian) Fort Union Formation, Wyoming (Estes, 1969a, 1975, 1981), and Paskapoo and Porcupine Hills formations, Alberta (Naylor, 1981; pers. obs., 1999). Other reported occurrences await verification. The genus has been reported in brief descriptive accounts and faunal lists for a further 15 formations: early Campanian (Aquilan) Wahweap Formation, Utah (Eaton et al., 1999:table 4); middle Campanian (Judithian) Foremost Formation (Peng, 1997:appendix II) and Oldman Formation (D. B. Brinkman, 1990:table 2; Peng, 1997:appendix II), Alberta, Judith River Formation, Montana (Sahni, 1972; Fiorillo, 1989), and "Mesaverde" Formation (sensu Lillegraven and McKenna, 1986), Wyoming (Breithaupt, 1985); late Campanian–early Maastrichtian (Edmontonian) St. Mary River Formation, Alberta (Langston, 1975, 1976; Fox, 1976), and Fruitland Formation, New Mexico (Armstrong-Zielger, 1978, 1980); late Maastrichtian (Lancian) Scollard Formation, Alberta (Naylor, 1981:table 1), Frenchman Formation, Saskatchewan (Fox, 1989; Tokaryk, 1997), and Laramie Formation, Colorado (Carpenter, 1979); lower and upper Paleocene parts (Puercan and Tiffanian in age, respectively) of the Ravenscrag Formation, Saskatchewan (Naylor, 1981:table 1); lower Paleocene (Puercan) Tullock Formation, Montana (Van Valen and Sloan, 1965:table 1; L. Bryant, 1989); middle Paleocene part (Torrejonian) of the Tonillo Formation, Texas (Standhardt, 1986); and lower Eocene (Clarkforkian) Polecat Bench and Willwood formations, Wyoming (Krause, 1980:table 1; Naylor, 1981).

Genus PRODESMODON Estes, 1964

Cuttysarkus Estes, 1964:139–140.

Type Species—Prodesmodon copei Estes, 1964; middle Campanian–late Maastrichtian (Judithian–Lancian), North American Western Interior.

Distribution—As for the type and only known species.

Diagnosis—As for the type species.

PRODESMODON COPEI Estes, 1964

(Figs. 11-5, 11-6)

Cuttysarkus mcnallyi Estes, 1964:139–140.

Holotype—UCMP 55783, trunk vertebra missing distal ends of prezygapophyses and entire postzygapophyses on both sides, posterior part of neural arch, and distal end of right transverse process (Estes, 1964:fig. 42f, g).

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Lance Formation; UCMP V-5620, Niobrara County, Wyoming, USA.

Referred Specimens—"Mesaverde" Formation, Wyoming: UCM 55840, trunk vertebra; Hell Creek Formation, Bug Creek Anthills: UCM 43504, UALVP 40075 atlantes; MCZ 3652a, 3652b, UCM 43328, trunk vertebrae; Lance Formation, Bushy Tailed Blowout: UALVP 12095, atlas; UALVP 40076, trunk vertebra; UALVP 40077, 40078, lots of five and three trunk vertebrae, respectively. This list does not include atlantes and trunk vertebrae (collections of the UCMP) listed by Estes (1964) from the Lance Formation or the remainder of the trunk vertebrae bulk catalogued as MCZ 3652 and reported by Estes et al. (1969) from the Hell Creek Formation.

Distribution—Campanian and Maastrichtian, North American Western Interior: middle Campanian (Judithian): Dinosaur Park Formation, Alberta, and "Mesaverde" Formation, Wyoming; late Campanian–early Maastrichtian (Edmontonian): Fruitland and Kirtland formations, New Mexico; and late Maastrichtian (Lancian): Hell Creek Formation, Montana, and Lance Formation, Wyoming.

Revised Diagnosis—Species of batrachosauroidid differing from all other batrachosauroidid taxa in four vertebral character states that are autapomorphic within the family: anterior cotyles on atlas compressed laterally and vertically oval in outline; anterior end of atlantal neural crest developed into a massive, swollen ball with convex anterior face; trunk centrum strongly opisthocoelous, with anterior end completely ossified into a bony ball; and vertebrarterial canal in inferred more posterior trunk vertebrae extends anteriorly, opening below base of prezygapophyseal process.

Although not included here, referred dentaries of Prodesmodon are distinctive among known batrachosauroidids in being short, in having the area for attachment of postdentary bones expanded dorsally and ventrally, and in having the teeth non-pedicellate, closely packed, pointed, and recurved.

Description

Vertebrae of Prodesmodon copei are known only as isolated specimens and have previously been described by Estes (1964, 1981) and Naylor (1979).

Atlas (Fig. 11-5)—The three atlantes at hand are nearly complete. The atlas is relatively small, yet blocky and robust in construction. The centrum is short and broad, with the midventral length ranging from about 1.7–2.2 mm and the intercotylar width ranging from about 3.6–4.4. The anterior cotyles are relatively large and deeply concave. In anterior view the cotyles are laterally compressed, elliptical in outline, and extend up about the ventral half of the neural arch. The lateral margin of each cotyle is tilted slightly posteriorly. The odontoid process is level with a point no higher than about one-third of the distance vertically along the long axis of the anterior cotyle. The process is an indistinct, anteriorly short and horizontal ridge, similar to that seen on some referred atlantes of Opisthotriton. No articular surfaces are evident on the odontoid process.

The posterior cotyle is small, especially compared to the anterior cotyles, and is slightly depressed dorsoventrally in posterior outline. The interior of the cotyle is shallowly concave, with the anterior part infilled by calcified cartilage and the notochordal pit closed. In lateral aspect, the ventral edge of the posterior cotyle lies slightly below the level of the ventral edges of the anterior cotyles and the dorsal edge of the posterior cotyle lies slightly above the level of the odontoid process. The ventral surface of the centrum is shallowly excavated in the middle and is perforated by one or more tiny subcentral foramina. A shallow ridge extends from the posterior face of the anterior cotyle, posteriorly along the ventrolateral margin of the centrum. At its posterior end and adjacent to the rim of the posterior cotyle, this ventrolateral ridge expands laterally to form a low, elongate bulge; this bulge evidently is the structure that Estes (1964:91) regarded as the basapophysis. The lateral wall of the centrum is penetrated by several small foramina and the most dorsal of these, the spinal foramina, opens between the base of the wall of the neural arch and the posterior face of the anterior cotyle.

In anterior outline the neural canal is taller than wide and somewhat oval in outline, with the ventral half pinched between the anterior cotyles. The neural arch is robust in build and relatively low. The walls are especially thick, compared to atlantes of comparable size from other salamanders. In dorsal view the roof of the arch is relatively broad and posteriorly short. The anterior two-thirds of the neural crest is swollen into a prominent ball-like structure. The three specimens at hand suggest that the anterior face of the neural crest changes with growth from nearly vertical to more inclined posteriorly. The posterior third of the neural crest continues as a low, thin keel that tapers posteriorly and terminates in a low, blunt neural spine. The neural spine is most prominent on the largest specimen, UALVP 12095. On the two smallest atlantes, UCM 43504 and UALVP 40075, a shallow ridge extends parallel to the neural crest, from the posterolateral base of the swollen ball to the posterior edge of the neural arch. A broad, shallow trough extends parallel to the midline and the lateral margin of the roof is demarcated by a low, moderately broad ridge. The postzygapophyses are short, stocky processes that project ventrally and slightly laterally and posteriorly. The articular facet is somewhat oval in ventral outline, with the broader end directed posteriorly, and the lateral and medial edges are warped downwards, producing a scoop-shaped articular surface.

Trunk Vertebra (Fig. 11-6)—Vertebrae figured here include a first trunk vertebra (Fig. 11-6A–D) and three specimens from more posterior positions—one each from the anterior (Fig. 11-6E, F), middle (Fig. 11-6G–J), and posterior (Fig. 11-6K) parts of the trunk series. The structure of the trunk vertebrae is best illustrated by UCM 43328 (Fig. 11-6E, F) and MCZ 3652a (Fig. 11-6G–J). Subtle differences, similar to those noted above for Opisthotriton, in the form of crests and processes suggest that UCM 43328 and MCZ 3652a are from, respectively, the anterior and middle parts of the trunk series.

MCZ 3652a and UCM 43328 are elongate and moderately delicate in construction. Both vertebrae are moderate in size: the centrum is 4.7 mm long in MCZ 3652a and about 5.2 mm long in UCM 43328. The centrum is deeply excavated ventrally and is strongly opisthocoelous. The anterior condyle is a small, prominent ball, with a minimally constricted base, that extends anteriorly to about the level of the leading edges of the prezygapophyses. MCZ 3652a and UCM 43328 exhibit the usual condition for

Prodesmodon in which the anterior face of the condyle is fully ossified and broadly rounded, but in some specimens the anterior face is indented by a shallow, median pit. The posterior cotyle is similarly small and subcircular in posterior outline. Internally the posterior cotyle is shallowly concave, the anterior part is infilled with calcified cartilage, and the notochordal pit is closed. The subcentral keel on UCM 43328 is broken, but MCZ 3652a preserves an intact subcentral keel that is thin, moderately deep, and runs the entire length of the centrum. In the latter specimen the keel arises from the anterior edge of the centrum and juts forward for short distance, below the base of the anterior condyle. The ventral edge of the keel is shallowly concave and extends posteriorly and slightly ventrally to the ventral edge of the posterior cotyle. MCZ 3652a also preserves intact posterior basapophyses. Each processes arises at about the midpoint of the centrum, extends posteroventrally along the wall of the centrum, and terminates in blunt point that extends slightly past the rim of the posterior cotyle. The proximal part of the basapophyses are more curved and extend further forward on UCM 43328; both features are consistent with this vertebra coming a more anterior position. One or two tiny subcentral foramina open on either side and about midway along the centrum, between the base of the subcentral keel and the medial edge of the basapophysis. No specimen available to me preserves an intact transverse process. Judging by the preserved base of the transverse process on both sides in UCM 43328, the transverse processes are unicipitate and extend posterolaterally; this accords well with the more nearly complete transverse processes on the holotype trunk vertebra (Estes, 1964:fig. 42f, g). On UCM 43328 the anterior alar process is a narrow ridge that extends along the anteroventral edge of the base of the transverse process and anteriorly onto the wall of the centrum, to the base of the prezygapophyseal process. MCZ 3652a preserves most of the anterior part of the anterior alar process on the right side and shows that, as in the holotype (cf., Estes, 1964:fig. 42g versus here:Fig. 11-5F) and other inferred middle trunk vertebrae, the alar process is a broader triangular flange that extends further anteriorly and the anterolateral corner projects slightly forward in a manner reminiscent of the so-called anterior basapophyses on trunk vertebrae of extant sirenids (see Chapter 10). Although not visible in Figure 11-6G, a tiny foramen penetrates the left wall of the neural arch in MCZ 3652a behind the transverse process, in approximately the position occupied by the spinal foramen in some other salamanders. I regard this foramen as an anomaly, because a complementary foramen is absent in the right side of MCZ 3652a and is absent entirely in other referred trunk vertebrae of Prodesmodon available to me.

The pattern of the vertebrarterial canal warrants special mention, because it exhibits unexpected variation. Estes (1964:90) stated that trunk vertebrae of Prodesmodon available to him were typical for caudates in having a short vertebrarterial canal that extends through the base of the transverse process and opens anteriorly and posteriorly through a foramen in a pit adjacent to the base of the process. UCM 43328 and other inferred anterior trunk vertebrae at hand have two small sediment-infilled openings, one in front of and one behind the base of the transverse process, that presumably represent the pits housing the foramina for the vertebrarterial canal. In the inferred middle trunk vertebra MCZ 3652a, however, the pits associated with the transverse processes are free of sediment and are clearly blind. The posterior foramen for the vertebrarterial canal instead lies just below and behind the base of the transverse process. A hair (not figured) inserted into this foramen shows that the vertebrarterial canal extends anteriorly and slightly dorsally through the wall of the neural arch, almost to the anterior end of the wall, and opens through a small, anteriorly facing foramen (arrow in Fig. 11-6G, I) below the base of the prezygapophyseal process, in the junction between the wall of the arch and the leading edge of the anterior alar process. Although the path of the vertebrarterial canal cannot be demonstrated as conclusively in other inferred middle trunk vertebrae or in the posterior trunk vertebra reported below, the configuration of sediment-infilled foramina in these implies that the vertebrarterial canal is similar to that in MCZ 3652a. UCM 43328 is unique among the referred vertebrae at hand in having two small openings in the right wall of the neural arch, below the base of the transverse process; judging by their positions, these two openings may be associated with the vertebrarterial canal.

The neural canal is lower then wide and the roof of the arch is flattened. In lateral view the posterior part of the roof is inclined dorsally at a low angle and extends a short distance past the posterior cotyle. The neural crest extends the length of the neural arch and is best developed midway along its length as a low, thin keel. In dorsal view the neural spine is weakly bifurcate or forked distally. The more steeply inclined neural arch and less prominent and less divergent neural spines on UCM 43328, compared to MCZ 3652a, are consistent with the former vertebra occupying a more anterior position along the trunk series. The pre- and postzygapophyseal processes are elongate, project anterolaterally at a shallow angle form the midline, and the lateral edges of each are titled slightly dorsally. The zygapophyseal articular facets are elliptical in outline and the articular face of each is nearly flat.

The first trunk vertebra has not previously been figured for Prodesmodon. The specimen shown here, MCZ 3652b (Fig. 11-6A–D), lacks the transverse process and zygapophyses on the left side and the distal ends of both basapophyses. This specimen closely resembles the first trunk vertebrae reported above for Opisthotriton kayi (cf., Fig. 11-4F–I), but differs notably as follows: posterior basapophyses more prominent; neural crest relatively shorter anteroposteriorly, but taller; notochordal pit closed in posterior cotyle; anterior cotyle ball-shaped and rounded anteriorly; and transverse process unicipitate. The last three features support the association of MCZ 3652b with the trunk vertebrae described above. Estes (1964:90) stated that the transverse processes were bicipitate and closely appressed, with the ventral one the larger, on an unfigured specimen available to him. Although the transverse process on MCZ 3652b may be broken distally, there is no evidence for the condition reported by Estes (1964). No specimens at hand appear to come from the region immediately behind the first trunk vertebra. Estes (1964:90) identified several such specimens and his published figure of one (UCMP 59510; Estes, 1964:64) shows that the dorsal surface of the postzygapophysis bore a pterypophyseal-like process similar to, but smaller than, those on some anterior trunk vertebrae of Opisthotriton.

UALVP 40076 (Fig. 11-6K) differs from the postcervical vertebrae described above and can be identified as a posterior trunk vertebra based on the following features: centrum relatively short, compared to width across the neural arch; ventral surface of centrum more excavated dorsally; posterior basapophyses less pronounced anteriorly and posteriorly; anterior alar process a broad, triangular flange; and neural crest a low ridge. A less nearly complete vertebra depicted by Estes (1964:fig. 42e) resembles UALVP 40076 and also appears to be from the posterior part of the trunk series.

Remarks

Estes (1964) named the new genus and species Prodesmodon copei on a trunk vertebra from the type area of the Lance Formation and described the taxon based on additional, referred vertebrae, premaxillae, maxillae, dentaries, and a femur from several localities in the formation. Estes (1964) originally interpreted Prodesmodon as a desmognathine plethodontid based on vertebral resemblances. Wake (1966:84–87) concurred and regarded Prodesmodon as "a specialized ... offshoot of a primitive desmognathine stock" (Wake, 1966:85). Estes (1969b) next allied Prodesmodon and Prosiren elinorae Goin and Auffenberg (Albian, Texas) in his new family Prosirenidae based on jaws then referred to each genus. By the mid 1970s, the Prosirenidae also included Ramonellus longispinus Nevo and Estes (Barremian, Israel) and Albanerpeton inexpectatum Estes and Hoffstetter (Miocene, France). Naylor (1979) described a vomer for Prodesmodon and, on the strength of stratigraphical occurrences and morphological evidence, convincingly argued: (1) the holotype and referred vertebrae of Prodesmodon were properly associated, but jaws originally referred to the genus belonged instead to Albanerpeton (then known only by the type species A. inexpectatum) or an Albanerpeton-like taxon; (2) the holotype and referred dentaries of the supposed squamate Cuttysarkus mcnallyi Estes (Edmontonian–Lancian, Western Interior) were instead referrable to Prodesmodon, making the name Cuttysarkus a junior subjective synonym of Prodesmodon (see also Estes et al. [1969] for remarks on the identity of jaws of Cuttysarkus); and (3) vertebral and dentary structure warranted transferring Prodesmodon to the Batrachosauroididae. Naylor's (1979) findings subsequently have not been challenged and P. copei remains the only recognized species in the genus.

Prodesmodon copei is reliably known from isolated atlantes, trunk vertebrae, dentaries, and vomers. Edwards (1976:308) listed, but neither described nor figured, two caudals for the species: UCMP 49509 from the Lance Formation and an unidentified specimen that was bulk catalogued as part of a collection of vertebrae (MCZ 3652) from the Hell Creek Formation. Neither identification can be verified. All vertebrae originally catalogued as MCZ 3652 are from the trunk region, as Estes et al. (1969) originally reported. Although I have not seen UCMP 49509, it is notable that Estes (1964:88) also listed this specimen as a trunk vertebra. No premaxillae or maxillae with diagnostic teeth (i.e., closely spaced, non-pedicellate, pointed, and recurved) have yet been identified, lending credence to Estes' (1981) suggestion that Prodesmodon lacked upper jaws. If correct, this differs from the condition in other well known batrachosauroidids, such as

Opisthotriton, Batrachosauroides, and Palaeoproteus, all which have well-developed upper jaws. Estes (1964) originally described a femur (UCMP 55782; Estes, 1964:fig. 44d, e) for Prodesmodon, then transferred the specimen (Estes, 1981) to Albanerpeton nexuosus. UCMP 55782 differs substantially from albanerpetontid femora and almost certainly belongs to a salamander (see Chapter 6), but at present there is no justification for referring the specimen to Prodesmodon.

Prodesmodon copei is convincingly known from Judithian–Lancian horizons in the Western Interior. Diagnostic vertebrae listed above confirm reports of Prodesmodon in the late Maastrichtian (Lancian) Hell Creek Formation, Montana (Estes et al., 1969; Naylor, 1979; Estes, 1981; L. Bryant, 1989), and Lance Formation, Wyoming (Estes, 1964, 1981; Naylor, 1979), and the middle Campanian (Judithian) "Mesaverde" Formation, Wyoming (Breithaupt, 1985). Occurrences in the first two formations are also supported by isolated, referred dentaries and vomers (Estes, 1964; Naylor, 1979, 1981). A second Judithian occurrence for the genus, in the Dinosaur Park Formation of Alberta, appears to be documented by an undescribed dentary lacking teeth in the collection of the UALVP. Reports of Prodesmodon in the intervening Edmontonian (late Campanian–early Maastrichtian) of the San Juan Basin in New Mexico (Armstrong-Ziegler, 1978, 1980; Naylor, 1979:table 1; Estes, 1981; Hunt and Lucas, 1993:table 1) are substantiated by Armstrong-Ziegler's (1980:13–15) description of referred trunk vertebrae of Prodesmodon and dentaries of "Cuttysarkus" from the Fruitland Formation, plus two undescribed jaws in the collection of the KUVP—a dentary from the Kirtland Formation and a vomer from the Fruitland Formation or Kirtland Formation.

Other published records for Prodesmodon are unsubstantiated. Fox's (1972, 1976) inclusion of Prodesmodon in preliminary faunal lists for the Milk River Formation, Alberta, and Sahni's (1972) description of a referred dentary (AMNH 8479) from the Judith River Formation, Montana, were based on jaws that are now recognized as belonging to albanerpetontids (Naylor, 1979; here:Chapter 6). Fox's (1989) report of Prodesmodon in the Frenchman Formation evidently relied on two uncatalogued dentaries in the collection of the UALVP: one jaw is too fragmentary to be identified with certainty beyond Caudata indet., whereas the second can be referred to Habrosaurus based on its shape and the characteristic enclosed groove along the labial surface. Prodesmodon has been reported in faunal lists for the Maastrichtian (NALMA uncertain) Harbell Formation, Wyoming (Breithaupt, 1985), and the lower Paleocene (Puercan) Tullock Formation (Van Valen and Sloan, 1965), but no diagnostic voucher specimens were listed, described, or figured to support either occurrence. If correct, the reported occurrence in the Tullock Formation would be the only post-Cretaceous record for the genus; it is worth noting, however, that L. Bryant (1989:32) did not identify any Prodesmodon specimens among the extensive series of microvertebrate fossils available to her from that formation.

Despite a temporal record stretching from the Judithian to Lancian, specimens of Prodesmodon are relatively uncommon at localities of this age, suggesting that individuals were not common in salamander assemblages of the day or lived in habitats outside of the depositional areas.

Genus ESTESERPETON, gen. nov.

Type Species—Esteserpeton robustus, sp. nov.; late Maastrichtian (Lancian), Wyoming.

Etymology—"Estes," after Dr. Richard Estes, in recognition of his contributions to the study of North American Cretaceous amphibians; combined with Latin, "erpeton," = creeping animal, a common suffix for caudate generic names.

Distribution—As for the type and only known species.

Diagnosis—As for the type species.

ESTESERPETON ROBUSTUS, sp. nov.
(Fig. 11-7A–F)

Holotype—USNM 482352, nearly complete atlas (Fig. 11-7A–F).

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Lance Formation; unrecorded locality in type area of formation, Niobrara County, Wyoming, USA.

Etymology-Latin, "robustus," = hard or strong, in reference to the robust build of the holotype atlas.

Distribution—Known only from the type locality.

Diagnosis—Species of batrachosauroidid that differs from all other batrachosauroidids in having atlas with neural crest not elaborated anteriorly and rear edge of neural arch roof upturned. Resembles Opisthotriton morph II atlantes and atlantes of Prodesmodon, Verdigriserpeton, and Peratosauroides in having neural arch posteriorly short; further resembles and differs from these as follows: resembles Opisthotriton morph II atlantes and atlantes of Prodesmodon in having notochordal pit closed, but differs from both in having ventral rim of posterior cotyle lying well below level of ventral rim of anterior cotyles, neural crest broadens posteriorly, and postzygapophyseal processes reduced; resembles Verdigriserpeton in having ventral rim of posterior cotyle lying well below level of ventral rim of anterior cotyles, but differs further in larger size, more robust build, in having notochordal pit closed, and in having neural crest lower, broader, and expanded posteriorly; resembles Peratosauroides in having ventral rim of posterior cotyle lying well below level of ventral rim of anterior cotyles and in having neural crest relatively broad and expanded posteriorly, but differs further in having notochordal pit closed, odontoid process reduced to a ridge, neural canal relatively larger and not lying between anterior cotyles, and dorsal surface of neural crest only slightly roughened for attachment of mandibular musculature.

Description

Atlas (Fig. 11-7A-F)—USNM 482352 is a nearly complete atlas that is broken transversely across the junction between the neural arch roof and both walls, but lacks only a small fragment from the right side of the neural arch. The bone is robust and blocky in construction and moderate in size. The centrum is about 2.6 mm long along the ventral midline and about 5.4 mm wide across the cotyles. The anterior cotyles are deeply concave, with the lateral margins tilted slightly posteriorly. In anterior view the cotyles are subcircular in outline and extend dorsally almost to the level of the midpoint of the neural canal. The odontoid process is an anteriorly short, horizontal ridge that extends between the medial edges of the anterior cotyles at about the level of the midpoint of the cotyles. No articular facets are present on the odontoid process. Although the dorsal rim is broken, when intact the posterior cotyle would have been subcircular in posterior outline and, in lateral view, the dorsal margin would have projected well above the level of the odontoid process. The ventral margin of the posterior cotyle lies well below the level of the ventral edges of the anterior cotyles. Internally the posterior cotyle is deeply concave, the notochordal pit is closed, and a patch of calcified cartilage covers the roof and adjacent surfaces. A cluster of four tiny subcentral foramina penetrate the ventral surface of the centrum. A low, broad ridge extends along the ventrolateral margin of the centrum, between the posterior face of the anterior cotyle and the rim of the posterior cotyle. The spinal foramen opens laterally in the junction between the wall of the arch and the posterior surface of the anterior cotyle.

In anterior view the neural canal is taller than wide and orbicular in outline, with the ventral part pinched between the anterior cotyles. In lateral view the neural arch is moderately tall and increases in height posteriorly, rising at about 30° from the horizontal. In dorsal view the roof of the neural arch is relatively broad, tapers minimally, and projects only slightly past the posterior cotyle. The neural crest is a thick, broad ridge, with a shallowly convex and slightly roughened dorsal surface. The crest runs the length of the arch and broadens posteriorly, before terminating in an indistinct neural spine. The posterior lip of the arch is slightly upturned and the posterior face is thick and nearly vertical. To either side of the neural crest, the roof of the arch is broad and slopes gently towards the midline. The postzygapophyses are small, stout processes that are directed ventrally and slightly laterally. The postzygapophyseal facets are broader than long, elliptical in outline, and the articular surface is shallowly convex.

Remarks

USNM 482352 can be identified as a batrachosauroidid atlas on the strength of its diagnostic anterior cotyles and odontoid process. Among known batrachosauroidid atlantes, USNM 482352 most closely resembles referred morph II atlantes of Opisthotriton kayi in size, build, and overall form, but it differs significantly from examples of the latter and atlantes of all other batrachosauroidids in numerous details of the neural arch. The most important of these are: neural arch relatively shorter, broader, and less tapered posteriorly; rear edge of neural arch roof truncate and upturned, with posterior face thickened and nearly vertical; neural crest not elaborated anteriorly, broadens posteriorly, and smooth dorsally; and postzygapophyses reduced. This combination of features is distinctive and at least two—anterior end of neural crest not elaborated and posterior edge of neural arch roof upturned—appear to be unique among batrachosauroidids. I thus regard USNM 482352 as sufficiently distinctive to justify erecting it as the holotype of the new genus and species Esteserpeton robustus.

At present Esteserpeton is known only by the holotype atlas and is restricted to the Lance Formation of Wyoming. Given the similarities between USNM 482352 and certain referred atlantes of Opisthotriton, some previously identified atlantes of Opisthotriton may prove referable to Esteserpeton upon closer examination. Judging by the closed notochordal pit, moderate size, and robust build of USNM 482352, postatlantal vertebrae of Esteserpeton can be predicted to resemble those of Prodesmodon in being opisthocoelous, but differ in being considerably larger and more robust. I have not identified any such trunk vertebrae in collections available to me.

Genus VERDIGRISERPETON, gen. nov.

Type Species—Verdigriserpeton bifurcatus, sp. nov., early Campanian (Aquilan), Alberta.

Etymology—"Verdigris," in reference to the holotype locality in Verdigris Coulee, Alberta; combined with "erpeton," = creeping animal, a common suffix for caudate generic names.

Distribution—As for the type and only known species.

Diagnosis—As for the type species.

VERDIGRISERPETON BIFURCATUS, sp. nov.

(Fig. 11-7G-R)

Holotype—UALVP 16252, incomplete atlas (Fig. 11-7G-L).

Holotype Horizon and Locality—Early Campanian (Aquilan); Deadhorse Coulee Member, Milk River Formation; UALVP MR-20, Verdigris Coulee, Alberta, Canada.

Etymology—Latin, "bifurcatus," = forked, in reference to the paired anterior projections arising off the anterior end of the atlantal neural arch.

Referred Specimens—Deadhorse Coulee Member, Milk River Formation, two localities, Alberta: UALVP MR-9: UALVP 16521, atlas; UALVP MR-6: UALVP 40079, trunk vertebra.

Distribution—Early Campanian (Aquilan), Deadhorse Coulee Member, Milk River Formation, Alberta.

Diagnosis—Species of batrachosauroidid differing from all other batrachosauroidid taxa in having atlas with leading end of neural crest bearing two anterior projections and in having trunk vertebrae with amphicoelous centrum and prominent posterior basapophyses.

Description

Atlas (Fig. 11-7G–O)—Two incomplete specimens are available: the holotype UALVP 16252 (Fig. 11-7G–L) and UALVP 16251 (Fig. 11-7M–O). Both specimens are broken transversely in front of the postzygapophyses and lack the more posterior part of the roof of the neural arch. UALVP 16251 also lacks the lateral part of the right anterior cotyle, whereas UALVP 16251 lacks the anterior end of the neural arch and the dorsal rim of the posterior cotyle. Both specimens are relatively gracile in build and small. The holotype is about 1.6 mm long along the ventral midline of the centrum and, when the right anterior cotyle was intact, the width across the cotyles was probably about 3.4 mm. UALVP 16251 is slightly smaller: the midventral length is about 1.5 mm and the intercotylar width is about 3.1 mm.

The anterior cotyles are deeply concave, subcircular in anterior outline, and extend up the ventral third of the neural arch. The odontoid process lies just above the level of the midpoint of the anterior cotyles. The process is an anteriorly short bar with a truncate leading edge on the holotype, but it is slightly more elongate and has a more convex leading margin on the referred atlas. The posterior cotyle is deflected ventrally: the dorsal rim lies slightly below the level of the odontoid process and the ventral rim lies well below the ventral margin of the anterior cotyles. The posterior cotyle is subcircular in outline. Internally the cotyle is shallowly concave, the anterior part is infilled with calcified cartilage, and the notochordal pit opens in the dorsal half. The ventral surface of the centrum is perforated by a cluster of tiny subcentral foramina. A shallow ridge, which is better developed on UALVP 16251, extends along the ventrolateral margin of the centrum. The spinal foramen opens laterally in the junction between the base of the neural arch and the posterior face of the anterior cotyle.

The neural canal is relatively large and slightly taller than wide in anterior view, with the ventral third pinched between the anterior cotyles. The neural crest is moderately high. In dorsal view the crest is bulbous anteriorly and tapers posteriorly. Anterolaterally the crest bears two short processes that project anteriorly past the anterior cotyles and curve inwards towards the midline; these processes are largely intact on the holotype, but are broken on the referred atlas. On both specimens a deep groove extends along the dorsal midline of the neural crest, between the bases of the anterior projections. The dorsal edge of the crest is horizontal in lateral aspect and it appears unlikely that the more posterior part of the crest, when complete, would have been inclined dorsally. To either side of the crest, the roof of the neural arch slopes away lateroventrally and a weak ridge extends along the lateral margin of the roof.

Trunk Vertebra (Fig. 11-7P-Q)—The sole available specimen, UALVP 40079, is an incomplete middle or posterior trunk vertebra that lacks the posteroventral part of the centrum, most of the transverse process on the right side and all of the process on the left side, and both prezygapophyses. The vertebra is delicate in build, moderately elongate, and small, with an estimated centrum length, when intact, of about 2.3 mm. The centrum is amphicoelous and the notochordal pit remains open. The subcentral keel is low and, judging from their preserved bases, the posterior basapophyses were small, but well developed. Subcentral foramina are present only on the left side. No spinal foramina are present. The neural arch bears a low neural crest and short, moderately divergent neural spines that project dorsally at a low angle. UALVP 40079 most closely resembles middle or posterior trunk vertebrae of Opisthotriton and differs from those of Prodesmodon as follows: centrum constricted medially, but not dorsally; transverse processes bicipitate and, evidently, closely appressed; vertebrarterial canal short and passes through base of transverse process; neural arch low anteriorly, but not depressed; and postzygapophyses (and by implication, prezygapophyses as well) more divergent laterally. UALVP 40079 differs further from middle and posterior trunk vertebrae of both genera in having the notochordal pit broadly open, the inner wall of both cotyles coated with only a modest layer of calcified cartilage, a narrower alar process, and, evidently, the transverse processes directed more nearly laterally.

Remarks

Assignment of the atlantes UALVP 16251 and 16252 to the Batrachosauroididae is supported by the diagnostic structure of the anterior cotyles and odontoid process, whereas the trunk vertebrae UALVP 40079 can be assigned to the family based on the infilling of calcified cartilage in the cotyles and detailed resemblances with trunk vertebrae of Opisthotriton. Differences between the first two specimens in the form of the odontoid process are within the range of variation seen in atlantes of Opisthotriton and Palaeoproteus. In all other preserved features, the two atlantes resemble one another and can be confidently associated on these grounds. The trunk vertebra is associated with the atlantes based on their provenance and similar size and build. The combination of a shallowly infilled anterior cotyle and relatively well-developed posterior basapophyses in the trunk vertebra is unique among those batrachosauroidids for which trunk vertebrae are known, and is an exception to the typical pattern in which the size of the posterior basapophyses increases with the amount of infilling of the anterior cotyle (Naylor, 1981).

Naylor (1983) originally figured and briefly described the atlas UALVP 16252. He concluded "The specimen differs from atlantes of all other known batrachosauroidids to at least the same degree that these differ from each other ... indicating that it probably represents a new genus of the family" (Naylor, 1983:51), yet he declined to formally name a new taxon because UALVP 16252 was the only specimen known to him. Atlantes and characters identified since confirm that UALVP 16252 is distinctive—the anteriorly bifurcate neural crest is unique among known batrachosauroidids, if not all salamanders—and additional vertebrae from the Milk River Formation now can be associated with the original atlas. Formal taxonomic recognition is now appropriate and I name the new genus and species Verdigriserpeton bifurcatus on the diagnostic atlas first reported by Naylor (1983).

Suborder AMBYSTOMATOIDEA Noble, 1931 (sensu Estes, 1981)

Family SCAPHERPETONTIDAE (Auffenberg and Goin, 1959)

Remarks—Scapherpetontids are known by isolated and rare associated elements from the latest Albian/earliest Cenomanian and early Campanian to middle Eocene of

North America (e.g., Auffenberg and Goin, 1959; Estes, 1964, 1965, 1969a, 1981; Naylor and Krause, 1981:table 1; Naylor, 1983). Previous reports (Nessov, 1981, 1988, 1997) of scapherpetontids from the Late Cretaceous of Middle Asia are unsubstantiated (see below) and the family appears to be endemic to North America. Scapherpetontid and batrachosauroidid vertebrae resemble each other in overall form and in certain details (e.g., trunk vertebrae have an elongate neural spine and lack spinal foramina), but vertebrae of scapherpetontids differ from those of batrachosauroidids in the following combination of characters: vertebrae having cotyles less infilled with calcified cartilage and notochordal pit consistently open; atlantes having base of odontoid process placed between medial edges of anterior cotyles, odontoid process generally well-developed and with articular surface spanning across ventral face, anterior cotyles dorsoventrally compressed and articular face typically nearly flat, neural arch tall and directed dorsally or dorsoposteriorly, and neural crest variably finished in cartilage; post-atlantal vertebrae consistently amphicoelous and lack basapophyses; and trunk vertebrae having transverse processes divergently bicipitate along most, if not all, of trunk series and the neural spine hollow, finished distally in cartilage, and consistently single. Differences in the outlines of cotyles on vertebrae, the form of the anterior and posterior cotyles, odontoid process, and neural arch on the atlas, and the form of the subcentral keel, transverse processes, and neural crest and spine on trunk vertebrae are useful for differentiating among scapherpetontid taxa.

Three monotypic scapherpetontid genera have previously been named from North America: Scapherpeton, Lisserpeton, and Piceoerpeton. The first two genera are known from the Campanian to Palaeocene of the Western Interior, whereas the type species of Piceoerpeton ranges from the late Paleocene–early Eocene of the Western Interior and the middle Eocene of the Canadian Arctic (e.g., Estes, 1981; Naylor and Krause, 1981). Naylor (1983) reported on a unique atlas from Bug Creek that he suggested may represent a Lancian species of Piceoerpeton. Below I present revised diagnoses and descriptions for Scapherpeton and Lisserpeton, name a new Lancian species of Piceoerpeton for the atlas reported by Naylor (1983) and additional vertebrae, and erect a new genus and species for distinctive atlantes from Bug Creek and Irvine. Other reported occurrences for the family are discussed in the second part of this chapter.

Genus SCAPHERPETON Cope, 1876a

Hemitrypus Cope, 1876a:358.
Hedronchus Cope, 1876b:259.

Type Species—Scapherpeton tectum Cope, 1876a; early Campanian–late Paleocene (Aquilan–Tiffanian), North American Western Interior.

Distribution—As for the type and only known species.

Diagnosis—As for the type species.

SCAPHERPETON TECTUM Cope, 1876a
(Fig. 11-8)

Scapherpeton laticolle Cope, 1876a:356–357; Auffenberg and Goin, 1959:fig. 1B, C.
Scapherpeton excisum Cope, 1876a:357.
Scapherpeton favosum Cope, 1876a:357–358.
Hemitrypus jordanianus Cope, 1876a:358–359; Auffenberg and Goin, 1959:fig. 1, D.
Hedronchus sternbergi Cope, 1876b:259.

Holotype—AMNH 5682, incomplete anterior trunk vertebra lacking distal ends of transverse processes on both sides, right prezygapophysis, left postzygapophysis, and distal end of neural spine (Auffenberg and Goin, 1959:fig.1F–H)

Holotype Horizon and Locality—Middle Campanian (Judithian); Judith River Formation; unrecorded locality in type area of formation, Chouteau County, Montana, USA.

Referred Specimens—Deadhorse Coulee Member, Milk River Formation, MR-9, Alberta: UALVP 40153, 40154, atlantes; Dinosaur Park Formation, Irvine, Alberta: UALVP 40080–40091, atlantes; UALVP 40110, trunk vertebra; Hell Creek Formation, Bug Creek Anthills, Montana: UALVP 40092–40104, atlantes; UALVP 40109, trunk vertebra; Lance Formation, Bushy Tailed Blowout, Wyoming: UALVP 40105–40108, trunk vertebrae.

None of the specimens listed above previously have been reported for the species.

Additional diagnostic atlantes and trunk vertebrae have been reported from Judithian–Torrejonian horizons elsewhere in the Western Interior (see "Remarks, below).

Distribution—Campanian to Paleocene, North American Western Interior: early Campanian (Aquilan): Deadhorse Coulee Member, Milk River Formation, Alberta; middle Campanian (Judithian): Dinosaur Park Formation, Alberta, Judith River Formation, Montana; late Maastrichtian (Lancian): Hell Creek Formation, Montana, and Lance Formation, Wyoming; middle Paleocene (Torrejonian): Tongue River Formation, Montana; late Paleocene (Tiffanian): Fort Union Formation, Wyoming, and Paskapoo and Porcupine Hills formations, Alberta.

Revised Diagnosis—Species of scapherpetontid differing from all other members of the family in having atlas with odontoid process that is scoop-shaped in dorsal or ventral outline and with trough extending along dorsal surface of process. Atlantal centrum differs further from other genera in having anterior cotyles more variably compressed dorsoventrally, typically to a lesser degree, and posterior cotyle typically slightly compressed laterally; from Piceoerpeton, but resembles Lisserpeton and Irvinetriton, in having articular surface of anterior cotyles nearly flat and odontoid process anteriorly elongate, with articular surface ventrally for contact with skull; from Piceoerpeton and Irvinetriton, but resembles Lisserpeton, in having base of odontoid process constricted and ventral edge of posterior cotyle in approximately the same horizontal plane as ventral edge of anterior cotyle. Atlantal neural arch differs from that of Lisserpeton and Piceoerpeton (arch unknown for Irvinetriton) in being relatively more elongate and more delicate, inclined posteriorly with distal end extending past level of posterior cotyle, and dorsal surface completely finished in bone; atlantal neural spine (unknown for Piceoerpeton and Irvinetriton) differs from Lisserpeton in being paired. Trunk vertebrae differ from those of Lisserpeton and Piceoerpeton (trunk vertebrae unknown for Irvinetriton) in having cotyles more compressed laterally, ranging from oval to teardrop shaped, and shallower due to anterior infilling by calcified cartilage, subcentral keel extending below level of cotyles, subcentral keel on some vertebrae having ventral edge notched and lateral face indented by prominent vertical groove, bicipitate transverse processes less divergent, dorsal transverse process consistently arising below level of dorsolateral edge of neural arch roof, neural crest relatively lower and extending posteriorly only onto base of neural spine, and zygapophyseal processes less divergent laterally. Trunk vertebrae differ further from Lisserpeton and resemble Piceoerpeton in lacking deep fossa to either side of ventral midline; from Piceoerpeton and resemble Lisserpeton in having subcentral keel narrower; and resemble Piceoerpeton and differ from large vertebrae of Lisserpeton in lacking zygapophyseal ridge.

Description

Vertebrae of Scapherpeton tectum previously have been described and figured by Auffenberg and Goin (1959) and Estes (1964, 1969a, 1981).

Atlas (Fig. 11-8A–II)—Two size series of referred atlantes are available, one each from Bug Creek Anthills (Fig. 11-8A–R) and Irvine (Fig. 11-8S–II). Specimens range in centrum length from about 1.6 to 8.8 mm and intercotylar width from about 2.0 to 11.7 mm. Most of these specimens are centra that preserve only the base of the wall of the neural arch on one or both sides. UALVP 40104 (Fig. 11-8M–R) is a nearly complete atlas that lacks only the right postzygapophysis and is the most nearly complete atlas known for Scapherpeton tectum. My description of the atlas focuses on this specimen.

The centrum of UALVP 40104 is massive, compared to the more delicate neural arch. The centrum in this specimen is moderately broad and elongate. The anterior cotyles are subcircular and are slightly compressed dorsoventrally. On some other specimens at hand, including the best preserved atlas (UALVP 40091; Fig. 11-8DD) from Irvine, the anterior cotyles are more compressed dorsoventrally and are more distinctly oval in outline. The articular surface on the anterior cotyles varies from nearly flat to shallowly concave from side to side. In UALVP 40104 the lateral edge of each cotyle projects lateroposteriorly at a pronounced angle. On some other specimens the cotyles extend more nearly laterally. The odontoid process on UALVP 40104 resembles a scoop: the process is moderately elongate, slightly broader than long, the base is weakly constricted, and the leading edge is shallowly convex in dorsal or ventral view. A shallow, broad trough extends along the dorsal surface and the ventral surface is convex from side to side. In lateral aspect the process is thickest at its base and shallows anteriorly to a blunt distal tip. Minor variation is seen among the 24 figured atlantes in the proportions and outline of the odontoid process, but the process maintains its characteristic scoop-like form. On all specimens the ventral surface of the process is covered by a broad articular surface, the margins of which may wrap around onto the lateral and anterior edges of the process. This articular surface is separate from those on the anterior cotyles.

The posterior cotyle on UALVP 40104 is slightly compressed laterally in posterior outline. Internally the cotyle is shallowly concave, the walls are lined with a moderately thick layer of calcified cartilage, and a modest-sized notochordal pit opens slightly dorsal to the midpoint. The ventral margin of the posterior and anterior cotyles are in approximately the same horizontal plane. The ventral surface of the centrum is essentially flat and is perforated by three subcentral foramina located in the posterior third of the centrum. On some other atlantes, such as UALVP 40091 (Fig. 11-8II), the ventral surface of the centrum is shallowly concave. An indistinct ridge extends along the ventrolateral edge of the centrum, between the margins of the anterior and posterior cotyles. The lateral wall of the centrum is indented by an elongate, deep fossa. More anteriorly, a relatively large spinal foramina opens in the posterior face of the anterior cotyle at the junction with the base of the neural arch wall.

The neural canal in UALVP 40104 is taller than wide and somewhat triangular in anterior and, especially, posterior outline. The neural arch is relatively tall. In lateral view the arch is inclined posterodorsally at a pronounced angle and the posterior end extends well past the level of the posterior cotyle. The base of the arch is relatively elongate, extending from just in front of the posterior cotyle to a point level with the base of the odontoid process, and the leading edge is nearly vertical. More dorsally, the wall tapers to its junction with the roof of the neural arch. Just above its base, the leading edge of the wall assumes a nearly horizontal orientation and extends posteriorly to a point approximately level with the spinal foramina. From this point, the leading edge of the wall changes direction again and extends dorsoposteriorly at a steep angle. The roof of the neural arch is tall and slopes steeply away from either side from the neural crest. The front of the neural arch and crest are expanded anteriorly, to form a deep projection that resembles a blunt sickle in lateral view. The neural crest is highest and thinnest along the dorsal surface of this projection. The remainder of the crest continues posterodorsally at a shallow incline, broadens, and grades into the roof just in front of the posterior edge. The neural spine is forked, but not as prominently as on some referred atlantes of

Opisthotriton. Each spine arises about midway along the roof of the neural arch, lateral and well below the neural crest, and extends posterodorsally as a low ridge. The spine terminates in a blunt tip that extends just slightly past the posterior edge of the roof. A shallow and triangular depression, with the apex directed anteriorly, spans across the distal tips of the spines. The granular surface of this depression suggests that, in life, the tip of the neural arch was finished in cartilage. The posterior face of the arch is deep, nearly vertical, and is indented to either side of the midline by a narrow, dorsoventral groove. The postzygapophyseal process is relatively elongate posteriorly, but appears to be essentially continuous with the neural arch because a deep flange extends medially from the posteromedial edge of the process to the adjacent part of neural arch. The postzygapophyseal facet is posteriorly elongate and oval in outline, with the posterior end slightly broader. The articular surface is shallowly concave and the lateral edge is tilted slightly dorsally.

Trunk Vertebrae (Fig. 11-8JJ–TT)—The best preserved specimen at hand is virtually complete (UALVP 40107; Fig. 11-8JJ–MM) and is interpreted as a first trunk vertebra based on its relatively short centrum, shallow subcentral keel, short transverse processes, steeply inclined leading edge of the neural crest, and steeply inclined, short neural spine. Scapherpetontid trunk vertebrae resemble those of amphiumids in some respects (Auffenberg and Goin, 1959) and given the lack of articulated vertebral series for scapherpetontids, comparisons with amphiumids are potentially useful for inferring the relative positions of other isolated Scapherpeton trunk vertebrae. Other specimens figured here are interpreted as coming from positions further along the series, although none is convincingly from the posterior region. The presence of a deep subcentral keel, with a straight ventral edge and no lateral grooves for passage of vessels from the subcentral foramina, and a steeply inclined neural spine suggest that UALVP 40108 came from near the anterior end of the column. I regard UALVP 40110 (Fig. 11-8OO–QQ) as having come from slightly further back, although probably still in the anterior third of the column, based on the notched ventral edge of the subcentral keel, prominent lateral grooves on the subcentral keel, and more depressed neural spine. Estes (1969a:caption for fig. 6A–D and 1981:caption for fig. 12M) identified a similar trunk vertebrae (AMNH 8135), with a more steeply inclined neural spine, as a posterior trunk vertebra, but he did not state the basis for his interpretation. UALVP 40109 (Fig. 11-8RR–TT) most closely resembles UALVP 40110, but the smooth and horizontal ventral edge on the subcentral keel implies a somewhat more posterior location along the trunk series. Estes (1976:fig. 2A, B) figured an incomplete trunk vertebra of Scapherpeton, from the middle Palaeocene Tongue River Formation, that is notable for having a shallower subcentral keel, with the ventral edge convex and no vertical groove in the lateral face; comparisons with amphiumids suggest this Palaeocene vertebra came from the posterior half of the trunk series.

The two largest trunk vertebrae at hand, UALVP 40108 and 40110, have centra lengths of about 6.8 mm. The centrum is moderately elongate, laterally compressed, and amphicoelous. The cotyles are laterally compressed and oval or teardrop shaped in outline, particularly in specimens inferred to be from the anterior part of the series. Cotyles are shallowly concave, partially infilled with calcified cartilage, and a modest-sized notochordal pit opens in the dorsal half to third. The subcentral keel is robust and deep, extending below the ventral rims of the cotyles. Multiple subcentral foramina may be present. The transverse processes are bicipitate, moderately divergent laterally, and are connected proximally by a web of bone. The base of the dorsal process arises from below the lateral edge of the neural arch roof and a prominent vertebrarterial canal extends anteroposteriorly through the base of the transverse processes. The anterior and posterior alar processes are narrow, short flanges. No spinal foramina or basapophyses are present.

The neural canal is shallow and the neural arch is low. The neural crest is relatively tall on the first trunk vertebra, but it is substantially shallower on more posterior vertebrae and extends only a short distance onto the neural spine. The neural spine is posteriorly elongate, thin, hollow, and open distally, indicating that the spine was finished, in life, with cartilage. The zygapophyseal processes are modest in size and, on most specimens, extend laterally at a shallow angle. Zygapophyseal facets are oval in outline and the lateral edges are tipped dorsally.

Remarks

The nomenclatural and taxonomic history of Scapherpeton was reviewed by Auffenberg and Goin (1959) and Estes (1964). In short, Cope (1876a) named two new genera and five new species of salamanders on isolated trunk vertebrae from the type area of the middle Campanian (Judithian) Judith River Formation, Montana: Scapherpeton tectum, S. laticolle, S. excisum, S. favosum, and Hemitrypus jordanianus. These were the first Mesozoic salamanders to be described. By page priority (Cope, 1876a:355–356), S. tectum is the type species of Scapherpeton (Auffenberg and Goin, 1959). Auffenberg and Goin (1959) subsequently interpreted the holotypes of S. laticolle, S. excisum, and S. favosum as regional variants of the taxon represented by S. tectum and, accordingly, placed the first three names in synonymy with the name S. tectum. They also erected the new family Scapherpetontidae for receipt of the monotypic genus. Auffenberg and Goin (1959) regarded H. jordanianus as a valid taxon of indeterminate salamander, perhaps related to Scapherpeton, and described additional vertebrae for both genera. Estes (1964) placed the name H. jordanianus as a junior synonym of the name S. tectum because, he argued, the holotype vertebra of the former taxon is a composite and the main part of the specimen, the centrum, is indistinguishable from that of Scapherpeton. Estes (1964) also reinterpreted the holotype of Hedronchus sternbergi as the anterior part of a broken vertebra of S. tectum and, therefore, placed the former name as a junior synonym of the latter; Cope (1876b) originally interpreted the holotype of Hedronchus sternbergi as the crown of a young tooth from a shark.

Until Estes' (1964) revision, Scapherpeton was known almost exclusively from vertebrae. Estes (1964) described additional isolated vertebrae (atlantes, trunk vertebrae, sacrals, and caudals) plus femora, jaws, a vomer, parietals, and exoccipitals, all from the type area of the Lance Formation. Estes (1964:62) intended to present a more "detailed morphological study" for the genus, but this was never published. Subsequent papers provided limited new information about the morphology and relationships of the genus (e.g., Estes, 1969a, 1976, 1981; Naylor and Krause, 1981).

Trunk vertebrae are distinctive for Scapherpeton, as previous authors have noted (Cope, 1876a; Auffenberg and Goin, 1959; Estes, 1964, 1969a, 1981; Naylor and Krause, 1981; Naylor, 1983). Trunk vertebrae of Scapherpeton can be readily associated and differentiated from those of other scapherpetontids (for which trunk vertebrae are known) based on the following combination of characters: cotyles laterally compressed and typically tear drop-shaped; cotyles shallowly concave internally, because anterior part is infilled with calcified cartilage; subcentral keel deep, extending below level of cotyles;

transverse processes weakly bicipitate, with dorsal process arising below level of lateral edge of neural arch; anterior alar process a short, narrow flange that does not form the dorsolateral wall of a fossa below it; neural crest low and extends only onto base of neural spine; zygapophyseal processes less divergent laterally; and interzygapophyseal ridge absent. Trunk vertebrae from the anterior part of the series, behind the first few positions, are further characterized by having the subcentral keel notched ventrally and indented laterally by a groove extending ventrally from the subcentral foramen. Several trunk characters previously regarded as diagnostic for the genus (e.g., neural spine elongate and inclined posteriorly; basapophyses absent; intercotylar process prominent and having a constricted base) are better regarded as primitive characters for the family as a whole.

The identity of atlantes previously referred to Scapherpeton has long been problematic. Published accounts implied that these atlantes were remarkably similar to isolated, referred atlantes of Lisserpeton and that there was considerable overlap between the two genera (Estes, 1965, 1981; Naylor, 1983). This confusion was particularly perplexing in light of the observation that the respective holotype and referred trunk vertebrae of the two genera are distinctive. Trunk vertebrae of Scapherpeton and Lisserpeton differ in at least three features that can be used to associate these with the appropriate atlantes: cotylar shape (more compressed laterally in Scapherpeton versus subcircular in Lisserpeton); calcified infilling of cotyles (anterior part infilled in Scapherpeton versus thin layer coating walls in Lisserpeton); and build of neural arch (more delicate in Scapherpeton compared to Lisserpeton). Maximum size may also be useful, because the largest available trunk vertebrae for Scapherpeton are about 70% the size of those for Lisserpeton; however, the discrepancy between the largest atlantes is less pronounced.

In retrospect, several factors conspired to create the perception that atlantes of Scapherpeton and Lisserpeton were all but indistinguishable: 1) incorrectly identified specimens; 2) small sample sizes; and 3) a preponderance of atlantes that preserved only the centrum. To deal briefly with the first point, an atlantal centrum figured by Auffenberg and Goin (1959:fig. 1A) is diagnostic for the new Lancian species of Piceoerpeton described below (see also Naylor, 1983) and the nearly complete atlas figured by Estes (1964:33c) belongs to Lisserpeton (see next account). Specimens now at hand for Scapherpeton and Lisserpeton include size series of referred atlantal centra from Lancian and Judithian horizons and a nearly complete atlas for each taxon from the Bug Creek Anthills. These specimens demonstrate that atlantes are reliably diagnostic for the two genera and differ from one another in numerous details of the centrum and neural arch. Compared to Lisserpeton, the atlas of Scapherpeton differs as follows: anterior cotyles less compressed dorsoventrally, ranging from subcircular to oval in outline; odontoid process scoop-shaped, with trough extending along dorsal face; posterior cotyle more laterally compressed and more shallowly concave, because anterior part is infilled with thick layer of calcified cartilage; atlantal neural arch more delicate and inclined posteriorly, with posterior end extending past level of posterior cotyle; roof of neural arch completely ossified; and neural spines paired. Differences in characters of the centrum are more subtle than those of the neural arch. Two features—the relative length of the centrum and number of subcentral foramina—used by Estes (1965) differentiate atlantes of Scapherpeton and Lisserpeton are uninformative. Minor differences are evident among atlantal centra here referred to both genera from Bug Creek and Irvine in the outlines of the anterior and posterior cotyles and the form of the odontoid process. This variation occurs irrespective of size or geological age, and I do not regard these differences as indicating the presence of separate Lancian and Judithian species for both genera.

Scapherpeton is a common component of Upper Cretaceous and Paleogene microvertebrate assemblages and has been reported from no fewer than a dozen early Campanian (Aquilan) to upper Palaeocene (Tiffanian) formations in the Western Interior (e.g., Estes, 1981; Naylor and Krause, 1981:table 1). Many of these reports are in faunal lists and await verification. Adequately published specimens and specimens available to me confirm the presence of Scapherpeton in at least the following units: early Campanian (Aquilan) Deadhorse Coulee Member, Milk River Formation, Alberta; middle Campanian (Judithian) Dinosaur Park Formation, Alberta, and Judith River Formation, Montana; late Maastrichtian (Lancian) Hell Creek Formation, Montana, and Lance Formation, Wyoming; middle Paleocene (Torrejonian) Tongue River Formation, Montana; and upper Paleocene (Tiffanian) Fort Union Formation, Wyoming, and Paskapoo and Porcupine Hills formations, Alberta (e.g., Auffenberg and Goin, 1959; Estes, 1964, 1969a, 1975, 1976, 1981; Estes et al., 1969; Fox, 1972, 1976; Naylor and Krause, 1981). Estes and Hutchison's (1978) report of Scapherpeton in the Eureka Sound Formation (middle

Eocene or Wasatchian) on Ellesmere Island has since been corrected; the dentary in question is now regarded as having come from a small individual of Piceoerpeton willwoodense (Estes and Hutchison, 1980; Naylor and Krause, 1981). This leaves the last occurrence of Scapherpeton in the late Paleocene.

Genus LISSERPETON Estes, 1965

Type Species—Lisserpeton bairdi Estes, 1965; middle Campanian to Paleocene (Judithian-Tiffanian), North American Western Interior.

Distribution—As for the type and only known species.

Diagnosis—As for the type species.

LISSERPETON BAIRDI Estes, 1965

(Fig. 11-9)

Holotype—AMNH 8123, trunk vertebra missing distal ends of transverse processes and postzygapophysis on left side and distal end of neural spine (Estes, 1965:fig.1).

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Hell Creek Formation; Bug Creek Anthills, McCone County, Montana, USA.

Referred Specimens—Dinosaur Park Formation, Irvine, Alberta: UALVP 40135-40144, atlantes; Hell Creek Formation, Bug Creek Anthills, Montana: 40123-40134, atlantes; UALVP 14892, 14893, 40145, 40146, trunk vertebrae. None of these specimens previously have been reported for the species.

Distribution—Middle Campanian to middle Paleocene, North American Western Interior: middle Campanian (Judithian): Dinosaur Park Formation, Alberta, and Judith River Formation, Montana; late Maastrichtian (Lancian): Hell Creek Formation, Montana, and Lance Formation, Wyoming; and middle Paleocene (Torrejonian): Tongue River Formation, Montana.

Revised Diagnosis—Species of scapherpetontid differing from all other members of the family in having atlas with odontoid process that is phallus-shaped in dorsal or ventral outline. Atlantal centrum differs further from Piceoerpeton, but resembles

Scapherpeton and Irvinetriton, in having articular surface of anterior cotyles nearly flat and odontoid process anteriorly elongate, with articular surface ventrally for contact with skull; from Scapherpeton, but resembles Piceoerpeton and Irvinetriton, in having anterior cotyles more consistently compressed dorsoventrally, odontoid process with flattened dorsal surface, and posterior cotyle less compressed laterally, if at all; from Piceoerpeton and Irvinetriton, but resembles Scapherpeton, in having base of odontoid process constricted and ventral edge of posterior cotyle in approximately the same horizontal plane as ventral edge of anterior cotyle. Atlantal neural arch differs from that of Scapherpeton and resembles Piceoerpeton (arch unknown for Irvinetriton) in being relatively shorter and more robust, directed dorsally, and portions of dorsal surface evidently finished in cartilage; atlantal neural spine (unknown for Piceoerpeton and Irvinetriton) differs from Scapherpeton in being single. Trunk vertebrae differ from those of Scapherpeton and Piceoerpeton (trunk vertebrae unknown for Irvinetriton) in having anterior alar process an elongate, moderately broad flange that forms the dorsolateral wall of a fossa to either side of ventral midline and in having dorsal transverse process arising consistently from dorsolateral margin of neural arch roof; large trunk vertebrae differ further in having an interzygapophyseal ridge. Trunk vertebrae differ further from those of Piceoerpeton, but resemble Scapherpeton, in having subcentral keel thin; differ further from Scapherpeton, but resemble Piceoerpeton, in having cotyles more subcircular in outline and deeper, bicipital transverse processes more divergent, neural crest relatively taller and extending further distally along neural spine, zygapophyseal processes extending more laterally, subcentral keel not extending below level of cotyles, and ventral edge and lateral faces of subcentral keel smooth.

Description

Vertebrae of Lisserpeton previously have been figured and described by Estes (1965, 1976, 1981).

Atlas (Fig. 11-9A–CC)—Two size series of atlantes are available: one from the Bug Creek Anthills (Fig. 11-9A–P) and the second from Irvine (Fig. 11-9Q–CC). Centra range in length from about 1.8 to 9.4 mm and intercotylar width from about 2.2 to 11.8

mm. One specimen, UALVP 40134 (Fig. 11-9K-P), preserves a nearly intact neural arch; in lateral view this specimen closely resembles an atlas (UCMP 61205) from the Lance Formation that Estes (1964:fig. 33c) referred to Scapherpeton tectum.

Atlantes here referred to Lisserpeton bairdi and Scapherpeton tectum are similar, more so in the structure of the centrum than the neural arch. In atlantes of L. bairdi the anterior cotyles tend to be more dorsoventrally compressed, giving the cotyles an oval or oblong shape. The odontoid process is elongate and the neck is constricted; however, the process is relatively narrower and more phallus- or arrowhead-shaped in dorsal or ventral view, and the dorsal surface is flatter. The posterior cotyle is subcircular in posterior outline and more deeply concave, because the inner walls are not lined with calcified cartilage. In other respects, the atlantal centrum resembles that of Scapherpeton.

The most nearly complete atlantes referred here to Scapherpeton (UALVP 40104) and Lisserpeton (UALVP 40134) are of similar size—in terms of their intercotylar widths and midventral lengths—yet the neural arch on the latter is shorter and stockier in build. The neural arch projects more nearly dorsally, such that the apex of the arch lies anterior to the level of the posterior cotyle. The wall of the neural arch is anteriorly longer and only the dorsal half of the leading edge is excavated. The neural arch roof and crest are expanded anteriorly. The neural crest is broadest anteriorly and narrows posteriorly. From its anterior end, the crest ascends steeply and terminates in a low, blunt neural spine. The posterior half of the dorsal surface of the crest is roughened for attachment of adductor muscles or ligaments. Two irregular excavations are present along the midline: one near the anterior end of the neural crest and the second behind the neural spine. Comparisons with extant ambystomatids suggest that, in life, these depressions were finished in cartilage. The posterior face of the neural arch roof is deep, inclined slightly anteriorly, and bears a broad median ridge. The postzygapophyseal process is intact on the right side. Compared to Scapherpeton, the postzygapophyseal process is relatively larger, projects more laterally, and the articular facet is broader and shorter.

Trunk Vertebrae (Fig. 11-9DD-NN)—Trunk vertebrae at hand from the Bug Creek Anthills include the first example of a first trunk vertebra (UALVP 40145; Fig. 11-9DD-GG). This specimen lacks the left anterior corner of the neural arch and the neural spine is broken on the right side. Identification of UALVP 40145 as a first trunk vertebra is based on many of the same features seen in the first trunk vertebra reported above for

Scapherpeton: centrum relatively short; subcentral keel shallow and ventrally descending; transverse processes short; neural crest relatively tall; and neural spine steeply inclined and relatively short. On the other two figured trunk vertebrae, UALVP 14892 (Fig. 11-9HH, II) and 14893 (Fig. 11-9JJ-NN), the subcentral keel is moderately deep and has a relatively straight ventral edge; these features indicate that both vertebrae occupied positions further back, in the anterior half or so of the series. The more steeply inclined neural spine on the former specimen suggests it occupied a more anterior position than the latter. The holotype (Estes, 1965:fig. 1d) has a markedly shallower subcentral keel with a dorsally concave ventral margin; these features suggest that this specimen came from the posterior part of the trunk series.

The largest trunk vertebrae, UALVP 14892 and 14893, have centra lengths of about 9.5 and 8.3 mm, respectively. In all specimens the centrum is amphicoelous. The cotyles are weakly compressed laterally and range in outline from subcircular to slightly oval. Internally the cotyles are deeply concave, lined with a thin layer of calcified cartilage, and a modest-sized notochordal pit opens in the dorsal half of the cotyle. The subcentral keel is thin and moderately deep, never extending below the level of the ventral margins of the cotyles. The ventral edge of the keel is nearly straight or concave, but never notched. One specimen, UALVP 14892, has a faint vertical groove on the left side of the subcentral keel for transport of a blood vessel from the subcentral foramen. One to three subcentral foramina, of varying sizes, are present. The anterior alar process is relatively broader and more elongate than in Scapherpeton, and forms the dorsolateral roof of a large fossa to either side of the subcentral keel. On specimens with intact transverse processes, these structures are tipped by shallow distal facets for articulation with ribs. Compared to Scapherpeton, the transverse processes are more divergent distally and the dorsal process arises from higher up on the neural arch, approximately level with the lateral edge of the roof. The paired transverse processes are connected basally by a thin web of bone. A prominent vertebrarterial canal extends through the base of the processes. No basapophyses or spinal foramina are present.

The neural canal is relatively broad and low. A low, ridge-like neural crest extends posteriorly along the roof of the neural arch onto the neural spine, to at least the level of the postzygapophyses. The neural spine is hollow, elongate, and inclined posteriorly at less than 30° from the horizontal. On UALVP 14892 and 14893 a distinct interzygapophyseal ridge runs along the lateral edge of the neural arch roof, between the bases of the prezygapophysis and dorsal transverse process. An unfigured trunk vertebra (UALVP 40146) about half the size of UALVP 14892 and from the same regions of the trunk series lacks the interzygapophyseal ridge, suggesting that this distinctive feature develops ontogenetically. In all other respects, UALVP 14892 resembles larger trunk vertebrae of Lisserpeton and can confidently be associated with them. The zygapophyseal processes are moderate in size and, compared to Scapherpeton, tend to project slightly more laterally. Zygapophyseal facets are flat, oval in outline, and their lateral edges are tipped dorsally.

Remarks

Estes (1965) described the new genus and species Lisserpeton bairdi for several small collections of isolated trunk vertebrae, atlantes, and skull bones from Bug Creek Anthills, Montana, and sites in the Lance Formation, Wyoming. Estes (1965) assigned Lisserpeton to the Scapherpetontidae and his original generic diagnosis relied on trunk vertebral characters alone to differentiate the genus from Scapherpeton. Estes's (1981) revised diagnosis again differentiated Lisserpeton from Scapherpeton (Piceoerpeton was not mentioned) and incorporated cranial characters. Additional information on referred vertebrae, dentaries, and vomers subsequently was provided by Estes (1976, 1981) and Naylor and Krause (1981). Estes and Hutchison (1980) reassigned a middle Paleocene dentary figured by Estes (1976:text-fig. 3I) to Piceoerpeton. Estes (1969a, 1981) and Naylor and Krause (1981) noted resemblances between the jaws, palatal bones, and trunk vertebrae of Lisserpeton and Piceoerpeton, and Estes (1969a:232) suggested that the former was ancestral to the latter.

Trunk vertebrae of Lisserpeton are distinctive among scapherpetontids and can be associated based on the following combination of features: cotyles subcircular in outline; cotyles relatively deep and walls lined with a thin layer of calcified cartilage; subcentral keel narrow, shallow, does not extend below level of cotyles, ventral surface not notched, and groove on lateral face faintly developed at best; transverse processes divergently bicipitate, with dorsal process arising at lateral edge of neural arch; anterior alar process an elongate, moderately broad flange that forms the dorsolateral wall of a fossa below it;

neural crest moderately tall and extends some distance along neural spine; and zygapophyseal processes directed anterolaterally. Many of these characters are shared with one or both species of Piceoerpeton. The prominent interzygapophyseal ridge is unique for Lisserpeton among known scapherpetontids, but only for large individuals.

Justifiable concerns have been expressed (Naylor and Krause, 1981; Naylor, 1983) over the distinctiveness of atlantes that have been referred to Lisserpeton, especially in comparison with those attributed to Scapherpeton, and the proper association of these with their respective, characteristic trunk vertebrae. As noted in the previous account, atlantes and trunk vertebrae can be associated based on details of the cotyles, neural arch, and, perhaps, size. Size series of atlantal centra from Bug Creek Anthills and Irvine, plus a nearly complete atlas from Bug Creek Anthills, confirm that atlantes of Lisserpeton differ from those of Scapherpeton, as follows: anterior cotyles relatively more compressed dorsoventrally, ranging from oval to oblong in outline; odontoid process somewhat phallus shaped, with dorsal face flat; posterior cotyle more weakly compressed laterally, if at all, and more deeply concave because only a thin layer of calcified cartilage coats the inner walls; atlantal neural arch more stocky and projects dorsally, with apex well anterior to level of posterior cotyle; roof of neural arch incompletely ossified; and neural spine single. Details of the odontoid process also differentiate atlantes of Lisserpeton from those of Piceoerpeton and Irvinetriton.

The published figure (Estes, 1964:fig. 33c) of an atlas (UCMP 61250) that Estes referred to Scapherpeton depicts a neural arch all but identical to that on the nearly complete atlas (UALVP 40134) referred here to Lisserpeton. Based on the shape of the neural arch, UCMP 61250 likely pertains to Lisserpeton and the same may be true for some of the other, unfigured atlantes with neural arches reported by Estes (1964) for Scapherpeton.

Jaws, vomers, and roofing elements reported by Estes (1965) and Naylor and Krause (1981) for Lisserpeton are distinctive. The jaws and vomers more closely resemble homologous bones in Piceoerpeton than Scapherpeton, yet little weight can be put on these resemblances until associations of cranial elements with vertebrae are critically re-examined for Scapherpeton and Lisserpeton. Estes's (1965) rational for referring skull bones to Lisserpeton seems to have been that homologous bones had already been referred by him to Scapherpeton, leaving Lisserpeton as the only Lancian scapherpetontid for which cranial elements were not then known.

Lisserpeton has been reported from fewer formations and a less extensive temporal range than Scapherpeton in the Western Interior (see Estes, 1981; Naylor and Krause, 1981:table 1). Specimens available to me and adequately published accounts indicate that Lisserpeton is reliably known from at least the following units: middle Campanian (Judithian) Dinosaur Park Formation, Alberta, and Judith River Formation, Montana; late Maastrichtian (Lancian) Hell Creek Formation, Montana, and Lance Formation, Wyoming; and middle Paleocene (Torrejonian) Tongue River Formation, Montana. Naylor and Krause (1981:table 1, pers. comm from R. Estes) reported a late Paleocene (Tiffanian) occurrence in the Polecat Bench Formation, Wyoming, but this record has not been substantiated. Fox (1972) listed Lisserpeton in a preliminary faunal list for the Deadhorse Coulee Member (Aquilan), Milk River Formation, Alberta, but I have not seen any convincingly diagnostic vertebrae for the genus in the collections of the UALVP. Based on current information, Lisserpeton is restricted to the middle Campanian (Judithian) to middle Palaeocene (Torrejonian).

Genus PICEOERPETON Meszoely, 1967

(Fig. 11-10)

Type Species—Piceoerpeton willwoodense (Meszoely); late Paleocene–middle Eocene (Tiffanian–Wasatchian), western and Arctic North America.

Included Species—Piceoerpeton willwoodense and P. naylori, sp. nov.

Distribution—Late Maastrichtian to early Eocene (Lancian–Clarkforkian), North American Western Interior, and middle Eocene (Wasatchian), Ellesmere Island.

Revised Diagnosis—Genus of scapherpetontid differing from all other members of the family in having atlas with articular surface of anterior cotyles deeply excavated and odontoid process reduced to a rudimentary, nipple-like projection that lacks articular surface ventrally for contact with skull. Atlantal centrum further differs from Scapherpeton and Lisserpeton, but resembles Irvinetriton, in having base of odontoid process not constricted and ventral edge of posterior cotyle lying below level of ventral edge of anterior cotyle. Atlantal neural arch differs from that of Scapherpeton and resembles Lisserpeton (arch unknown for Irvinetriton) in being relatively shorter and more robust, directed dorsally, and portions of dorsal surface evidently finished in cartilage. Trunk vertebrae differ from those of Scapherpeton and Lisserpeton in having broader subcentral keel; differ further from Lisserpeton and resemble Scapherpeton in lacking deep fossa to either side of ventral midline; and differ further from those of Scapherpeton and resemble Lisserpeton (trunk vertebrae unknown for Irvinetriton) in having cotyles more subcircular in outline and deeper, bicipital transverse processes more divergent, dorsal transverse process variably arising level with or below level of neural arch roof, zygapophyseal processes extend more laterally, neural crest relatively taller and extending further distally along neural spine, subcentral keel not extending below level of cotyles, and ventral edge and lateral faces of subcentral keel smooth. Trunk vertebrae resemble those of Scapherpeton and differ from larger trunk vertebrae of Lisserpeton in lacking interzygapophyseal ridges. Trunk vertebrae resemble those of Scapherpeton and differ from large vertebrae of Lisserpeton in lacking zygapophyseal ridges.

Remarks—Meszoely (1967) described the new genus and species Piceoerpeton willwoodensis, subsequently amended to P. willwoodense by Estes (1969a:232), for a broken trunk vertebra from the lower Eocene (Clarkforkian) Willwood Formation, Wyoming, and assigned the taxon to the Cryptobranchidae. Estes (1969a:232) reinterpreted P. willwoodense as a probable scapherpetontid and suggested it was "a late, large derivative" of Lisserpeton. Isolated limb elements and distinctive atlantes, trunk vertebrae, and skull elements subsequently were described for P. willwoodense from the middle Eocene (Wasatchian) of Ellesmere Island (Estes and Hutchison, 1980) and upper Paleocene (Tiffanian) localities in the Western Interior (Naylor and Krause, 1981). Examples of previously unfigured atlantes and a trunk vertebra previously reported by Naylor and Krause (1981) are shown in Figure 11-10A-H. Estes (1981) and Naylor and Krause (1981) retained Piceoerpeton in the Scapherpetontidae, and regarded the reduced odontoid process and deeply concave anterior cotyles on the atlas as convergent with batrachosauroidids. These two character states and the lack of a ventral articular surface on the odontoid process are unique to Piceoerpeton among scapherpetontids.

Naylor (1983) figured and briefly described a small scapherpetontid atlantal centrum (UALVP 14918) from the late Maastrichtian (Lancian) Bug Creek Anthills, Montana, that he suggested represented "an early, probably small, species of the genus Piceoerpeton" (Naylor, 1983:51). Naylor (1983) did not formally name this new species, in part, because he had only one specimen available to him and, in part, because additional specimens were then being studied by Richard Estes. Unfortunately, Estes' description was not published before his death. Two additional Lancian specimens, an atlas and a trunk vertebra, since identified in the collections of the UALVP substantiate Naylor's (1983) suspicion that UALVP 14918 pertained to a second species of Piceoerpeton. This new species is formally described below.

PICEOERPETON NAYLORI, sp. nov.

(Fig. 11-10I–V)

Holotype—UALVP 14918, atlantal centrum (Naylor, 1983:fig. 1; here:Fig. 11-10I–M).

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Hell Creek Formation; Bug Creek Anthills, McCone County, Montana, USA.

Etymology—Specific epithet recognizes Dr. Bruce Naylor, who first reported the presence of this new species based on the atlas selected here as the holotype.

Referred Specimens—Hell Creek Formation, Bug Creek Anthills, Montana: UALVP 40122, trunk vertebra. Lance Formation, Bushy Tailed Blowout, Wyoming: UALVP 43920, atlas. See "Remarks" below for comments on other specimens.

Distribution—Late Maastrichtian (Lancian), Western Interior: Hell Creek Formation, Montana, and Lance Formation, Wyoming.

Diagnosis—Species of Piceoerpeton primitively differing from type species in inferred smaller body size, in having an atlas with a relatively larger odontoid process and neural canal, and in having a layer of calcified cartilage lining walls of both cotyles in trunk vertebrae and infilling the anterior part of the posterior cotyle in the atlas.

Description

Naylor (1983) briefly described and figured the atlantal centrum here selected as the holotype. In the same paper Naylor (1983:fig. 2A) presented a composite reconstruction of the atlas, in anterior view.

Atlas (Fig. 11-10I-Q)—The two specimens at hand preserve the centrum and the base of the neural arch on both sides. The holotype is moderate in size, with a centrum length of about 2.6 mm and intercotylar width of about 5.3 mm. The referred atlas is slightly smaller, measuring about 2.5 mm in length and 4.3 mm in intercotylar width. The centrum is relatively robust in construction. The anterior cotyles are shallowly compressed dorsoventrally: in the holotype the cotyles are oval in outline, whereas in UALVP 43920 the cotyles are more orbicular in shape, with the upper edge more steeply convex dorsally. On the latter specimen, the right cotyle is narrower than the left and its lateral edge is more broadly rounded. The articular faces of the anterior cotyles are moderately concave from side to side and top to bottom, much more so than on non-Piceoerpeton atlantes of equivalent size. The lateral ends of the anterior cotyles project slightly posteriorly on UALVP 14918 and nearly laterally on UALVP 43920. The medial rim of the anterior cotyle on both specimens is drawn forward from the main body of the centrum, forming a tiny vertical ridge to either side of the odontoid process. The odontoid process is a thick, but flattened, nipple-like projection. In dorsal or ventral view the process is short, accounting for only about 10% of the total length of the centrum, is relatively narrow, and tapers anteriorly to an acutely rounded tip. The base of the odontoid process is not constricted and it lies between the medial edges of the anterior cotyles. The dorsal and ventral surfaces of the odontoid process are flat to shallowly convex and no articular surface is present ventrally.

The posterior cotyle is subcircular in outline. The interior of the cotyle is deeply concave, infilled anteriorly with a layer of calcified cartilage, and a moderate-sized notochordal pit opens at about the center of the cotyle. The ventral rim of the posterior cotyle lies slightly below the level of the ventral rims of the anterior cotyles. In contrast with large atlantes of the type species, the ventral surface on both Lancian centra is relatively smooth. Two ridges extend anterolaterally-posteromedially on either side of the ventral midline. The more medial ridge runs from about the midpoint of the ventral edge of the anterior cotyle to either side of the posterior midline; this ridge is low and broad on UALVP 43920 and a sharp crest on UALVP 14918. The more lateral ridge is a narrow, horizontal crest that runs along the ventrolateral edge of the centrum, between the ventrolateral corners of the anterior and posterior cotyles. The area enclosed by the medial pair of ridges is shallowly concave and perforated by a cluster of three (UALVP

43920) or five (UALVP 14918) small subcentral foramina. The ventrolateral and lateral surfaces of the centrum are perforated by foramina of varying sizes, most of which are infilled with matrix. Several foramina lie on the posterior face of anterior cotyle, around the dorsolateral rim; the dorsalmost foramen opens into a canal that extends into the neural canal and is identified as the spinal foramen.

Atlantes available to me preserve only the base of the neural arch. Judging by the positions and structure of the broken bases, the neural canal was relatively broader and, perhaps, taller, than in atlantes of Piceoerpeton willwoodensis. Naylor's (1983:fig. 2A) composite reconstruction of the atlas of P. naylori depicts a moderately broad and tall neural arch, with a thin neural crest. Naylor (1983:caption for figure 2) stated that his reconstruction was founded on an atlantal centrum (UALVP 14918), Auffenberg and Goin's (1959:fig. 1A) drawing of a second atlantal centrum (part of CMNH 6467) referred by them to Scapherpeton, and an unpublished sketch provided by Richard Estes. Estes' sketch appears to have been the basis for the reconstructed neural arch, yet it was not reported whether his sketch was taken directly from undescribed Lancian atlantes with intact neural arches or extrapolated from atlantes of the type species. As such, the structure of the atlantal neural arch in Naylor's (1981:fig. 2A) reconstruction is open to question.

Trunk Vertebra (Fig. 11-10R–V)—The available trunk vertebra, UALVP 40122, is incomplete: the neural spine is broken across its base, the neural crest is broken posteriorly, the transverse processes are broken on both sides, and both prezygapophyses are damaged. The specimen is moderate in size, with a centrum length of about 4.9 mm. Judging by its shallowly concave subcentral keel and the lateral edges of the postzygapophyses that are tilted steeply dorsally, the vertebra is from the posterior part of the trunk series.

The centrum is amphicoelous and the cotyles are round in outline. Both cotyles are deeply concave, the walls are lined with a thick layer of calcified cartilage, and a relatively large notochordal pit opens in about the center of the cotyle. The ventral surface of the centrum is smooth. The subcentral keel is low, relatively broad (less so than in the trunk vertebra figured for Piceoerpeton willwoodense; Fig. 11-10G), and the ventral surface is concave in lateral aspect. Judging from the broken bases, the transverse processes were divergently bicipitate and a web of bone connected the processes, at least near the base. The dorsal transverse process arises below the lateral edge of the roof of the neural arch. The anterior alar process is a moderately broad flange that, together with the subcentral keel, defines a deep fossa to either side of the ventral midline. No subcentral or spinal foramina or basapophyses are present.

The neural canal is moderately broad and relatively flat. The neural crest is a keel-like structure that arises level with the bases of the prezygapophyses and becomes taller posteriorly; although broken across the base of the neural spine, neural crest almost certainly would have extended onto the neural spine for some distance. Judging by its broken base, the neural spine was thin and projected dorsoposteriorly. No interzygapophyseal ridges are present. The prezygapophyses are damaged, but these evidently were moderate in size, relatively robust, and directed somewhat laterally. The postzygapophyseal process are similar, but extend more posteriorly. The postzygapophyseal facets are broad, oval in outline, and the lateral edges are tipped steeply dorsally.

Remarks

The three vertebrae reported above can be assigned to Piceoerpeton and associated with one another based on four characters states that are unique to the genus among known scapherpetontids: anterior cotyles on atlas deeply excavated; odontoid process greatly reduced in length and width; odontoid process lacks articular surface ventrally for contact with skull; and subcentral keel on trunk vertebra shallow and broad. Notable differences between these Lancian specimens and those of the type species P. willwoodense are as follows: (1) elements are no more than 25% the size of the largest homologous specimens of P. willwoodense reported by Naylor and Krause (1981:510–511), which implies a correspondingly smaller body size; (2) odontoid process on atlas relatively larger, but still markedly reduced compared to other scapherpetontids; (3) neural canal in atlas relatively larger and, probably, comparable in size to other scapherpetontids; and (4) cotyles on trunk vertebra lined internally with a moderately thick layer of calcified cartilage and posterior cotyle in atlas partially infilled anteriorly with calcified cartilage (versus no calcified cartilage inside vertebral cotyles in P. willwoodense). These differences are of sufficient magnitude to warrant erecting a new species, namely P. naylori, for the distinctive Lancian specimens. The diagnostic character states for P. naylori are probably primitive relative to the P. willwoodense, implying that the Lancian species may be ancestral to the Tertiary type species.

Besides Naylor's (1983) original account, there are at least three reports in the literature of Piceoerpeton-like vertebrae of Lancian age. The first is an atlantal centrum (part of CM 6467) that Auffenberg and Goin (1959:fig. 1A) figured and referred to Scapherpeton tectum. Judging from their published figure, the specimen is diagnostic for Piceoerpeton in the deeply excavated anterior cotyles and for P. naylori in size and in having a reduced, nipple-like odontoid process. The second report is of specimens from the Hell Creek formations that were being studied by Richard Estes (Naylor, 1983:48), but were never described. I have not been able to locate the whereabouts of these specimens, but presumably at least some of them pertain to P. naylori. The third report is of an atlantal centrum (UCMP 123524; unfigured) from the Hell Creek Formation that L. Bryant (1989:33) identified as "cf. Piceoerpeton sp." My examination of UCMP 123424 confirms that it resembles the two atlantes described here for P. naylori in most respects, but it differs in having the odontoid process flatter, more shelf-like, and broader, spanning between the medial edges of the anterior cotyles. The configuration of the odontoid process on UALVP 123524 is strikingly reminiscent of batrachosauroidids and argues against assigning the specimen to Piceoerpeton. At present, I cannot offer any further opinion on the identity of this curious atlas.

Genus IRVINETRITON, gen. nov.

Type Species—Irvinetriton elongatus, sp. nov.; middle Campanian–late Maastrichtian (Judithian–Lancian), North American Western Interior.

Etymology—"Irvine," the name of the locality that has yielded the greatest number of specimens; combined with Latin, "triton," = salamander, a common suffix for caudate generic names.

Distribution—As for the type and only known species.

Diagnosis—As for the type species.

IRVINETRITON ELONGATUS, sp. nov..

(Fig. 11-11)

Holotype—UALVP 40121, atlantal centrum (Fig. 11-11A–F).

Holotype Horizon and Locality—Middle Campanian (Judithian); Dinosaur Park Formation; Irvine, Alberta, Canada.

Etymology—Latin, "elongatus," = to prolongate or stretch, in reference to the diagnostic, prong-like odontoid process on the atlas.

Referred Specimens—Dinosaur Park Formation, Irvine, Alberta: UALVP 40114–40120, atlantes; Hell Creek Formation, Bug Creek Anthills, Montana: UALVP 40111–40113, atlantes.

Distribution—Middle Campanian-late Maastrichtian, North American Western Interior: Dinosaur Park Formation (Judithian), Alberta, and Hell Creek Formation (Lancian), Montana.

Diagnosis—Species of scapherpetontid differing from all other members of the family in having atlas with anterior cotyles strongly compressed dorsoventrally and odontoid process prong-like. Atlas differs further from that of Piceoerpeton, but resembles Scapherpeton and Lisserpeton, in having articular face of anterior cotyles nearly flat and in having odontoid process elongate and with broad articular surface ventrally for contact with skull; from Scapherpeton and Lisserpeton, but resembles Piceoerpeton, in lacking constriction at base of odontoid process and in having ventral edge of posterior cotyle lying below level of ventral edge of anterior cotyles; and from Scapherpeton and P. naylori, but resembles Lisserpeton and P. willwoodense, in having walls of posterior cotyle lined with thin layer of calcified cartilage. Largest available atlantes are comparable in size to those of P. naylori, but about half the size of largest Scapherpeton and Lisserpeton atlantes, and about one-quarter the size of largest P. willwoodense atlantes.

Description (Fig. 11-11)—Figured atlantes include a size series of eight specimens from Irvine (Fig. 11-11A–M) and three small specimens from Bug Creek Anthills (Fig. 11-11N–P) that range in centra length from about 1.5 to 4.9 mm and intercotylar width from about 2.1 to 5.4 mm. The holotype is the largest and one of the most nearly complete of the available specimens. No specimen preserves an intact neural arch. The largest atlantes of Irvinetriton are less than half the size of the largest atlantes at hand for Scapherpeton and Lisserpeton.

Compared to atlantes of Scapherpeton and Lisserpeton, the atlantal centrum of Irvinetriton is more delicate in build and relatively flatter. The anterior cotyles are strongly compressed dorsoventrally, markedly broader than tall, and oblong in outline. The articular face of the anterior cotyles is flat or shallowly concave from side to side. The lateral edges of the anterior cotyles extend laterally or slightly posterolaterally. The odontoid process is an elongate, relatively narrow process with an unconstricted base, relatively straight lateral margins, and a blunted rounded distal tip. The dorsal surface is flattened and the ventral surface is convex from side to side. A broad articular surface extends across the ventral, lateral, and anterior faces of the process and, on some specimens, wraps around the anterior end onto the dorsal surface.

The posterior cotyle may be weakly compressed laterally and ranges in posterior outline from subcircular to oval. Internally the cotyle is deeply concave, the walls are lined with a thin layer of calcified cartilage, and a notochordal pit opens in approximately the center of the cotyle. The ventral rim of the posterior cotyle lies well below the level of the ventral rim of the anterior cotyles. The ventral surface of the centrum is relatively flat or shallowly concave and is perforated by several subcentral foramina. An indistinct ridge extends along the ventrolateral margin of the centrum. The lateral surface is perforated by two moderate-sized foramina, one just in front of the posterior cotyle and the second, the spinal foramen, opens in the junction between the posterior face of the anterior cotyle and the neural arch wall.

Most specimens, including the holotype, preserve the base of the wall on at least one side. These bases are most reminiscent of the nearly intact neural arch on the referred atlas (UALVP 40104) of Scapherpeton, and suggest that, when intact, the walls of the atlantal neural arch in Irvinetriton were similarly narrow.

Remarks—Atlantal centra of the kind described above have not previously been reported. These new atlantes can be assigned to the Scapherpetontidae based on the dorsoventrally compressed anterior cotyles, prominent odontoid process, and overall form. The new atlantes resemble one another and differ from atlantes of other scapherpetontids in the unique, prong-like shape of the odontoid process and the more dorsoventrally compressed anterior cotyles and in a unique combination of other characters, including:

walls of posterior cotyle lined with thin layer of calcified cartilage (versus anterior part of cotyles infilled with cartilage in Scapherpeton and Piceoerpeton naylori); ventral edge of posterior cotyle lies below level of ventral edge of anterior cotyles (versus ventral edges of cotyles approximately in line in Scapherpeton and Lisserpeton); odontoid process not constricted at base (versus constricted in Scapherpeton and Lisserpeton); odontoid process elongate and with articular surface ventrally (versus short and lacking ventral articular surface in Piceoerpeton); and articular face of anterior cotyles nearly flat (versus deeply excavated in Piceoerpeton). The new atlantes are also relatively small: the largest specimen (UALVP 40121) is approximately the same size as the two atlantes at hand for P. naylori and only about half the size of the largest available atlantes for Scapherpeton and Lisserpeton. The new atlantes are not transitory ontogenetic variants of atlantes referred here to Scapherpeton and Lisserpeton, because size series of atlantes for the last two genera demonstrate that the characteristic atlantal features of both are established early in ontogeny, in specimens equivalent in size to the new atlantes in question, and remain fixed thereafter. Many of the differences that characterize the new atlantes are subtle, yet they are consistent with differences that separate other scapherpetontid genera. On balance, these observations support erecting a new genus and species, namely Irvinetriton elongatus, for receipt of these characteristic, previously unrecognized atlantes.

At present, no other elements have been identified that can be associated with atlantes of Irvinetriton. The lack of trunk vertebrae is perplexing, but not surprising considering that atlantes of Irvinetriton are small, somewhat delicate, and not abundant in collections of the UALVP from Irvine and the Bug Creek Anthills.

Genus and Species Indeterminate
(Fig. 11-12)

Specimens—UALVP 40147–40149, sacrals or anteriormost caudals; UALVP 40150, anterior caudal; UALVP 40151, posterior caudal. All specimens are from the late Maastrichtian (Lancian) Bug Creek Anthills, Hell Creek Formation, Montana.

Description (Fig. 11-12)–Five scapherpetontid vertebrae are identified as coming from the post-trunk region based on the following features: ventral surface of centrum concave; subcentral keel shallow or absent; transverse processes unicipitate and ventrally deflected or absent; and opening(s) for spinal nerve present in posterior half of neural arch. Specimens shown in Figure 11-12 are the first figured examples of scapherpetontid post-trunk vertebrae. All specimens are moderate in size, with centra lengths ranging from about 6.1–7.8 mm.

Three specimens (UALVP 40147–40149) are either sacrals or anteriormost caudals. The two figured specimens, UALVP 40147 (Fig. 11-12A–D) and 40148 (Fig. 11-12E–G), resemble generalized scapherpetontid trunk vertebrae in having the centrum uncompressed, the neural crest low and the neural spine moderately elongate, and zygapophyses prominently developed. All three specimens differ, however, in that the transverse processes are shorter, unicipitate, and directed lateroventrally and the anterior alar process is broader, extending nearly to the distal end of the transverse process. In UALVP 40147 the spinal nerve exited through a notch in the posterior edge of the neural arch wall on the left side, but through a pair of enclosed spinal foramina on the right side (Fig. 11-12A, B). The subcentral keel is low and broad on UALVP 40147 (Fig. 11-12D) and essentially non-existent on UALVP 40149 (unfigured). UALVP 40148 lacks the subcentral keel; instead a low, ridge-like haemal spine extends along the centrum to either side of the ventral midline.

UALVP 40150 (Fig. 11-12H, I) is interpreted as an anterior caudal, from a slightly more posterior location than the three specimens reported above, on the strength of the following features: ridge-like, paired haemal spines deeper and with posterior ends projecting ventroposteriorly; transverse process reduced in length and directed more ventrally; and zygapophyses, particularly posterior pair, reduced in size. Facets on the postzygapophyseal processes are about half the size of those on the prezygapophyseal processes. The structure of UALVP 40151 (Fig. 11-12J–M) is typical for a posterior caudal: the centrum is constricted medially; the neural arch is narrow; the prezygapophyses are small; and the haemal arch is elongate, projects ventroposteriorly, and is enclosed ventroposteriorly by bone. Both walls of the haemal arch are pierced by a large opening and laterally bear short, laterally directed prongs—one on the right wall and two on the left. The neural spine is a posteriorly inclined, elongate tube, with an accessory crest on either side running along the dorsolateral edge of the spine. The posterolateral corners of the neural arch are smooth rounded and lack even a trace of having borne postzygapophyseal processes. A pair of small spinal foramina are present on both sides.

Remarks—The five vertebrae reported above are characteristic for scapherpetontids in being amphicoelous and in lacking the diagnostic crests and processes of other contemporaneous salamanders. Among known scapherpetontids, the vertebrae in question are appropriate in size for Scapherpeton or Lisserpeton, yet all specimens lack the laterally compressed and infilled cotyles seen in trunk vertebrae of Scapherpeton and the interzygapophyseal ridges characteristic of large trunk vertebrae of Lisserpeton. The specimens more closely resemble trunk vertebrae of Lisserpeton in having a thin layer of calcified cartilage lining the inner walls of the cotyles and, in most specimens, the cotyles are subcircular in outline. The posterior cotyle on UALVP 40149 is compressed dorsoventrally; this condition has not reported for any scapherpetontid trunk vertebrae and may indicate that cotylar shape is more variable among post-trunk vertebrae than appears to be the case for presacrals. For the present, I conservatively identify the five post-trunk vertebrae as Scapherpetontidae Indeterminate and, possibly, representing more than one species.

Regardless of their precise affinities, the specimens in question confirm Edward's (1976) report that spinal foramina exit intravertebrally in post-trunk vertebrae of scapherpetontids. Spinal foramina have never been identified in scapherpetontid trunk vertebrae, indicating that spinal nerves exited intervertebrally in the trunk region. Intravertebral exit of spinal nerves limited to post-trunk vertebrae was considered by Edwards (1976) to be a derived condition that united scapherpetontids with dicamptodontines and rhyacotritonines.

FOSSIL RECORD AND PHYLOGENY

Batrachosauroididae

Fossil Record—The fossil record of batrachosauroidids is best documented in North America, where eight genera and nine species ranging in age from early Campanian to Pliocene are recognized: Verdigriserpeton, early Campanian, Alberta; Opisthotriton early Campanian–late Palaeocene, and Prodesmodon, middle Campanian–late Maastrichtian, both North American Western Interior; Parrisia, Campanian, New Jersey;

Batrachosauroides (two species), early Eocene–middle Miocene, southern and western USA; and Peratosauroides, Pliocene, California (e.g., Estes, 1981; Naylor, 1981; Denton and O'Neill, 1998; this study). My earlier report (Gardner, 1994) of batrachosauroidids in the upper part (latest Albian/earliest Cenomanian in age) of the Cedar Formation in Utah relied on several incomplete dentaries and a trunk vertebra; additional vertebrae now available indicate that the specimens in question are from scapherpetontids (Cifelli et al., 1999). Eaton et al. (1999) recently reported "cf. Batrachosauroides sp." in faunal lists for the Dakota Formation (middle–late Cenomanian) and the Smoky Hollow Member (late Turonian) of the Straight Cliffs Formation, both in Utah, but no diagnostic elements were figured or described to support these records.

Batrachosauroidids have a temporally extensive European record, but just one Tertiary genus has been formally named: Palaeoproteus includes two species, one from the late Paleocene of France and the second from the middle Eocene of Germany (Herre, 1935; Estes et al., 1967; Estes, 1981). Two Cretaceous occurrences on the continent are substantiated by diagnostic vertebrae and, perhaps, dentaries from the Purbeck Limestone Formation (Berriasian), England (Ensom et al., 1991; Evans and McGowan, unpublished) and from Champ-Garimond (Campanian), France (Estes, 1981; Duffaud, 1995; Sigé et al., 1997). The former record is the geologically oldest known occurrence for the family. Sanz et al. (1988) briefly reported on small articulated skeletons, with remnants of gill arches, from Las Hoyas (Barremian), Spain, that may represent a new batrachosauroidid genus (Evans and Milner (1996).

The sole reported Asian genus is Mynbulakia Nessov, which includes two species known by isolated elements from the Turonian–Coniacian of Uzbekistan (Nessov, 1981, 1988, 1997). Mynbulakia has been accepted as a batrachosauroidid (Duellman and Trueb, 1986; Milner, 1993; Denton and O'Neill, 1998), but this familial assignment is questionable. Both congeners are named on incomplete jaws (Nessov, 1981:pl. 8, fig. 11 and pl. 11, fig. 10), neither of which are demonstrably batrachosauroidid in construction to judge from published photographs. Photographs (Nessov, 1981:pl. 11, fig. 14) of an atlas referred to the type species M. surgayi Nessov clearly show a prominent odontoid process and shallowly concave anterior cotyles; both features argue against referring this specimen to the Batrachosauroididae. The genus and its two species are best excluded from the family. As an aside, it must be pointed out that the paper attributed by Denton and O'Neill (1998:493) to Nessov (1988), with the title "A description of Mynbulakia surgayi, a new salamander from the Coniacian of Central Asia," does not exist (A. Averianov, pers. comm., 1999). The only descriptions for Mynbulakia and its two species are Nessov's (1981) original Russian language description. Nessov (1988:431) also devoted a short paragraph to the genus in his English language review paper on Mesozoic lizards and amphibians from Middle Asia.

Phylogenetic Relationships—Cranial and vertebral characters and inferences about vertebral musculature provide compelling evidence that batrachosauroidids and proteids are each other's closest relatives (Naylor, 1978, 1979, 1981; Estes, 1981). Although there is no consensus on the position of these families within the Caudata, most schemes place proteids and, when included, batrachosauroidids at an intermediate position somewhere between the more basal hynobiids and cryptobranchids and the more crownward ambystomatids, salamandrids, and plethodontids (e.g., Edwards, 1976; Milner, 1983; Duellman and Trueb, 1986; Larson, 1991, Larson and Dimmick, 1993; R. Cloutier, unpublished analysis cited by Trueb, 1993:fig. 6.9). Monophyly of the Batrachosauroididae is provisionally supported by a unique combination of vertebral synapomorphies: odontoid process an anteriorly shortened, shelf-like process or ridge, that spans between the medial edges of the anterior cotyles and generally lacks articulation anteriorly with the skull; anterior cotyles on atlas deeply concave; and neural spine on trunk vertebrae posteriorly elongate and finished distally in bone. Recent identifications of spinal foramina in the posterior caudals of Opisthotriton (this study) and, perhaps, caudals of Parrisia (Denton and O'Neill, 1998) suggest this derived condition (Edwards, 1976) may be more widespread in batrachosauroidids than previously realized and may prove to be another synapomorphy for the family. The characteristic subcircular anterior cotyles on the atlas are better regarded as a primitive feature (contra Denton and O'Neill, 1998).

Naylor (1981) briefly discussed variation in vertebral morphology among known batrachosauroidids and made three important observations that have phylogenetic implications. First, the condition of the neural crest (= neural spine of Naylor) on the atlas varies among genera. Atlantes identified since confirm that the neural crest is indeed highly variable among batrachosauroidids (Naylor, 1983; Denton and O'Neill, 1998; this study). Naylor (1981) suggested that differences in the form of the atlantal neural crest reflect differences in the cranio-mandibularis muscles and associated ligaments that attached posteriorly onto the roof of atlas. Second, trunk vertebrae for genera then recognized form a morphocline documenting progressive reduction of the calcified infilling of the anterior centrum, as follows: Prodesmodon (strongly opisthocoelous with ball-shaped plug) — Opisthotriton — Batrachosauroides — Palaeoproteus and, likely, Peratosauroides (amphicoelous with minimal infilling). Third, the degree of opisthocoely correlates with the relative size of the posterior basapophyses—i.e., basapophyses are most pronounced on more opisthocoelous vertebrae and are lacking on more amphicoelous vertebrae. Elsewhere Naylor (1979) suggested that opisthocoely and posterior basapophyses in salamanders act in concert to strengthen the vertebral column and provide increased areas of attachment for trunk muscles.

From these and other lines of evidence, Naylor (1981:fig. 5) presented a hand drawn tree of inferred relationships among the five batrachosauroidid genera in which: (1) the Cretaceous genera Opisthotriton and Prodesmodon are each other's closest relatives and occupy a basal position on the tree; (2) the Tertiary genera Batrachosauroides, Palaeoproteus, and Peratosauroides are more derived and are united by reduced opisthocoely and loss of the posterior basapophyses; (3) Batrachosauroides and Palaeoproteus most closely resemble one another and "are readily derivable from a structural ancestor represented by Opisthotriton, either separately or through a common ancestor" (Naylor, 1981:11); and (4) the geologically youngest genus, Peratosauroides, "is perhaps derivable from within Batrachosauroides" (Naylor, 1981:11). The basis for Naylor's (1981) inferred groupings cannot easily be assessed because many character states were not explicitly identified; however, the pattern of relationships he proposed remains testable.

Denton and O'Neill (1998) recently published a cladistic analysis based on three cranial and 16 vertebral characters that yielded one shortest tree, of unreported length, with the following topology: Parrisia (Prodesmodon (Opisthotriton (Batrachosauroides + Palaeoproteus))). Although this topology is appealing on the grounds that it accords well with the stratigraphic and geographic ranges of the batrachosauroidid genera, there are numerous problems with Denton and O'Neill's (1998) analysis that caution against accepting their topology. The most notable of these problems are as follows: (1) of the three outgroup taxa (the proteid Necturus, the plethodontid Plethodon, and the scapherpetontid Scapherpeton) used to polarize characters, only the first is informative—the latter two belong in families that are generally regarded as being crownward of batrachosauroidids and, as such, are uninformative for assessing the relative polarities of character states within the Batrachosauroididae; (2) only Scapherpeton and a hypothetical all zero ancestor were included as outgroups in the analysis—again, Necturus would have been more appropriate because it is a member of the inferred sister-taxon, the Proteidae; (3) five characters can be rejected because they are uninformative and each of the remaining 14 characters is compromised by some combination of misinterpreted polarities, inadequately defined states, and incorrect scores; (4) the geologically youngest genus, Peratosauroides, was unjustifiably excluded from the analysis; (5) the authors evidently restricted their examination of actual specimens to just Parrisia and Opisthotriton; and (6) levels of relative support for clades were not reported. My re-analysis of Denton and O'Neill's (1998:appendix 2) published matrix recovered the same shortest tree, but identified weak support for the clades: their Batrachosauroididae has decay and bootstrap values of four steps and 78%, respectively, but the less inclusive clades collapse in one or two steps and have bootstrap values below 50%.

My examination of intra-familial relationships among batrachosauroidids is at a preliminary stage—in part, because I have not been able to examine representative specimens of Batrachosauroides, Palaeoproteus, Parrisia, and Peratosauroides and, in part, because I have not been able to resolve to my satisfaction the identities of the two atlantal morphs reported above for Opisthotriton. Nevertheless, initial results of my cladistic analysis are worth mentioning because they differ notably from both Naylor's (1981) and Denton and O'Neill's (1998) hypotheses. In addition, I have tried to use my analysis as an opportunity to gauge whether the two atlantal morphs of Opisthotriton can reasonably be accommodated in the same genus or species. The most recent version of my analysis used 20 informative characters scored for three out-group taxa (the representative basal urodeles Hynobius and Cryptobranchus, plus Necturus as a representative of the Proteidae, the inferred sister-taxon of the Batrachosauroididae), and nine in-group taxa (the seven non-Opisthotriton genera; "Opisthotriton A," scored on referred morph I atlantes; and "Opisthotriton B," scored on referred morph II atlantes and the Paleocene skeleton, UALVP 16274 that has this kind of atlas). Further details are given in Appendices 11-1 and 11-2. Six shortest trees of 38 steps were recovered, each with a monophyletic Batrachosauroididae. The strict consensus tree identified the following topology within the family: Palaeoproteus ((Batrachosauroides + Peratosauroides) + ("Opisthotrion A" + "Opisthotriton B" + Parrisia + (Verdigriserpeton (Esteserpeton + Prodesmodon)))). Support for the Batrachosauroididae is high (decay index > four steps; bootstrap = 100%), but support for the less inclusive clades identified in the strict consensus tree much weaker, with decay indices of one or two steps and bootstrap values of 27 to 69%.

The topology of my consensus tree differs from previous hypotheses in shifting the three Tertiary genera to the base of the tree, with the result that Palaeoproteus and Batrachosauroides + Peratosauroides become successive sister-taxa to a less inclusive clade of North American Campanian to Palaeocene terminal taxa. If correct, this arrangement (1) suggests that Naylor's (1981) morphocline leading from opisthocoely to amphicoely is not an evolutionary transition, a possibility he freely acknowledged, and (2) implies that the three inferred basal genera are the Tertiary end products of events that predate the Campanian. The latter point receives some support from the observation that the Campanian trunk vertebra from Champs-Garimond more closely resembles those of Batrachosauroides than any other known batrachosauroidid (Duffaud, 1995 and pers. comm, 2000; Sigé et al., 1997). The inferred sister-pair of Batrachosauroides + Peratosauroides is not inconsistent with Naylor's (1981) proposed ancestor-descendant relationship between the two genera. Within the North American Cretaceous and Paleocene clade, relationships are unresolved both among Parrisia, "Opisthotriton A", and "Opisthotriton B" and between these and the remaining three genera. Much of this uncertainty presumably stems from the fact that trunk and dentary characters cannot be scored for all taxa. My association of the two atlantal morphs of Opisthotriton within a single species receives little support, because "Opisthotriton A" and "Opisthotriton B" are identified as sister-taxa in just one of the six shortest trees; this arrangement hinges on one reversal (teeth pedicellate) that cannot be scored for "Opisthotriton A" and is only identified using the ACCTRAN optimization.

The only consensus that emerges from these three studies is that we lack a robust phylogenetic framework that can be used with much confidence to interpret the evolutionary history of the Batrachosauroididae. My revision of North American Campanian and Maastrichtian taxa—although admittedly unsatisfactory with regards to the identities of the two referred atlantal morphs of Opisthotriton—is an important step in this direction. Further work on these and other batrachosauroidid taxa and specimens is clearly warranted, and may help clarify intra-familial relationships. Specimens that promise to be particularly informative in this regard include the various skeletons from the Palaeocene of Wyoming (Estes, 1969a, 1975) and Alberta (collection of the UALVP) have been referred to Opisthotriton and skeletons of the suspected batrachosauroidid (Evans and Milner, 1996) from the Lower Cretaceous of Spain.

Scapherpetontidae

Fossil Record-In North America scapherpetontids are known from the late Albian/early Cenomanian to late Paleocene in the Western Interior and from the middle Eocene of Ellesmere Island, in the Canadian Arctic Archipelago. Four genera and five species are formally recognized: Scapherpeton, early Campanian-late Paleocene; Lisserpeton, middle Campanian-middle Paleocene; Piceoerpeton (two species), late Maastrichtian-middle Eocene; and Irvinetriton, middle Campanian-late Maastrichtian. Eaton et al. (1999) reported "Scapherpetontidae new genus and species" in a preliminary faunal list for the middle Campanian (Judithian) Kaiparowits Formation, Utah, but they did not provide any descriptions or figures of specimens. In a larger faunal review paper on vertebrates from the upper part (latest Albian/earliest Cenomanian) of the Cedar Mountain Formation, Cifelli et al. (1999) briefly reported on isolated scapherpetontid trunk vertebrae, atlantes, and dentaries. Atlantes in this collection suggest the presence of two taxa, which may be distinct at the generic level: one kind of atlas resembles that of Lisserpeton and the second resembles that of Piceoerpeton.

Reports of scapherpetontids from outside of North America are founded on isolated bones from the Cretaceous of Middle Asia (e.g., Nessov, 1981, 1988, 1997) and have been accepted without debate (Duellman and Trueb, 1986; Milner, 1993). These elements have been assigned to two genera and three species: Eoscapherpeton Nessov (two species) from the late Albian-Santonian and, perhaps, early Campanian of Uzbekistan, Kazakhstan, and Tadjikistan, and Horezmia Nessov from the late Albian-late Cenomanian and, perhaps, early Turonian of Uzbekistan (Nessov, 1981, 1988, 1997). Published figures of atlantes of Eoscapherpeton (e.g., Nessov, 1988:pl. 15, figs. 1-4) and

Horezmia (e.g., Nessov, 1988:pl. 8, fig. 17) indicate that these differ substantially from atlantes of North American scapherpetontids in having the anterior cotyles circular in Horezmia or compressed laterally in Eoscapherpeton (versus compressed dorsoventrally), in having the neural arch broadly rounded dorsally and bearing massive postzygapophyseal processes (versus pointed distally and having more delicate postzygapophyses), and in bearing a prominent, keel-like hypapophyseal spine ventrally (versus no ventral processes). Published figures (Nessov, 1981:pl. 12, fig. 1a) of a referred trunk vertebra of E. asiaticum Nessov further show a shallowly inclined and, evidently, short neural spine; this differs from the steeply inclined and posteriorly elongate neural spine that is diagnostic for North American scapherpetontid trunk vertebrae. Eoscapherpeton and Horezmia are distinctive and, almost certainly, closely related salamanders, but neither can be accommodated within the Scapherpetontidae as that family is currently understood. Pending further study, the two Asian genera are better regarded as Caudata indeterminate.

Phylogenetic Relationships—Relationships among scapherpetontids have not been analyzed cladistically. Although sufficient taxa (five species) and vertebral characters are now available to permit such an analysis, I have deferred doing so until (1) associations of cranial elements that have been referred to Scapherpeton and Lisserpeton are better corroborated, (2) character state distributions are adequately surveyed among appropriate out groups, and (3) character state polarities are better established. Because I place scapherpetontids within the Ambystomatoidea (sensu Estes, 1981), members of the three other ambystomatoid groups (ambystomatids, dicamptodontines, and Rhyactotriton) are the most appropriate out groups for judging character state polarities. Evidence from vertebral structure and comparisons with Ambystoma Tschudi, the type species of the Ambystomatidae Hallowell, allows for a preliminary assessment of character state polarities and relationships within the Scapherpetontidae.

No autapomorphies are recognized for the Scapherpetontidae, but monophyly of the family is provisionally supported by a unique combination of vertebral character states that I interpret as being derived within caudates: basapophyses absent; anterior cotyles on atlas dorsoventrally compressed; neural spine on trunk vertebrae developed into a posteriorly elongate, spike-like process; and transverse processes divergently bicipitate along vertebral column. Vertebrae of Scapherpeton exhibit a number of character states that appear to be derived with respect to other ambystomatoids (e.g., trunk vertebrae with laterally compressed condyles and deep, elaborated subcentral keel; atlas with neural arch elongate, posteriorly inclined, finished dorsally in bone, and neural spine paired), but these elements exhibit no features that nest the genus in a less inclusive clade within the family. Scapherpeton thus appears to be the basalmost member of the family, a position that is consistent with its earlier (early Campanian) first appearance.

A less inclusive clade of Lisserpeton, Irvinetriton, and Piceoerpeton is provisionally supported by three derived character states: vertebral cotyles less infilled with calcified cartilage, relative to the condition in Scapherpeton; anterior cotyles on atlas more dorsoventrally compressed; and odontoid process flattened dorsally. Relationships within this less inclusive clade cannot be satisfactorily resolved at present. A close relationship between Lisserpeton and Piceoerpeton has been suggested previously (Estes, 1969a, 1981; Naylor and Krause, 1981), and Naylor and Krause (1981:516) listed a number of vertebral resemblances between the two genera in support of this idea. Of the suite of features identified by Naylor and Krause (1981), only the more divergent transverse processes and taller, more posteriorly elongate neural crest are probable synapomorphies. Unfortunately, neither of these characters can be determined for Irvinetriton. Other features noted by Naylor and Krause (1981) are either probably primitive resemblances (trunk vertebral cotyles subcircular; subcentral keel shallow; zygapophyseal processes laterally divergent) or their distribution is more complex than was previously realized. For example, cotyles are coated internally with a thin layer of calcified cartilage in Lisserpeton and P. willwoodense, but with a thicker layer in P. naylori. Although the dorsal transverse process consistently originates at the laterodorsal corner of the neural arch roof in Lisserpeton, the process originates below this point in the one trunk vertebra available for P. naylori and it is now evident that both conditions occur in P. willwoodense (cf., Naylor and Krause, 1981:text-fig. 2B versus here:Fig. 11-10E). Naylor and Krause (1981:517) also noted that the medial part of the pars palatinum is expanded posteriorly on referred premaxillae of Lisserpeton and Piceoerpeton; this probably is a derived condition and, depending on the proper allocation of the maxillae traditionally referred to Lisserpeton, could be further evidence for a close relationship between the two genera. At present, however, this character cannot be scored for Irvinetriton. The other possible sister-pairing, between Piceoerpeton and Irvinetriton, is supported by two evidently derived atlantal character states: base of odontoid process unconstricted and ventral rim of posterior cotyle lies below level of ventral rims of anterior cotyles.

Although preliminary, the hypothesized relationships outlined above present a framework that can be tested in the future by a rigorous cladistic analysis. Ideally such an analysis would include cranial characters, a broader representation of outgroup taxa, and any additional scapherpetontid taxa that may be recognized in the meantime.

CONCLUSIONS

Study of batrachosauroidid and scapherpetontid salamanders, with particular reference to vertebrae from the latest Cretaceous (Campanian and Maastrichtian) of the North American Western Interior, yields the following findings:

(1) The Batrachosauroididae are reliably known by isolated elements and occasional skeletons from the Campanian to Pliocene of North America and the Berriasian, Campanian, and late Paleocene-early Eocene of Europe. The Scapherpetontidae are an exclusively North American family and are known by isolated elements from the latest Albian/earliest Cenomanian and Campanian-middle Eocene. Reports of batrachosauroidids from the Turonian and Coniacian and of scapherpetontids from the Cenomanian-Campanian of Middle Asia are rejected. For taxa that are known by isolated elements, associations of vertebrae (atlantes, trunk vertebrae, and caudals) are generally well understood; associations of vertebrae with cranial and appendicular elements generally are less well corroborated.

(2) Diagnostic atlantes and trunk vertebrae permit the identification of four batrachosauroidid species in the Campanian and Maastrichtian of the Western Interior: *Opisthotriton kayi* early Campanian-late Paleocene), *Prodesmodon copei* (middle Campanian-late Maastrichtian), and the new genera and species *Esteserpeton robustus* (late Maastrichtian), and *Verdigriserpeton bifurcatus* (early Campanian).

(3) The name *Opisthotriton gidleyi*, erected on a fragmentary and poorly preserved skull from the middle Paleocene of Montana, is judged to be a *nomen dubium*. Two distinctive atlantal morphs are described and illustrated for the type species *O. kayi*. Although these morphs differ from one another to the same extent that each differs from

atlantes of other batrachosauroidid genera, both morphs are conservatively retained in O. kayi because neither can be associated with more confidence than the other with the diagnostic holotype vertebra of O. kayi and because examples of both atlantal morphs occur in referred Palaeocene skeletons of O. kayi having trunk vertebrae all but identical to the holotype vertebra. A posterior caudal with spinal foramina is described for O. kayi; this is the second report of spinal foramina in caudal vertebrae of batrachosauroidids.

(4) Four scapherpetontid species are identified on the basis of characteristic vertebrae from the Campanian and Maastrichtian of the Western Interior: Scapherpeton tectum (early Campanian-late Paleocene), Lisserpeton bairdi (middle Campanian–late Palaeocene), the new species Piceoerpeton naylori (late Maastrichtian), and the new genus and species Irvinetriton elongatus (middle Campanian–late Maastrichtian). Size series of atlantal centrum and an atlas with a nearly complete arch are described and figured for both S. tectum and L. bairdi; these demonstrate that atlantal centra differ subtly, yet consistently, between the two species, whereas the atlantal neural arches are markedly different.

(5) Relationships within both families are not well understood. A preliminary cladistic analysis of relationships within the Batrachosauroididae differs from previous hypotheses in placing European and North American Tertiary genera basal to a less inclusive clade containing all North America Cretaceous genera. Although relationships with the Scapherpetontidae have not been subjected to cladistic analysis, distributions of vertebral character states suggest that Scapherpeton is the basalmost taxon and the sister of a clade consisting of Lisserpeton + Piceoerpeton + Irvinetriton. Both hypotheses provide frameworks that can be tested in the future by more rigorous cladistic analyses.

FIGURE 11-1. Undescribed skeleton of Opisthotriton kayi Auffenberg; Genesee, late Paleocene (Tiffanian), Paskapoo Formation, Alberta. **A**, **B**, UALVP 16244, nearly complete skeleton, (**A**) exposed in approximately dorsal aspect, with white box indicating area shown in (**B**) anterior part of skeleton, exposed in dorsal and slightly right lateral view; note presence of "morph II" atlas (cf., Fig. 11-3). Figures at different scales: top scale bar (**A**) = 7 cm and bottom scale bar (**B**) = 3 mm.

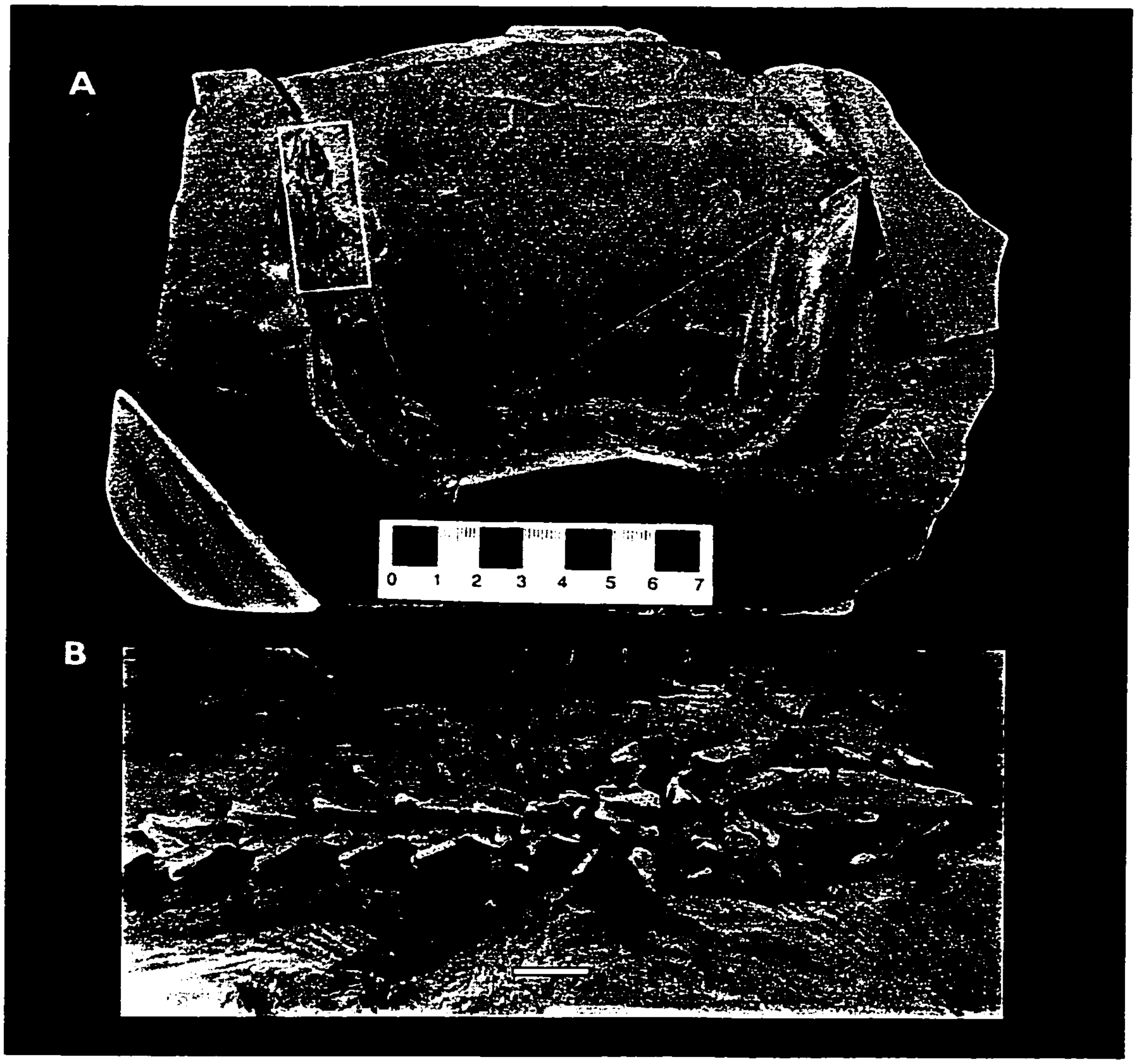
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FIGURE 11-2. Size series of "morph I" atlantes of Opisthotriton kayi Auffenberg; Bug Creek Anthills, late Maastrichtian (Lancian), Hell Creek Formation, Montana. **A–C**, UALVP 40056, in (**A**) anterior, (**B**) left lateral, and (**C**) dorsal views; **D–F**, UALVP 40057, in (**D**) anterior, (**E**) right lateral, and (**F**) dorsal views; **G–K**, UALVP 40058, in (**G**) anterior, (**H**) posterior, (**I**) right lateral, (**J**), dorsal, and (**K**) ventral views; **L–N**, UALVP 40059, in (**L**) anterior, (**M**) right lateral, and (**N**) dorsal views; **O–Q**, UALVP 40061, in (**O**) anterior, (**P**) right lateral, and (**Q**) dorsal views. Specimens at same scale: scale bar = 1 mm.

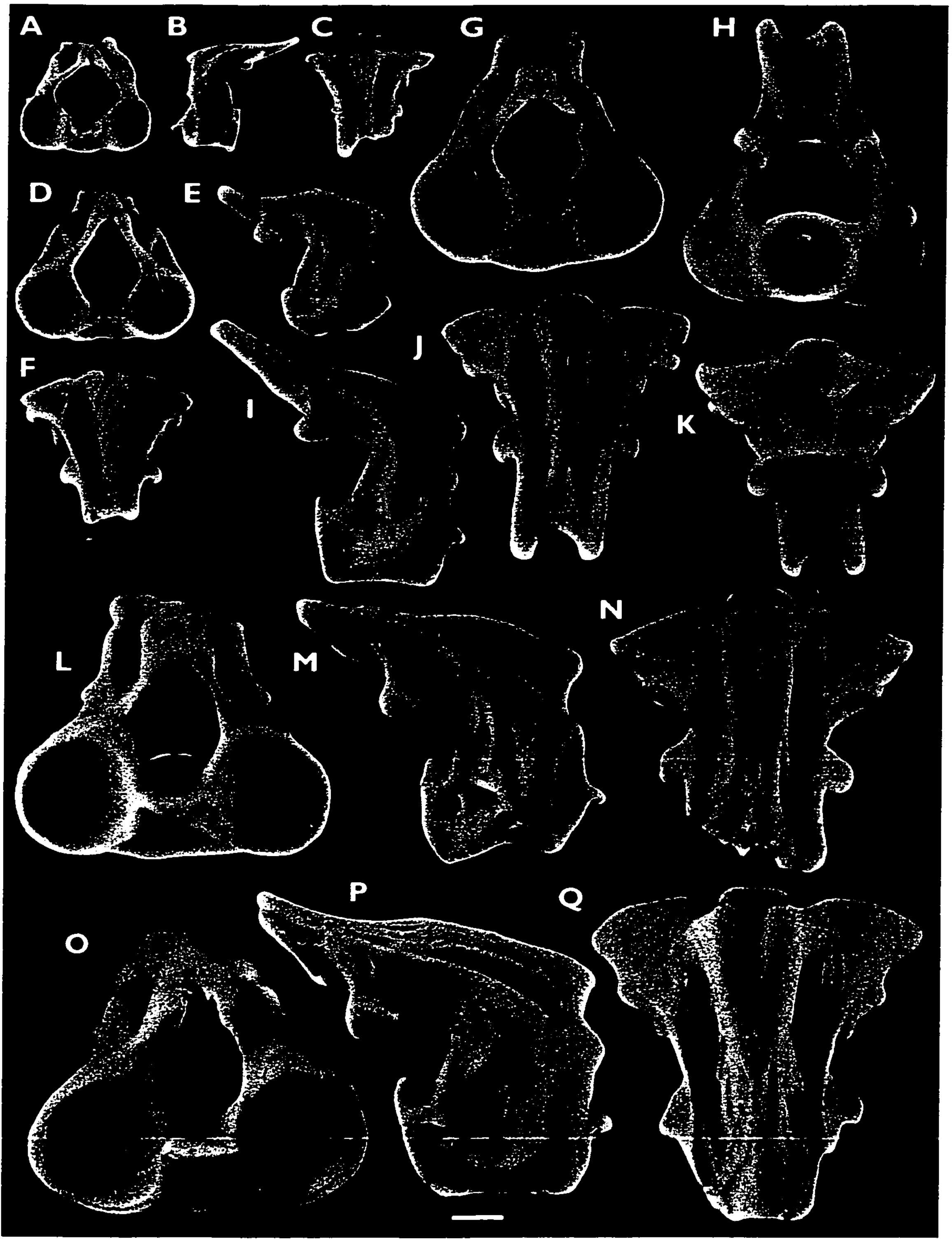
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FIGURE 11-3. "Morph II" atlantes of Opisthotriton kayi Auffenberg; early and middle Campanian (Aquilan and Judithian) and late Maastrichtian (Lancian), North American Western Interior. **A–C**, UALVP 40063, in (**A**) anterior, (**B**) right lateral, and (**C**) dorsal views; **D–H**, UALVP 40064, in (**D**) anterior, (**E**) posterior, (**F**) left lateral, (**G**) dorsal, and (**H**) ventral views; **I–K**, UALVP 40066, in (**I**) anterior, (**J**) right lateral, and (**K**) dorsal views; **L–P**, UALVP 12096, in (**L**) anterior, (**M**) posterior, (**N**) left lateral, (**O**) dorsal, and (**P**) ventral views; **Q**, UALVP 40067, in right lateral view; **R**, **S**, UALVP 40068, in (**R**) anterior and (**S**) right lateral views. Provenances: UALVP 40063, 40064, Bug Creek Anthills (Lancian), Hell Creek Formation, Montana; UALVP 40066, Bushy Tailed Blowout (Lancian), Lance Formation, Wyoming; UALVP 12096, 40067, Irvine (Judithian), Dinosaur Park Formation, Alberta; UALVP 40068, MR-9 (Aquilan), Deadhorse Coulee Member, Milk River Formation, Alberta. Specimens at different scales: bottom left (**A–Q**) and bottom right (**R**, **S**) scale bars = 1 mm.

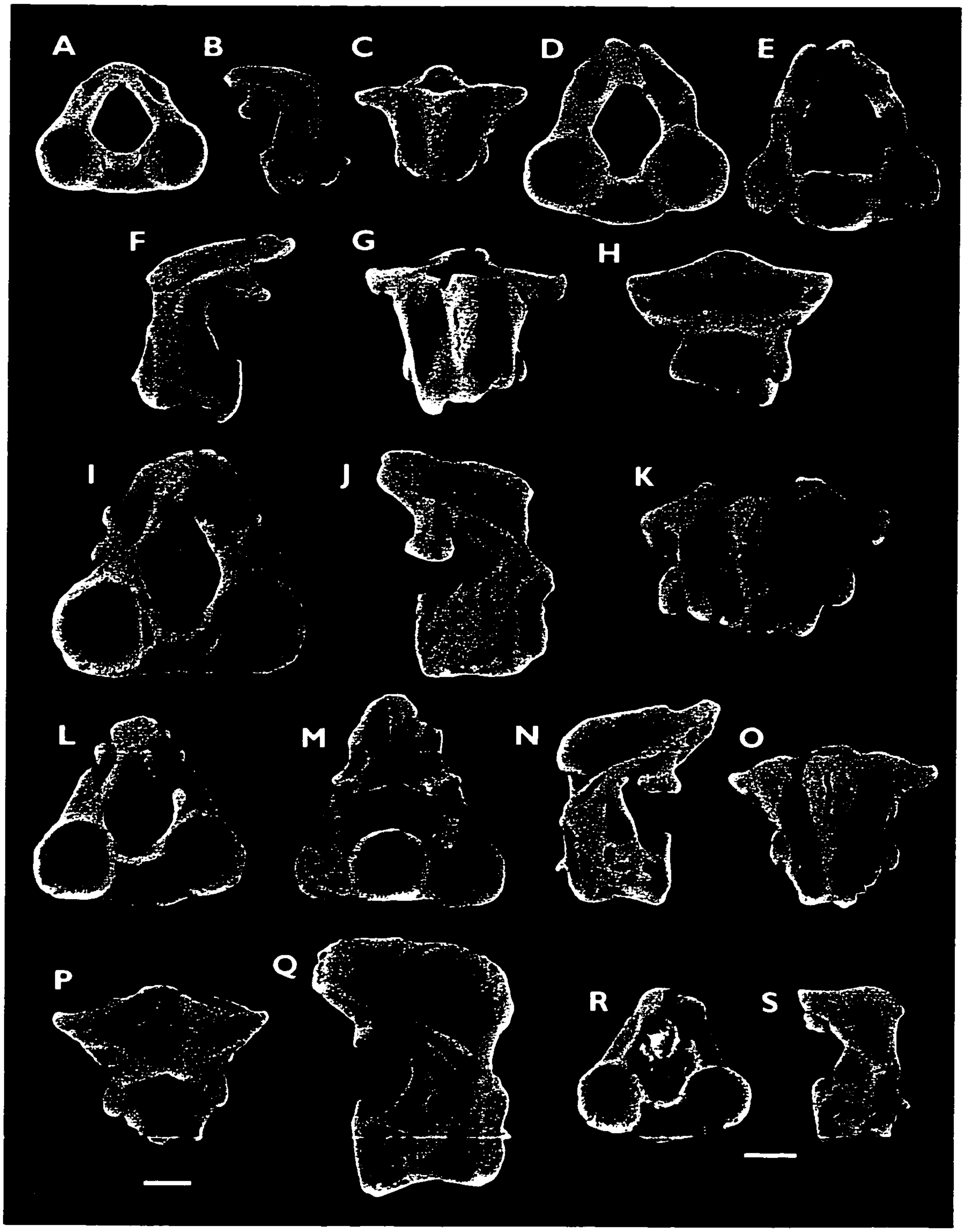
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FIGURE 11-4. Post-atlantal vertebrae of Opisthotriton kayi Auffenberg; late Maastrichtian (Lancian), USA. **A–E**, UALVP 40071, post-cervical anterior trunk vertebra, in (**A**) right lateral, (**B**) dorsal, (**C**) ventral, (**D**) anterior, and (**E**) posterior views; **F–I**, UALVP 40069, first trunk vertebra, in (**F**) right lateral, (**G**) oblique (anterior and right lateral), (**H**) dorsal, and (**I**) ventral views; **J**, UALVP 40070, second trunk vertebra, in oblique (right lateral and slightly anterior) view; **K**, **L**, UALVP 40072, middle trunk vertebra, in (**K**) left lateral and (**L**) dorsal views; **M**, UALVP 40073, posterior trunk vertebra, in left lateral view; **N–R**, UALVP 40074, caudal vertebra, in (**N**) right lateral view and with hair passing through spinal foramen and in (**O**) dorsal, (**P**) ventral, (**Q**) anterior, and (**R**) posterior views. Provenances: UALVP 40071, Bushy Tailed Blowout, Lance Formation, Wyoming; other specimens are from Bug Creek Anthills, Hell Creek Formation, Montana. Specimens at same scale: scale bar = 1 mm.

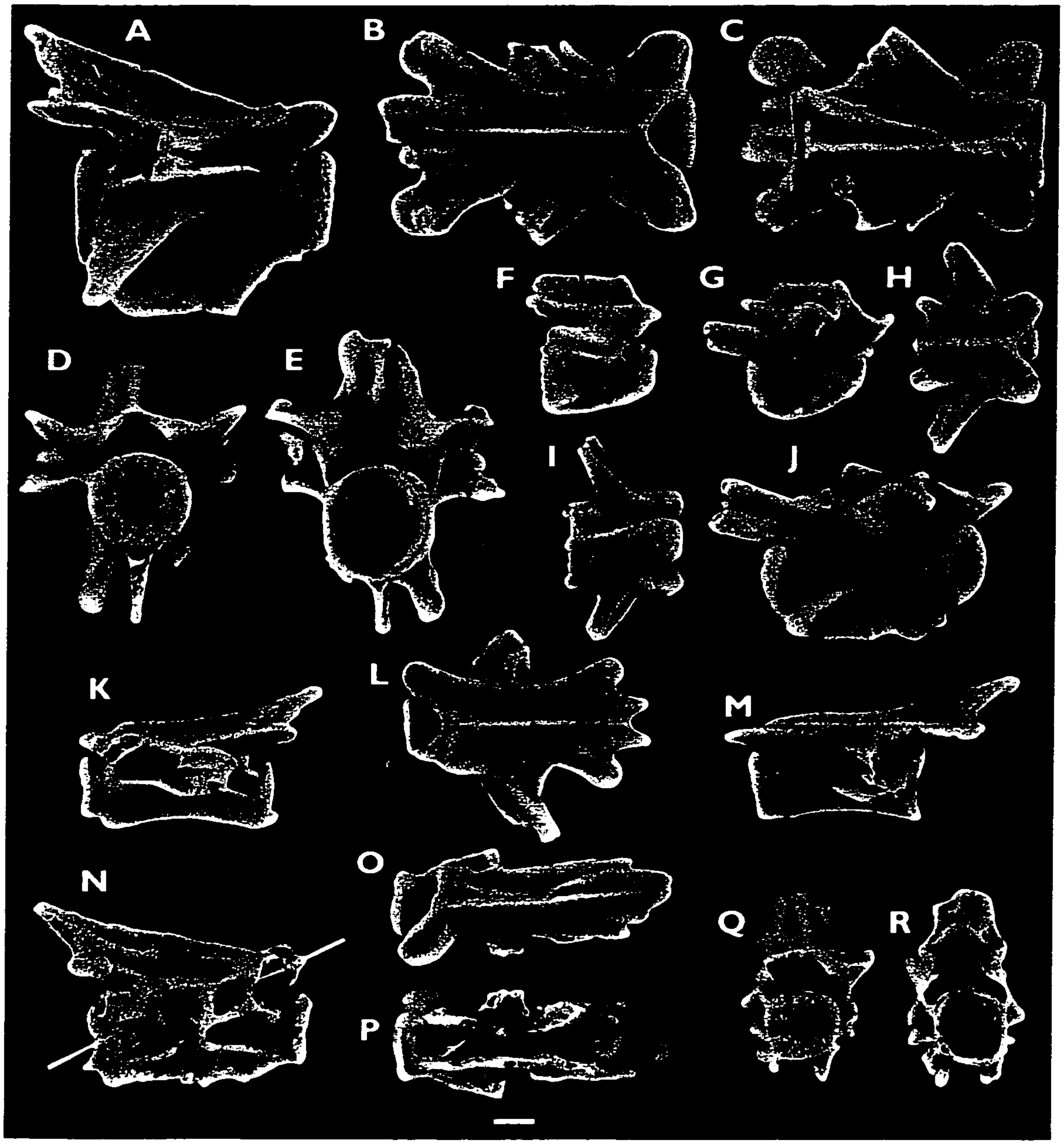
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FIGURE 11-5. Atlantes of Prodesmodon copei Estes; late Maastrichtian (Lancian), USA. **A–C**, UALVP 40075, in (**A**) anterior, (**B**) right lateral, and (**C**) dorsal views; **D–G**, UCM 43504, in (**D**) anterior, (**E**) right lateral, (**F**) dorsal, and (**G**) ventral views; **H–M**, UALVP 12095, in (**H**) anterior, (**I**) posterior, (**J**) right lateral, (**K**) dorsal, (**L**) oblique (dorsoanterior), and (**M**) ventral views. Provenances: UALVP 40075, 12095, Bushy Tailed Blowout, Lance Formation, Wyoming; UCM 43504, Bug Creek Anthills, Hell Creek Formation, Montana. Specimens at same scale: scale bar = 1 mm.

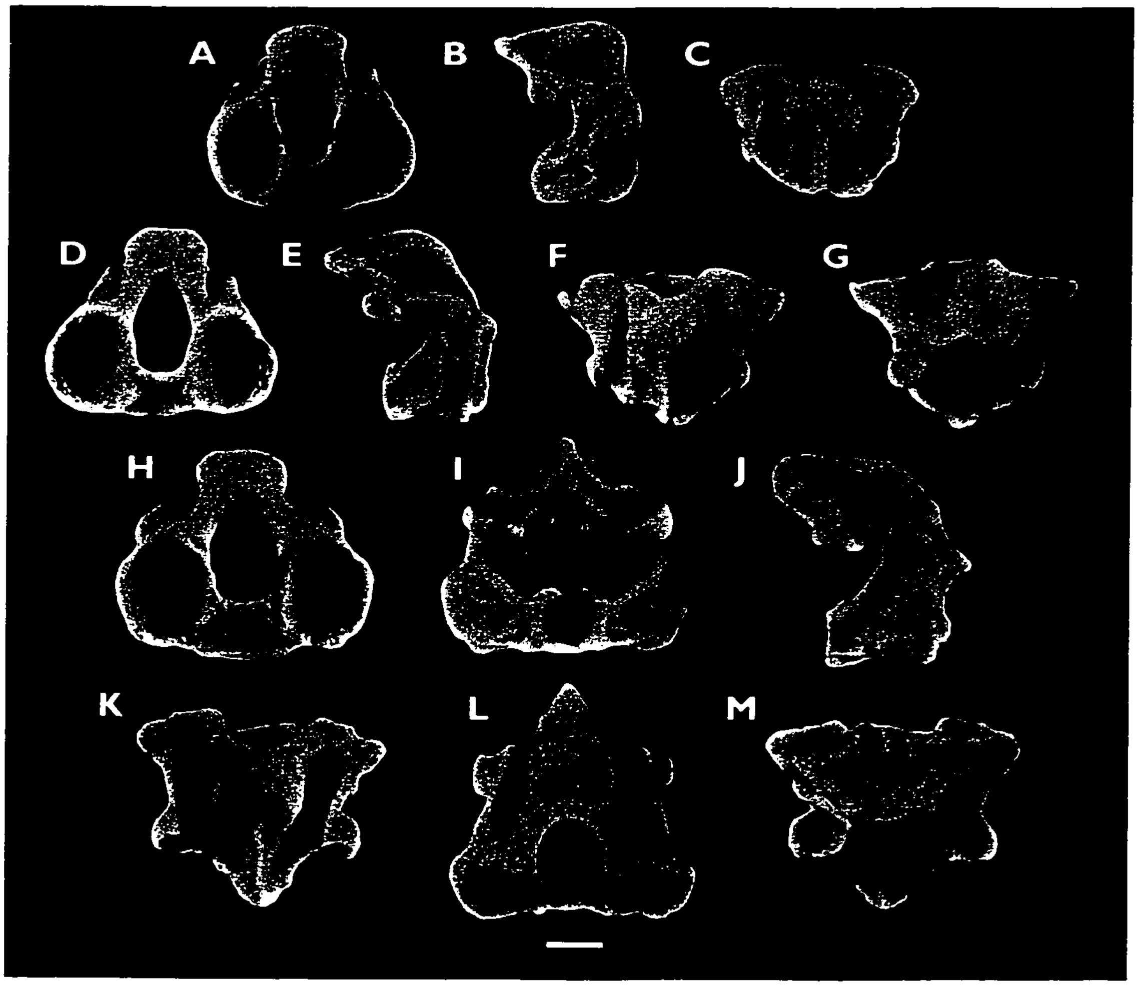
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FIGURE 11-6. Trunk vertebrae of Prodesmodon copei Estes; late Maastrichtian (Judithian), USA. **A–D**, MCZ 3652a, first trunk vertebra, in (**A**) right lateral, (**B**) oblique (anterior and right lateral), (**C**) dorsal, and (**D**) ventral views; **E**, **F**, UCM 43328, post-cervical anterior trunk vertebra in (**E**) right lateral and(**F**) dorsal views; **G–J**, MCZ 3652"b", middle trunk vertebra, in (**G**) left lateral, (**H**) dorsal, (**I**) anterior, and (**J**) posterior views, with arrows (**G**, **I**) pointing to anterior opening of vertebrarterial canal; (**K**) UALVP 40076, posterior trunk vertebra, in dorsal view. Provenances: MCZ 3652a, 3652b, UCM 43328, Bug Creek Anthills, Hell Creek Formation, Montana; UALVP 40076, Bushy Tailed Blowout, Lance Formation, Wyoming. Specimens at same scale: scale bar = 1 mm.

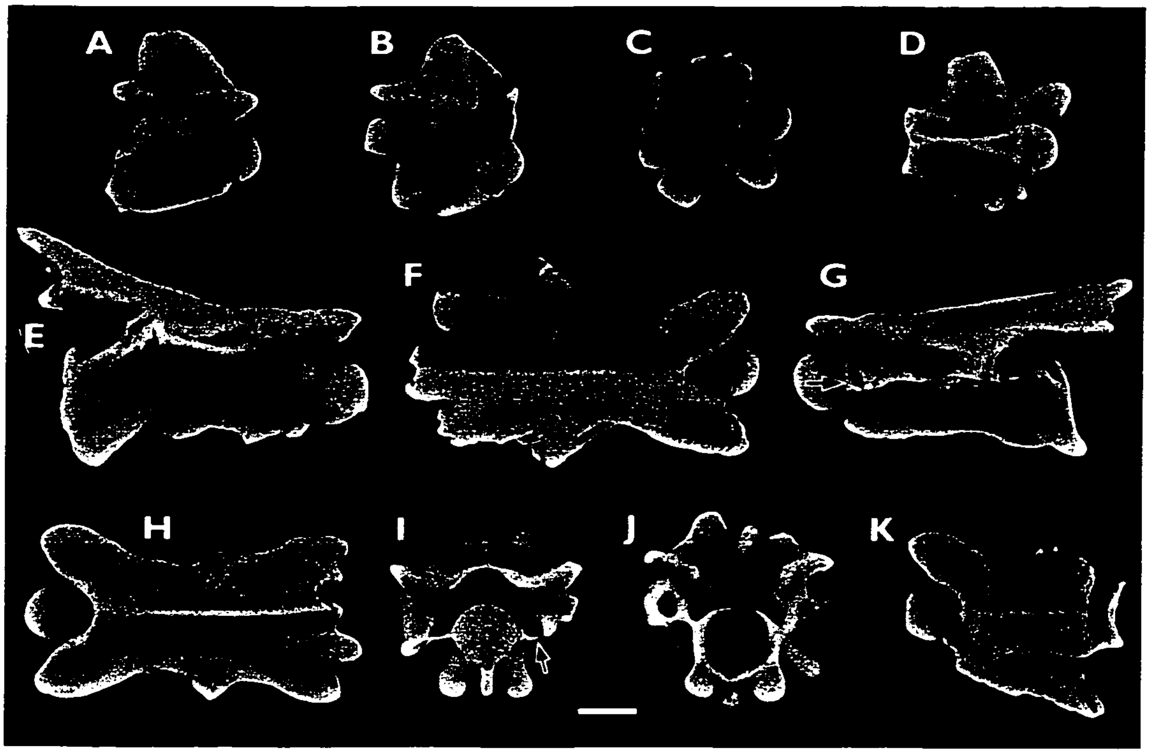
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FIGURE 11-7. Vertebrae of new batrachosauroidid genera and species; early Campanian (Aquilan) and late Maastrichtian (Lancian), North American Western Interior. Esteserpeton robustus, gen. et sp. nov. (A–F); unknown site, late Maastrichtian (Lancian), type Lance Formation, Wyoming: USNM 482352, holotype, nearly complete atlas, in (A) anterior, (B) posterior, (C) left lateral, (D) right lateral, (E) dorsal, and (F) ventral view. Verdigriserpeton bifurcatus, gen. et sp. nov. (G–R); MR localities, early Campanian (Aquilan), Deadhorse Coulee Member, Milk River Formation, Alberta: **G–L**, UALVP 16252, holotype, nearly complete atlas missing outer edge of right anterior cotyle and posterior end of neural arch, in (G) anterior, (H) posterior, (I) left lateral, (J) oblique (dorsoanterior), (K) dorsal, and (L) ventral views; **M–O**, UALVP 16251, atlas, in (M) anterior, (N) ventral, and (O) dorsoanterior views; **P–R**, UALVP 40079, trunk vertebra, in (P) right lateral, (Q) dorsal, and (R) ventral views. Specimens at different scale: middle (A–F), bottom left (G–O), and bottom right (P–R) scale bars = 1 mm.

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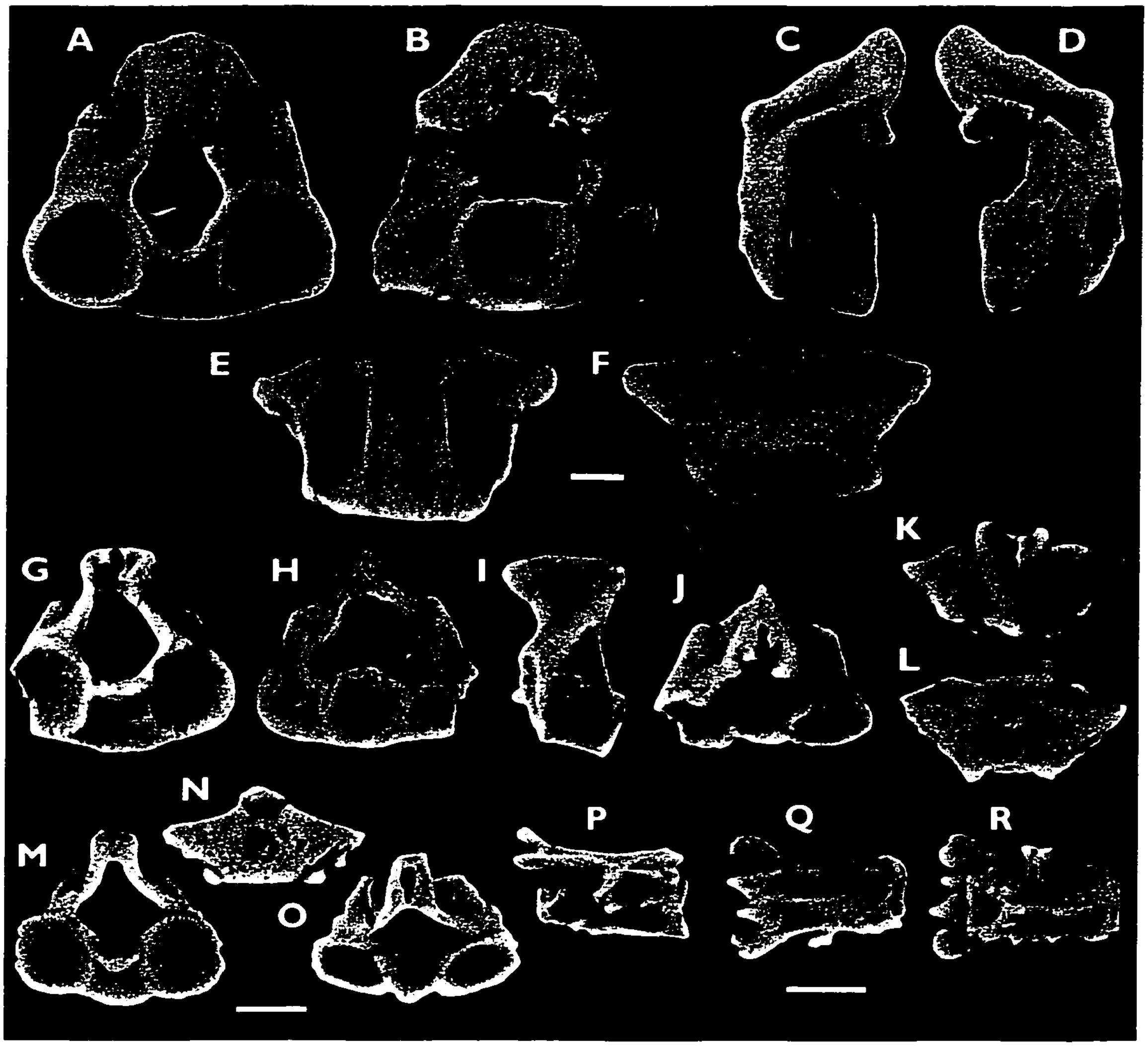

FIGURE 11-8. Atlantes and trunk vertebrae of Scapherpeton tectum Cope; middle Campanian (Judithian) and late Maastrichtian (Lancian), North American Western Interior. Atlantes (**A–II**): **A–L**, UALVP 40092–40103, respectively, size series of 12 atlantal centra, all in dorsal view; **M–R**, UALVP 40104, nearly complete atlas, missing right postzygapophysis, in (**M**) anterior, (**N**) posterior, (**O**) right lateral, (**P**) left lateral, (**Q**) dorsal, and (**R**) ventral views; **S–CC**, UALVP 40080–40090, respectively, size series of 11 atlantal centrum, all in dorsal view: **DD–II**, UALVP 40091, atlantal centrum, in (**DD**) anterior, (**EE**) posterior, (**FF**) right lateral, (**GG**) left lateral, (**HH**) dorsal, and (**II**) ventral views. Trunk vertebrae (**JJ–TT**): **JJ–MM**, UALVP 40107, first trunk vertebra, in (**JJ**) left lateral, (**KK**) dorsal, (**LL**) ventral, and (**MM**) posterior views; **NN**, UALVP 40108, post-cervical anterior trunk vertebra, in left lateral view; **OO–QQ**, UALVP 40110, middle trunk vertebrae, in (**OO**) left lateral, (**PP**) anterior, and (**QQ**) posterior views; **RR–TT**, UALVP 40109, posterior trunk vertebra, in (**RR**) left lateral, (**SS**) dorsal, and (**TT**) ventral views. Provenances: UALVP 40092–40104, 40109, Bug Creek Anthills (Lancian), Hell Creek Formation, Montana; UALVP 40107, 40108, Bushy Tailed Blowout (Lancian), Lance Formation, Wyoming; UALVP 40080–40091, 40110, Irvine (Judithian), Dinosaur Park Formation, Alberta. Specimens at same scale: scale bar = 1 mm.

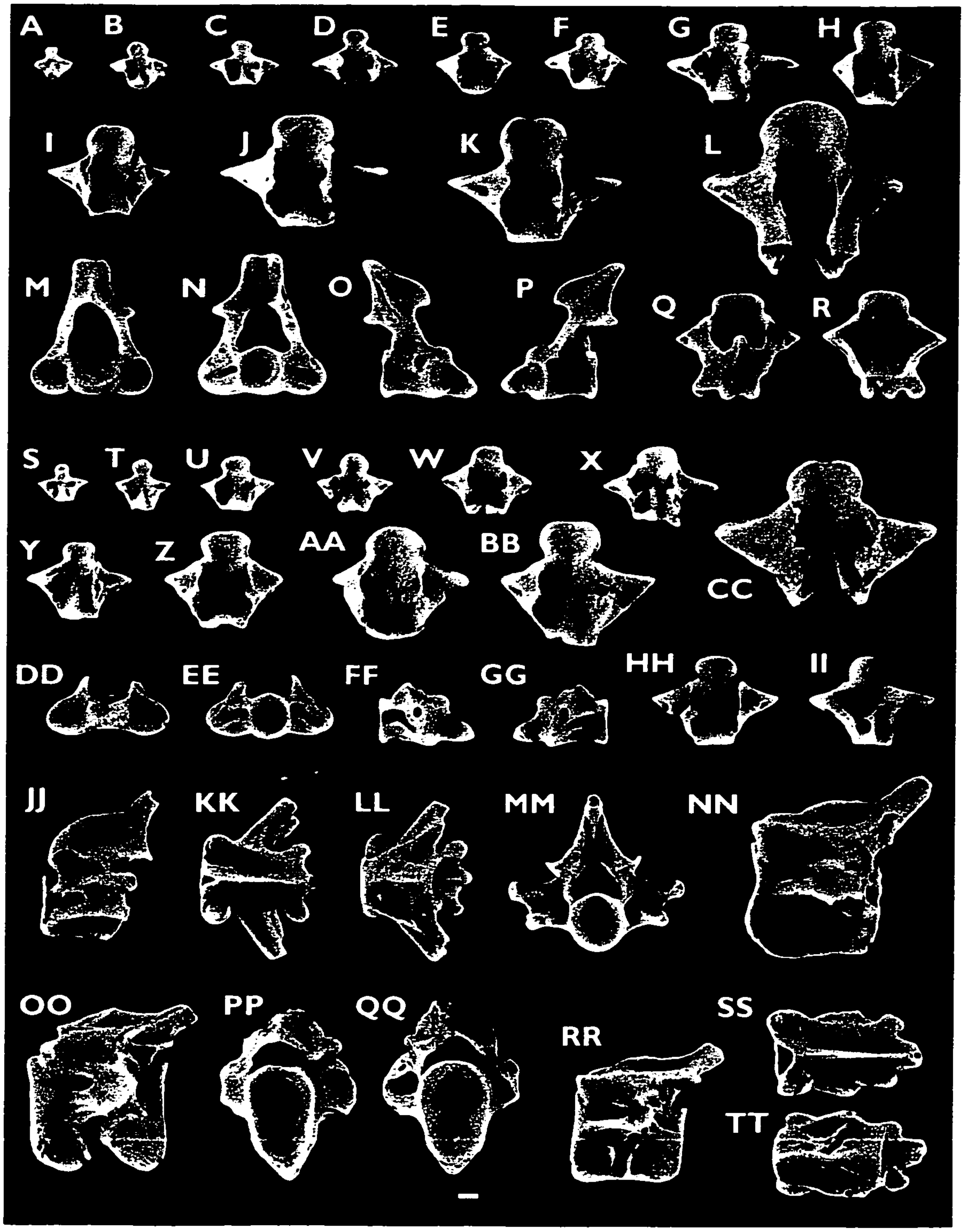
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FIGURE 11-9. Atlantes and trunk vertebrae of Lisserpeton bairdi Estes; middle Campanian (Judithian) and late Maastrichtian (Lancian), North American Western Interior. Atlantes (**A–CC**): **A–J**, UALVP 40123–40131 and 40133, respectively, size series of ten atlantal centra, all in dorsal view; **K–P**, UALVP 40134, nearly complete atlas, missing most of left postzygapophysis, in (**K**) anterior, (**L**) posterior, (**M**) right lateral, (**N**) left lateral, (**O**) dorsal, and (**P**) ventral views; **Q–Y**, UALVP 40135–40143, respectively, size series of nine atlantal centrum, all in dorsal view: **Z–CC**, UALVP 40144, atlantal centrum, in (**Z**) anterior, (**AA**) posterior, (**BB**) right lateral, and (**CC**) left lateral views. Trunk vertebrae (**DD–NN**): **DD–GG**, UALVP 40145, first trunk vertebra, in (**DD**) right lateral, (**EE**) dorsal, (**FF**) ventral, and (**GG**) posterior views; **HH**, **II**, UALVP 14892, post-cervical anterior trunk vertebra, in (**HH**) left lateral and (**II**) dorsal views; **JJ–NN**, UALVP 14893, middle or posterior trunk vertebra, in (**JJ**) left lateral, (**KK**) dorsal, (**LL**) ventral, (**MM**) anterior, and (**NN**) posterior views. Provenances: UALVP 40123–40134, 40145, 14892, 14893, Bug Creek Anthills (Lancian), Hell Creek Formation, Montana; UALVP 40135–40144, Irvine (Judithian), Dinosaur Park Formation, Alberta. Specimens at different scales: middle (**A–CC**) and bottom (**DD–NN**) scale bars = 1 mm.

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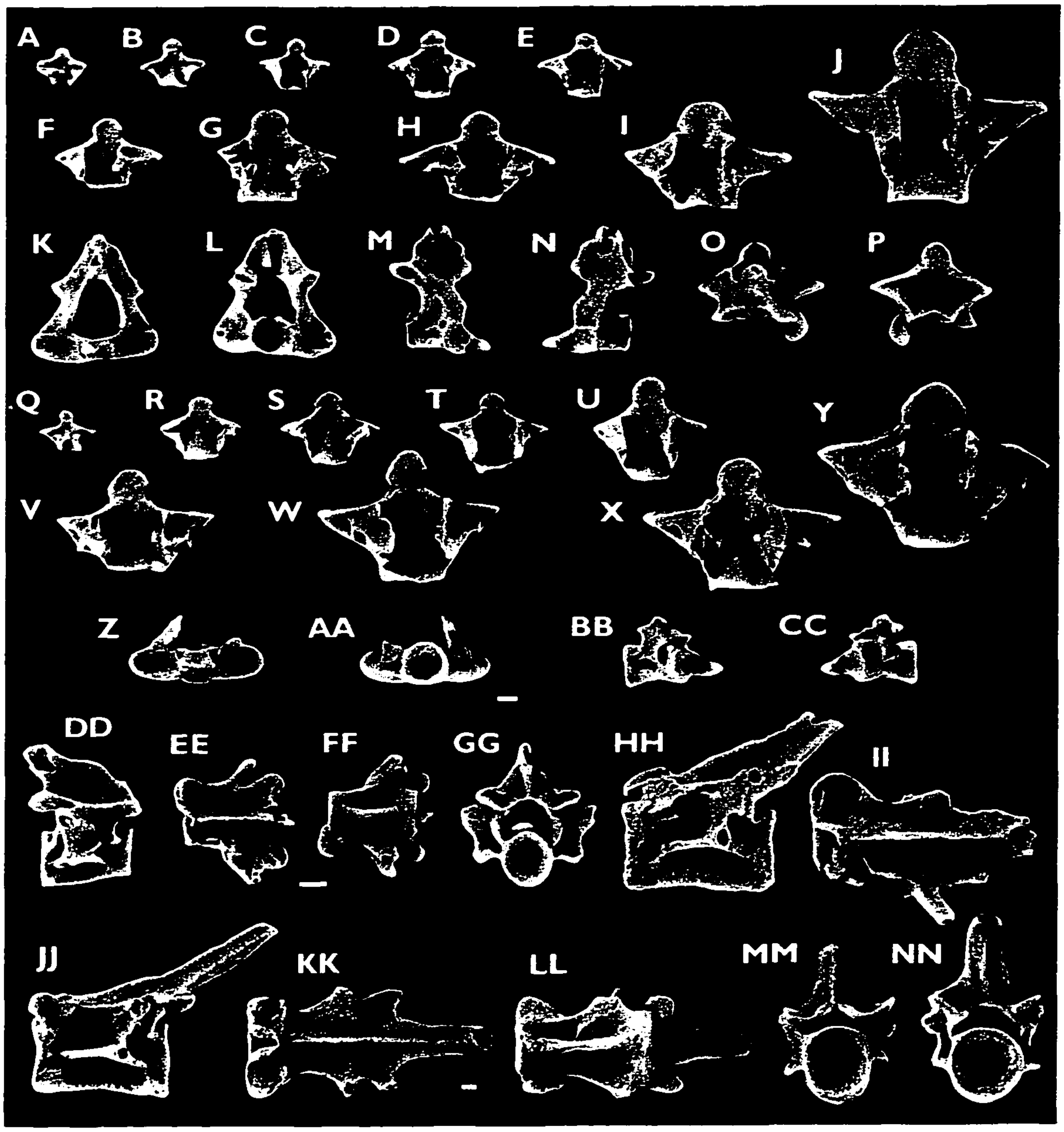
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FIGURE 11-10. Atlantes and trunk vertebrae of Piceoerpeton Meszoely; late Maastrichtian (Lancian) and late Paleocene (Tiffanian), USA. Piceoerpeton willwoodensis Meszoely, type species (**A–H**): **A**, UALVP 11771, atlas missing posterior part of neural arch, in anterior view; **B–D**, UALVP 11766, atlantal centrum, in (**B**) anterior, (**C**) dorsal, and (**D**) ventral views; **E–H**, SMM P76.28.238, trunk vertebra, in (**E**) left lateral, (**F**) dorsal, (**G**) ventral, and (**H**) oblique (left lateral, anterior, and slightly and dorsal) views. Provenances: UALVP 11771, 11766, Roche Percée localities, Ravenscrag Formation, Saskatchewan; SMM P76.28.238, Wannagan Creek Quarry, Tongue River Formation, North Dakota; all Tiffanian in age. Piceoerpeton naylori, sp. nov. (**I–V**); **I–M**, UALVP 14918, holotype, atlantal centrum, in (**I**) anterior, (**J**) posterior, (**K**) right lateral, (**L**) dorsal, and (**M**) ventral views; **N–Q**, UALVP 43920, atlantal centrum, in (**N**) anterior, (**O**) right lateral, (**P**) dorsal, and (**Q**) ventral views; **R–V**, UALVP 40122, middle or posterior trunk vertebra, in (**R**) right lateral, (**S**) dorsal, (**T**) ventral, (**U**) anterior, and (**V**) posterior views. Provenances: UALVP 14918, 40122, Bug Creek Anthills, Hell Creek Formation, Montana; UALVP 43920, Bushy Tailed Blowout, Wyoming; all Lancian in age. Specimens at different scales: top (**A–D**), middle (**E–H**), and bottom (**I–V**) scale bars = 1 mm.

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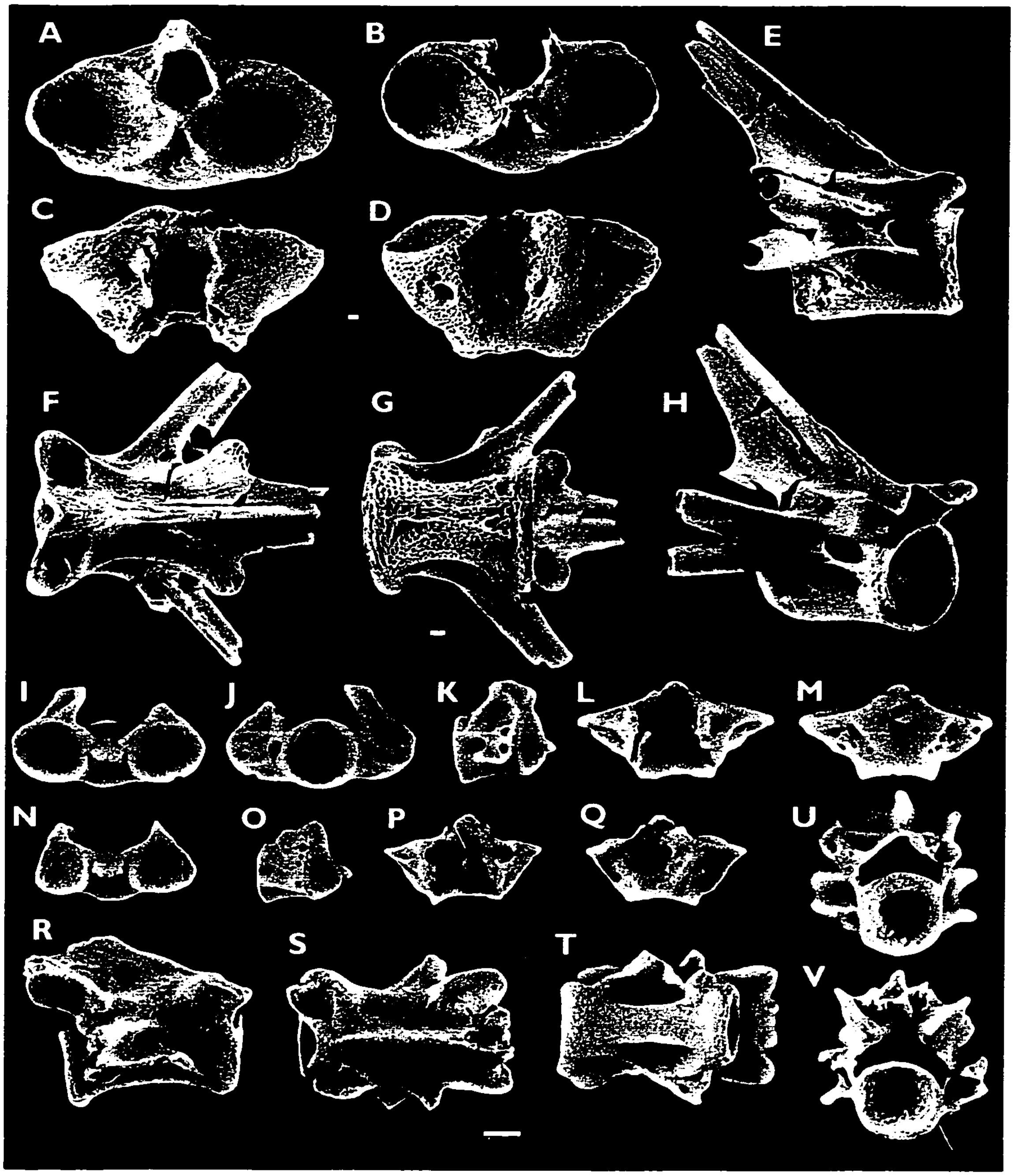

FIGURE 11-11. Atlantes of Irvinetriton elongatus gen. et sp. nov.; middle Campanian (Judithian) and late Maastrichtian (Lancian), North American Western Interior. **A–F**, UALVP 40121, holotype, atlantal centrum, in (**A**) anterior, (**B**) posterior, (**C**) right lateral, (**D**) left lateral, (**E**) dorsal, and (**F**) ventral views; **G–M**, UALVP 40114–40120, respectively, size series of seven atlantal centra; **N–P**, UALVP 40111–40113, respectively, size series of three atlantal centra. Provenances: UALVP 40114–40121, Irvine (Judithian), Dinosaur Park Formation, Alberta; UALVP 40111–40113, Bug Creek Anthills (Lancian), Hell Creek Formation, Montana. Specimens at same scale: scale bar = 1 mm.

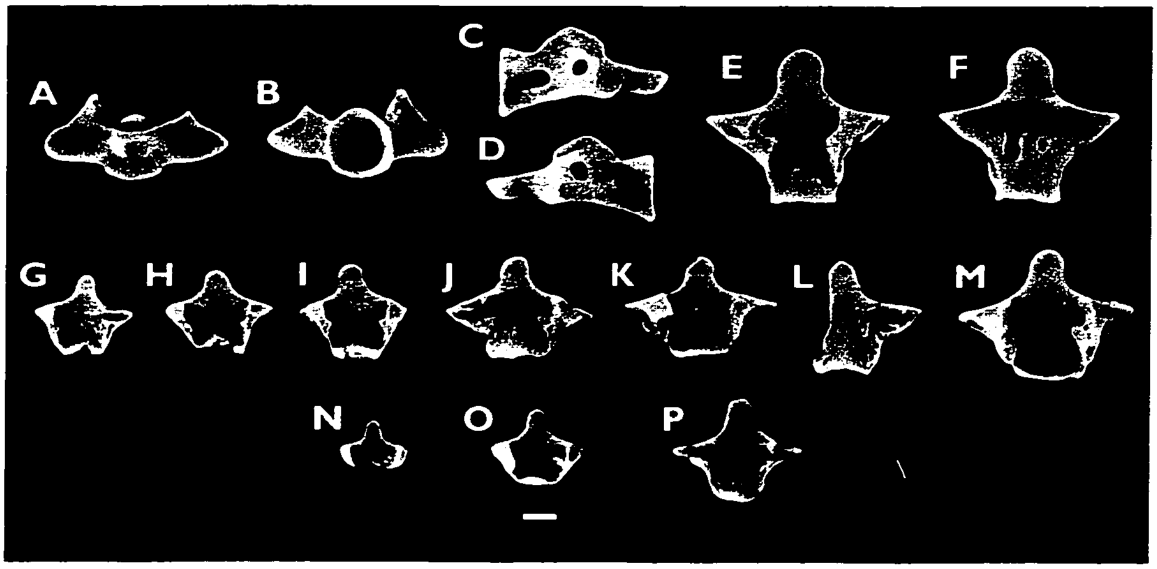
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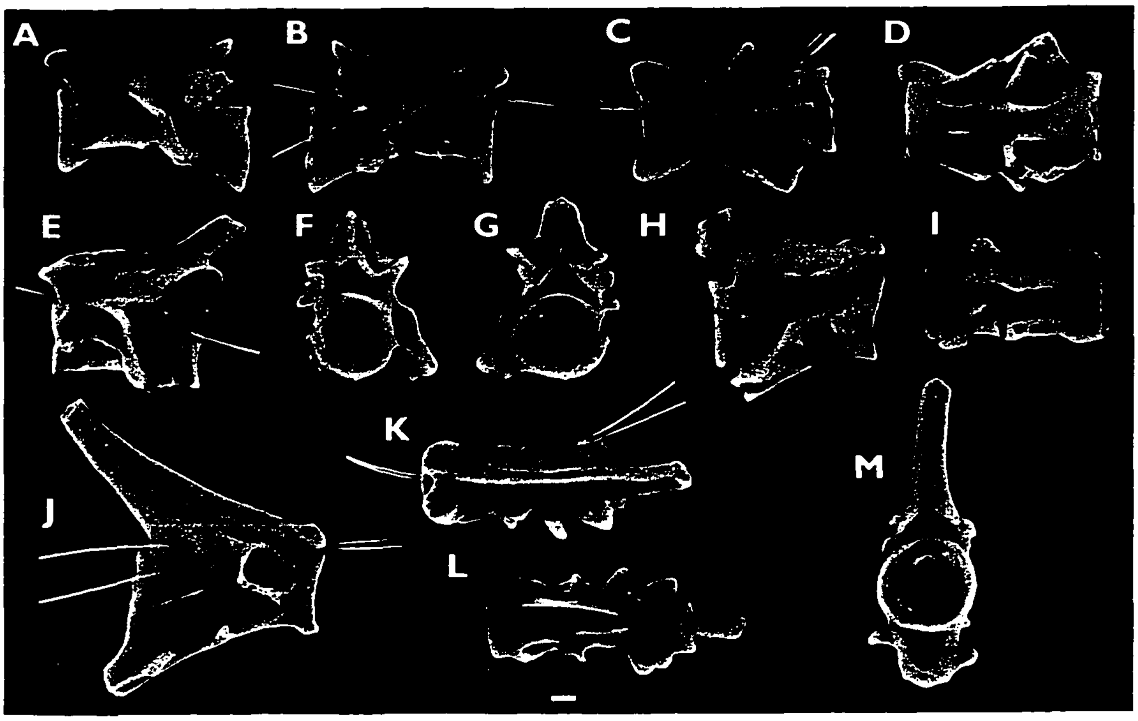
FIGURE 11-12. Post-trunk vertebrae of Scapherpetontidae indeterminate; Bug Creek Anthills, late Maastrichtian (Lancian), Hell Creek Formation, Montana. Sacrals or anteriormost caudals (A–G): **A–D**, UALVP 40147, in (A) left lateral view, (B) right lateral and (C) dorsal views, with hairs passing through paired spinal foramina in right wall of neural arch, and (D) ventral view; **E–G**, UALVP 40148, in (E) left lateral view, with hair passing through single spinal foramen in wall of neural arch, and (F) anterior and (G) posterior views. Caudals (H–M): **H, I**, UALVP 40150, anterior caudal, in (H) right lateral and (I) ventral views; **J–M**, UALVP 40151, posterior caudal, in (J) right lateral and (K) dorsal views, with hairs passing through paired spinal foramina in right wall of neural arch, and (L) ventral and (M) posterior views. Specimens at same scale: scale bar = 1 mm.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APPENDIX 11-1. General information and character descriptions for preliminary assessment of relationships within the Batrachosauroididae

General Information

My preliminary analysis relies on 20 informative characters (13 modified from Denton and O'Neill, 1998) scored for three out-group taxa (Hynobius, Cryptobranchus, and Necturus) and nine in-group taxa: the seven non-Opisthotriton genera, "Opisthotriton A," and "Opisthotriton B." Another four characters (12, 14, 18, and 21) are uninformative for assessing relationships and were excluded form all searches, but are retained in the matrix because they are potentially useful for diagnosing taxa. "Opisthotriton A" is scored on referred morph I atlantes (see Fig. 11-2) and "Opisthotriton B" is scored on referred morph II atlantes and the Paleocene skeleton, UALVP 16274, that has this kind of atlas (see Figs. 11-3 and 11-1, respectively). Vertebral character states for Prodesmodon, Esteserpeton, and Verdigriserpeton are scored on specimens reported in the respective species accounts in this chapter and character states of the dentary for Prodesmodon are scored on specimens in the collection of the UALVP listed by Naylor (1979). Character state scores for other batrachosauroidid taxa are taken from the literature, as follows: Batrachosauroides (Taylor and Hesse, 1943; Auffenberg, 1958; Estes, 1963, 1969a, 1981; Hinderstein and Boyce, 1977; J. Bryant, 1991; Albright, 1994); Palaeoproteus (Herre, 1935; Estes et al., 1967), Parrisia (Denton and O'Neill, 1998), Peratosauroides (Naylor, 1981). PAUP 3.3.1 (Swofford, 1993) was used for searches and to compute consensus trees and tree statistics. All characters were run unordered and unweighted. Hynobius was used to root the tree and monophyly of the Batrachosauroididae was not enforced.

Character Descriptions

Atlas (1-15):

1. Position of posterior cotyle relative to anterior cotyles: 0, approximate in line; 1, displaced ventrally.

2. Notochordal pit in posterior cotyle: 0, open; 1, closed.

3. Relative thickness of calcified cartilage infilling posterior cotyle: 0, thin; 1, thick.

4. Relative depth of anterior cotyles: 0, nearly flat to shallowly excavated; 1, deeply excavated.

5. Outline of anterior cotyles: 0, subcircular; 1, compressed dorsoventrally; 2, compressed lateromedially.

6. Form of odontoid process: 0, anteriorly elongated knob; 1, dorsoventrally flattened and reduced in length; 2, dorsoventrally flattened and reduced further to a horizontal bar.

7. Position of neural canal relative to anterior cotyles: 0, above; 1, partly between; 2, between.

8. Size of neural canal relative to anterior cotyles: 0, approximately equal to or greater than; 1, smaller than.

9. Posterior extent of neural arch roof: 0, extends slightly past posterior cotyle; 1, extends well past posterior cotyle.

10. Dorsal outline of posterior margin of neural arch roof: 0, truncate or pointed; 1, forked.

11. Dorsal outline of neural crest: 0, broadens posteriorly; 1, narrows posteriorly.

12. Shape of anterior end of neural crest: 0, not elaborated; 1, swollen into massive ball; 2, paired anterior processes.

13. Postzygapophyses: 0, prominent and laterally divergent; 1, smaller and directed more ventrolaterally.

14. Supracondylar process: 0, absent; 1, present.

15. Condition of neural crest and spine: 0, finished in cartilage; 1, finished in bone.

Trunk vertebrae (16–21):

16. Form of centrum: 0, amphicoelous; 1, semi-opisthocoelous; 2, fully opisthocoelous.

17. Posterior basapophyses: 0, absent; 1, small; 2, large.

18. Height of neural spine: 0, low; 1, high.

19. Form of transverse processes in anterior part of trunk series, excluding first trunk vertebra: 0, bicipitate and appressed; 1, bicipitate and divergent; 2, unicipitate.

20. Condition of neural spine: 0, finished in cartilage; 1, finished in bone.

21. Prominent, V-shaped hypapophyses: 0, absent; 1, present.

Dentary (22–24):

22. Tooth form: 0, pedicellate; 1, subpedicellate; 2, non-pedicellate.

23. Shape of dentary: 0, elongate and lacking coronoid process; 1, short and having coronoid process.

24. Lateral groove: 0, absent; 1,shallow; 2, deep.

APPENDIX 11-2. Data matrix of the 24 characters scored for three non-batrachosauroidid outgroups and nine batrachosauroidid terminal taxa used in preliminary analysis of relationships within the Batrachosauroididae. Conventions: a, polymorphic for states 0 and 1; b, polymorphic for states 1 and 2; ?, state unknown. Final column is percentage of missing records.

	00000	00001	11111	11112	2222	percent
	12345	67890	12345	67890	1234	missing
Hynobius	00000	00000	00000	00000	0000	0
Cryptobranchus	00000	00000	00000	00000	0000	0
Necturus	00001	00000	00000	00010	0100	0
Batrachosauroides	0??10	111??	?0?0?	10111	0202	29
Verdigriserpeton	10110	110??	12?0?	110a1	0???	29
"Opisthotriton A"	00110	b101a	10101	?????	????	38
"Opisthotriton B"	01110	b1000	10101	12011	0001	0
Palaeoproteus	0??10	b1?01	??00?	00011	1a12	25
Parrisia	0??10	11011	00111	22010	0201	08
Peratosauroides	10?12	1210?	00101	?0?1?	0???	33
Esteserpeton	11110	21000	00101	?????	????	38
Prodesmodon	11112	21000	11101	21021	0211	0

CHAPTER 12 — FROGS FROM THE CAMPANIAN AND MAASTRICHTIAN OF THE NORTH AMERICAN WESTERN INTERIOR

INTRODUCTION

The latest Cretaceous (Campanian and Maastrichtian) record of frogs in North America is sparse and consists largely of isolated elements. In the Western Interior, frogs of this age are best documented from the late Maastrichtian (Lancian) Lance Formation of Wyoming (Estes, 1964; Fox, 1976a; Breithaupt, 1982; Estes and Sanchíz, 1982) and the Hell Creek Formation of Montana (Estes et al., 1969; Estes and Sanchíz, 1982; L. Bryant, 1989). Five species and three families have been reported from these units: the palaeobatrachid Palaeobatrachus occidentalis Estes and Sanchíz; the discoglossids (sensu lato) Scotiophryne pustulosa Estes and Paradiscoglossus americanus Estes and Sanchíz; the pelobatid (sensu lato) Eopelobates Parker; and the incertae sedis taxon Theatonius lancensis Fox (Estes, 1964, 1970; Estes et al., 1969; Fox, 1976a; Estes and Sanchíz, 1982; Breithaupt, 1982, 1985; L. Bryant, 1989; Sanchíz, 1998). Occurrences of pre-late Maastrichtian and Campanian frogs in the Western Interior are less well documented. No taxa have been formally named from older horizons and published reports are limited to brief descriptive accounts (e.g., Sahni, 1972; Armstrong-Ziegler, 1980; Rowe et al., 1992; Peng, 1997) and citations in faunal lists (Fox, 1972, 1976b; Breithaupt, 1985; D. B. Brinkman, 1990). Where identified to familial level, membership of these pre-Lancian taxa in the Discoglossidae sensu lato and Pelobatidae sensu lato has also been suggested (Sahni, 1972; Fox, 1972, 1976b; Armstrong-Ziegler, 1980; Breithaupt, 1985). Palaeobatrachids, discoglossids sensu lato, and pelobatids sensu lato are generally viewed as "archaic" anurans that are known elsewhere from the Mesozoic and Cenozoic of Eurasia (see Sanchíz, 1998 and references therein) and, in the case of the last two families, have also been identified in the Upper Jurassic Morrison Formation of Wyoming (Evans and Milner, 1993). These North American occurrences have important biogeographical implications, because they have been taken as evidence that the three families were Holarctic in distribution during the latter part of the Mesozoic (e.g., Estes and Reig, 1973; Savage, 1973; Estes and Sanchíz, 1982; Duellman and Trueb, 1986).

Our understanding of latest Cretaceous anurans from the Western Interior rests largely on Estes' (1964) descriptions of isolated elements from the Lance Formation and on the type descriptions for *Scotiophryne* (Estes, 1969), *Theatonius* (Fox, 1976a), and *Paradiscoglossus* and *Palaeobatrachus occidentalis* (Estes and Sanchíz, 1982). Sanchíz (1998) recently included accounts for these taxa in his compendium of fossil salientians, but his comments were limited and no new specimens were described or figured. Examination of all important published specimens from the Lance and Hell Creek formations, plus undescribed material from these units and from Judithian and Aquilan horizons in Alberta provides an opportunity to consider the latest Cretaceous record of frogs in the Western Interior in greater detail than has previously been possible. My objectives here are threefold. First, I review previously reported Lancian taxa. Where appropriate, revised diagnoses are presented and new specimens and character states are reported. Second, I report on distinctive, but taxonomically indeterminate Lancian maxillae and ilia from the Lance Formation and briefly describe two unnamed taxa from the Judithian of Alberta. Third, I discuss some problems inherent in studying fossil anurans from isolated elements, with reference to specimens reported herein from the Western Interior.

SYSTEMATIC PALAEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order SALIENTIA Laurenti, 1768
Crown-order ANURA Rafinesque, 1815
Family PALAEOBATRACHIDAE Cope, 1865

Remarks—The Palaeobatrachidae are early Campanian to middle Pleistocene frogs (Sanchíz, 1998) that are interpreted as having been highly aquatic and the Laurasian equivalents (Špinar, 1972) of the closely related pipids (e.g., Ford and Cannatella, 1993; Báez and Trueb, 1997). Palaeobatrachids are best known from Europe, where four genera are currently recognized (Sanchíz, 1998; Hossini and Rage, 2000): the monotypic *Albionbatrachus* Meszoely et al. (late Eocene, England), *Messelobatrachus* Wuttke (middle Eocene, Germany), *Pliobatrachus* Fejérváry (Pliocene–middle Pleistocene, Central and Eastern Europe), and Palaeobatrachus Tschudi. The last genus contains five European late Paleocene–Pliocene species and, questionably, the North American late Maastrichtian species considered below (Sanchíz, 1998; Hossini and Rage, 2000).

PALAEOBATRACHUS? OCCIDENTALIS (Estes and Sanchíz, 1982)
(Fig. 12-1A–H)

cf., Barbourula sp. Estes, 1964:55–57, figs. 28, 29b.
Palaeobatrachus occidentalis Estes and Sanchíz, 1982:15–17, figs. 1c–f, 4A, B.
Palaeobatrachus? occidentalis Sanchíz, 1998:39.

Holotype—UCMP 55704, incomplete right ilium missing posterior part of dorsal acetabular expansion and distal end of ilial shaft (Estes and Sanchíz, 1982: figs. 1c, d, 4A; here:Fig. 12-1A–C).

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Lance Formation; Lull 2 Locality (UCMP V-5620), Lance Formation, Niobrara County, Wyoming, USA. Locality reported incorrectly as UMCP V-5720 by Estes and Sanchíz (1982:15) and Sanchíz (1998:39).

Revised Diagnosis (modified from Estes and Sanchíz, 1982; Sanchíz, 1998)—Species of palaeobatrachid differing from Pliobatrachus and other species of Palaeobatrachus in the following evidently unique combination of ilial character states: dorsal margin of ilium above acetabulum relatively straight in lateral aspect; sulcus wraps around anteroventral and anterior margin of dorsal tubercle, separating tubercle anteriorly from ilial shaft; dorsal tubercle oval in dorsal outline, slightly elongated, and not divided; iliofibularis-iliofemoralis attachment area small, lenticular in outline, and low; dorsal acetabular expansion relatively low; anterior margin of acetabulum squarish in lateral outline; and ilial synchondrosis on medial surface relatively large. Atlas differs from that of Pliobatrachus in having anterior cotyles paired, not confluent, and from Albionbatrachus in lacking a median "intercotylar process" between the anterior cotyles. Differs further from Palaeobatrachus robustus Hossini and Rage and Pliobatrachus in inferred smaller body size.

Referred Specimens—Lance Formation, Bushy Tailed Blowout (UCMP V-5711), Wyoming: UCMP 55705, left ilium. Hell Creek Formation, Bug Creek Anthills, Montana: UALVP 40163, fused atlas and first trunk vertebra.

Distribution—Late Maastrichtian (Lancian), USA: Lance Formation, Wyoming, and Hell Creek Formation, Montana.

Remarks—Estes and Sanchíz (1982) named the new species Palaeobatrachus occidentalis on a distinctive ilium (UCMP 55704; Fig. 12-1A–C) from the type Lance Formation and referred to the species two ilia: UCMP 55705 (Fig. 12-1D) from the same formation and MCZ 3653 (not figured here) from Bug Creek Anthills, in the Hell Creek Formation of Montana. The last specimen is a poorly preserved ilium that only superficially resembles the holotype and is not diagnostic for the Palaeobatrachidae (pers. obs., 1999). The only additional specimen available to me that can be associated with the two topotypic ilia is a previously unreported fused atlas and first trunk vertebra (UALVP 40163; Fig. 12-1E–H) from Bug Creek Anthills.

UCMP 55704 and 55705 originally were identified by Estes (1964) as pertaining to "cf., Barbourula sp.", within the Discoglossidae sensu lato. Subsequently, Vergnaud-Grazzini and Hoffstetter (1972) and Estes and Reig (1973) independently reinterpreted the Lancian ilia as belonging to palaeobatrachids. This familial assignment is supported by detailed resemblances between the two Lancian ilia and those of European palaeobatrachids—e.g., dorsal crest absent; dorsal tubercle small and separate from attachment area for iliofibularis and iliofemoralis muscles; ventral acetabular expansion virtually absent; acetabulum relatively large, incomplete posteriorly, expanded laterally, and ventral rim projects anteroventrally to overhang subacetabular area; and interiliac synchondrosis prominent (see Vergnaud-Grazzini and Hoffstetter, 1972; Holman, 1996; Hossini and Rage, 2000). The fused atlas and first trunk vertebra (UALVP 40163) compares favorably with homologous European specimens (Vergnaud-Grazzini and Hoffstetter, 1972; Špinar, 1972; Sanchíz and Mlynarski, 1979; Rage and Ford, 1980; Meszoely et al, 1984) and is characteristic for the Palaeobatrachidae in being solidly fused and in having a foramen for exit of the first spinal nerve at the line of fusion, the posterior cotyle broader than wide, a narrow (although distally incomplete) transverse process, the neural arch elongate posteriorly, low, and simple in construction, and the postzygapophyseal processes unelaborated. In those pipids in which the atlas and first trunk vertebra are also fused the transverse process ranges from absent to wing-like, the neural arch is often posteriorly shorter and may bear an enlarged neural spine, and the zygapophyses may be elaborated in various ways to enhance articulation with adjacent vertebrae (see Báez and Trueb, 1997; Báez and Rage, 1998).

The specific and generic identities of the Lancian ilia and of the fused atlas and first trunk vertebra within the Palaeobatrachidae are less certain, mainly because most European taxa are known by articulated skeletons in which detailed features of the ilia and atlas complex cannot readily be observed (Špinar, 1972; Sanchíz, 1998). Comparisons with the limited number of published, isolated palaeobatrachid ilia and atlantal complexes from Europe (e.g., Vergnaud-Grazzini and Hoffstetter, 1972; Sanchíz and Mlynarski, 1979; Meszoely et al., 1984; Holman, 1996; Hossini and Rage, 2000), suggest that the Lancian specimens are sufficiently different to be retained within their own species. The generic placement of this Lancian species remains problematic, however, because the characters of the ilium and atlantal complex are not widely used to differentiate palaeobatrachid genera (e.g., Špinar, 1972; Meszoely et al., 1984; Sanchíz, 1998; Hossini and Rage, 2000). I thus conservatively follow Sanchíz (1998) and Hossini and Rage (2000) in provisionally assigning the Lancian species to Palaeobatrachus as Palaeobatrachus? More diagnostically informative elements—ideally frontoparietals—will be needed to better establish the generic affinities of the Lancian palaeobatrachid species.

Family Indeterminate

SCOTIOPHRYNE PUSTULOSA Estes, 1969

(Fig. 12-1I–T)

Holotype—MCZ 3623, incomplete left ilium missing ventral part of ventral acetabular expansion and distal part of ilial shaft (Estes, 1969:fig. 1c. d). Armstrong-Ziegler (1980:10) erroneously stated that a maxilla identified by her as MCZ 3626 and figured by Estes (1969:fig. 2c,d) was the holotype; in fact, this maxilla was explicitly identified by Estes (1969:2) as a referred specimen and one of "14 anterior and posterior fragments of maxillae" catalogued together as MCZ 3652.

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Hell Creek Formation; Bug Creek Anthills, McCone County, Montana, USA.

Revised Diagnosis (modified from Estes, 1969; Sanchíz, 1998)—Anuran species differing from other known anurans, especially other North American Cretaceous anurans, in the following unique combination of character states: inferred moderate body size; ilium lacks dorsal crest and has dorsal tubercle poorly developed, preacetabular region anteriorly short, dorsal acetabular expansion low, and ventral acetabular expansion moderate, with depth greater than height of dorsal acetabular expansion; maxilla, nasal, squamosal, and frontoparietal ornamented externally with shagreen of fine, bead-like tubercles that rarely contact one another; maxilla dentate, with pre- and postorbital regions moderately high and subequal in height, palatine and pterygoid processes moderately well developed, and pars palatinum a thick, well defined ridge; squamosal dorsally elongate, inclined slightly posteriorly, and with obtuse bend midway along length, base broadly sutured with maxillae, dorsal end blunt and free; frontoparietals paired and evidently not in broad contact anteriorly with nasals, sphenethmoid, or both.

Referred Specimens—Hell Creek Formation, Bug Creek Anthills, Montana: AMNH 26422, UALVP 40155, ilia; UALVP 40156, 40157, maxillae; UALVP 40158, nasal; UALVP 40159, squamosal; UALVP 40160, frontoparietal. This list does not include topotypic ilia and maxillae from the Hell Creek Formation or a maxilla, squamosal, and ilium from the Lance Formation, all listed by Estes (1969:2).

Distribution—Late Maastrichtian (Lancian), USA: Hell Creek Formation, Montana, and Lance Formation, Wyoming.

Remarks—Estes (1969) described the new genus and species Scotiophryne pustulosa for isolated and incomplete Lancian ilia, a squamosal, maxillae, and humeri (Estes, 1964:figs. 1-3) from the Lance and Hell Creek formations and questionably referred to the species a fragmentary ilium and three humeri (Estes, 1969:fig. 4) from the middle Palaeocene (Torrejonian) Tongue River Formation, Montana. Estes (1969) assigned Scotiophryne to the Discoglossidae sensu lato and suggested affinities with the extant European Bombina Oken. Estes and Sanchíz (1982) reviewed the affinities of Scotiophryne and provisionally retained the genus within the Discoglossidae sensu lato, although they noted similarities with extant pelodytids. Sanchíz (1998:20) maintained this familial placement, despite having conceded that "assignment of this distinct taxon to a family group is uncertain because no synapomorphies are observable."

Aside from a line drawing of a referred humerus (Estes and Sanchíz, 1982:fig.

3c), no additional specimens of Scotiophryne pustulosa have been illustrated since Estes' (1969) type description. New specimens figured here (Fig. 12-1I–T) from the holotype locality include ilia, maxillae, and a squamosal, and the first examples for the species of a nasal and a frontoparietal. Examples of the first three elements compare favorably with specimens described by Estes (1969), but reveal some new features. Both ilia (AMNH 26422 and 40155; Fig. 12-1I–K), preserve more of the acetabular region than did specimens figured by Estes (1969:fig. 1), and demonstrate that the ventral acetabular expansion is relatively deeper than the height of the dorsal acetabular expansion. The two incomplete maxillae (UALVP 40156 and 40157; Fig. 12-1L–O) overlap one another in the region of the palatine process and collectively reveal most of the structure of this element. The two topotypic maxillary specimens (bulk catalogued as part of MCZ 3626) figured by Estes (1969:fig. 2c–f) are more worn than is evident from his drawings and they no longer overlap one another, because the anterior part of the more posterior specimen has since been broken away (pers. obs., 1995). The equivalent specimen (UALVP 40156) illustrated here that preserves the posterior part of the bone differs slightly in lacking the posterior facet in the labial face of the maxilla for contact with a more posterior element, presumably the quadratojugal (cf., Estes, 1969:fig. 2c; here:Fig. 12-1O). UALVP 40156 also preserves the first examples for this taxon of intact teeth: these are non-pedicellate or, at most, weakly pedicellate and bear labiolingually, bicupsid crowns on which the cupsules are disc-shaped and separated by a sulcus. The squamosal UALVP 40159 (Fig. 12-1Q, R) is more nearly complete than the specimen figured by Estes (1969:fig. 2a,b). This new specimen shows that the bone is narrow, inclined slightly posteriorly, and has an obtuse bend midway along its length, causing the dorsal part to be inclined more posteriorly. The base of the bone is slightly expanded anteroposteriorly and ventrally bears a prominent suture scar, for contact with the complementary processus zygomatico-maxillaris on the maxilla. The nasal UALVP 40158 (Fig. 12-1P) is incomplete anteriorly and medially, yet the bone clearly was broad and bears a prominent, prong-like and distally blunt processus paraorbitalis for articulation with the maxilla. UALVP 40160 (Fig. 12-1S, T) is the anterior end of a right frontoparietal; judging by the preserved margins, the frontoparietals were paired in life and did not broadly contact more anterior elements.

Cranial elements reported here can be associated with one another and with the squamosal and maxillae reported by Estes (1969) on the strength of their characteristic beaded ornamentation. The nasal and frontoparietal reported here demonstrate that this ornamentation is maintained onto the skull roof, although the beads tend to coalesce towards the margins of the frontoparietal. Association of these referred cranial elements with the holotype and referred ilia is less certain, but is reasonable based on the provenance, size, and relative frequencies of specimens. The Torrejonian ilium and some of the topotypic and Torrejonian humeri that Estes (1969) referred to Scotiophryne pustulosa may pertain to this taxon, but this is not certain.

Based on specimens available to me and adequately published accounts, Scotiophryne pustulosa is best regarded as a Lancian species, restricted to the Lance Formation of Wyoming and the Hell Creek Formations of Montana. Armstrong-Ziegler (1980:10) reported a fragmentary, supposed left anuran maxilla having "prominent pustulate sculpturing," said to resemble that on referred Lancian maxillae of Scotiophryne, from the Fruitland Formation (Edmontonian) of New Mexico. I have not been able to examine this specimen and the published figures (Armstrong-Ziegler, 1980:pl. 1a, b) are too insufficiently detailed to establish its identity with any confidence. Scotiophryne has also been reported from the "El Gallo" formation, Baja California (Estes and Sanchíz, 1982:14) and "Mesaverde" Formation, Wyoming (Breithaupt, 1985), both Judithian in age, and from the Tullock Formation (Puercan), Montana (L. Bryant, 1989). These records await verification.

THEATONIUS LANCENSIS Fox, 1976a
(Fig. 12-2A–J)

Holotype—UALVP 12073, nearly complete left maxilla, missing two chips out of occlusal margin (Fox, 1976a:fig. 1; here:Fig. 12-2A–D).

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Lance Formation; Bushy Tailed Blowout, Niobrara County, Wyoming, USA.

Revised Diagnosis (modified from Fox, 1976a; Sanchíz, 1998)—Anuran species differing from other known anurans, especially other North American Cretaceous anurans, in the following unique combination of character states: inferred small body size; maxilla, squamosal, and frontoparietal ornamented externally with moderate-sized, tightly packed pustules; maxilla edentulous, pars palatinum an indistinct ridge, preorbital area taller than postorbital area, palatine process massive, projecting more medially, and with prominent facet developed dorsally for sutured contact with nasal, groove for ductus nasolacrimalis deep and extending labially across base of palatine process to orbital margin, pterygoid process lingually short but broad and bearing prominent articular facet that wraps posterodorsally onto dorsal edge of processus zygomatico-maxillaris, processus posterior bluntly pointed; squamosal having lamella alaris a broad plate, with tiny spines along posteroventral margin; and frontoparietals relatively short and broad, paired, broadly sutured along midline, anterior end transverse and bearing extensive facet ventrally for broad sutured contact with palatine, sphenethmoid, or both, lateral process broadly expanded laterally, probably roofing over prootic, and bearing extensive facet ventrally for sutured contact laterally with squamosal, supraorbital roof narrow and developed only along orbital margin of lateral process, and ventrally bearing a thick, ventrally descending flange that parallels lateral edge of bone and undivided incrassatio frontoparietalis more medially.

Referred Specimens—Holotype locality: UALVP 12075, maxilla; UALVP 12074, 12076–12078, 40161, frontoparietals; UALVP 12079, 12080, 40162, squamosals.

Distribution—Known only from the holotype locality.

Remarks—Fox (1976a) described the new genus and species Theatonius lancensis for distinctive skull elements (two maxillae, four frontoparietals, and two squamosals) from Bushy Tailed Blowout. Fox (1976a) regarded T. lancensis as an incertae sedis anuran, an interpretation that has been universally followed (Estes and Sanchíz, 1982; Duellman and Trueb, 1986; Sanchíz, 1998) and is accepted here. Aside from the fragmentary frontoparietal and squamosal (UALVP 40161 and 40162, respectively) listed above, no new specimens have been identified for T. lancensis. Specimens figured here include the two known maxillae (UALVP 12073 and UALVP 12075; Fig. 12-2A–E), the most nearly complete squamosal (UALVP 12080; Fig. 12-2F), and the two most nearly complete frontoparietals (UALVP 12074 and 12076; Fig. 12-2G–J).

The known cranial elements of Theatonius lancensis are distinctive and can be reliably associated based on their provenance, small size, evidence of broad and tightly sutured contacts, and characteristic ornament. This ornament resembles that of Scotiophryne pustulosa in consisting of convex tubercles, but differs in that the tubercles are relatively larger and are tightly packed, as compared to relatively smaller and rarely in contact on homologous bones of S. pustulosa. Sanchíz's (1998:fig. 134A, 135) drawings of the holotype maxilla of T. lancensis and of the referred frontoparietal UALVP 12074 do not accurately depict the ornamentation on these specimens.

Fox's (1976a) description of Theatonius is accurate and does not require repeating; however, two features not noted by Fox (1976a) are worth mentioning. First, on the maxilla the groove that carried the ductus nasolacrimalis (see Roček, 1980) is a relatively deep and broad channel that wraps around the labial base of the palatine process and opens posteriorly in the anteroventral corner of the orbital margin. Where present in other Cretaceous anuran maxillae available to me, this groove is considerably shallower and less pronounced. Second, on the frontoparietal the incrassatio frontoparietalis, which demarcates the area of attachment of the dura mater onto the undersurface of the skull roof (Špinar, 1976), is undivided and slightly broader posteriorly than anteriorly.

Available skull bones of Theatonius lancensis are small, approximately one-half the size of the largest homologous specimens available for Scotiophryne pustulosa. Nevertheless, a suite of features suggest that the skull of T. lancensis was robust and solidly ossified, in a manner analogous to that in so-called "casque-headed" species of extant anurans. Features consistent with this interpretation include the following: maxilla, squamosal, and frontoparietal robust in construction, heavily ornamented, and show evidence of having been in broad, tightly sutured contact with adjacent elements; maxilla relatively short, bearing relatively massive palatine process; squamosal with broad, plate-like lamella alaris; and frontoparietal having lateral process broadly expanded laterally, probably roofing over prootic to suture broadly with squamosal. Among extant anurans of similar body size, such skulls are typical of, but not unique to, terrestrial and fossorial taxa.

Theatonius lancensis is the only Mesozoic frog taxon that unequivocally lacks teeth on the maxilla. Among extant anurans teeth either are present on both the maxilla and premaxilla or are absent from both elements, depending on the species (Trueb, 1973); this pattern suggests that the premaxilla of T. lancensis was also edentulous. I have not identified any such specimens in collections of Lancian anurans available to me.

Theatonius lancensis is reliably known only from Bushy Tailed Blowout, in the Lance Formation of Wyoming. Denton and O'Neill (1998:485) mentioned that the

Ellisdale locality (Campanian) of New Jersey has produced squamosals that "seem comparable to Theatonius," but they provided no further information on these specimens.

PARADISCOGLOSSUS AMERICANUS Estes and Sanchíz, 1982
(Fig. 12-2K, L)

Holotype—UCMP 125827, incomplete left ilium lacking distal end of ilial shaft and dorsal edge along anterior two-thirds of ilial crest.

Holotype Horizon and Locality—Late Maastrichtian (Lancian); Lance Formation; Bushy Tailed Blowout (UCMP V-5711), Niobrara County, Wyoming, USA.

Revised Diagnosis (modified from Estes and Sanchíz, 1982; Sanchíz, 1998)—Anuran species differing from other known anurans, especially other North American Cretaceous anurans, in the following unique combination of character states: inferred moderate body size; ilium bearing crest that is moderately tall, convex laterally and concave medially, and not having base demarcated by a groove, dorsal tubercle a low, elliptical, elongate knob placed dorsolaterally on proximal end of crest, dorsal acetabular expansion high and subacetabular expansion deep, and supracetabular fossa a relatively large, deep pit, open posterodorsally.

Referred Specimens—Lance Formation, Lull 2 Locality (UCMP V-5620), Wyoming: UCMP 125830, ilium.

Distribution—Late Maastrichtian (Lancian), Lance Formation, Wyoming.

Remarks—Estes and Sanchíz (1982) described the new genus and species Paradiscoglossus americanus largely on the holotype ilia (Fig. 12-2K, L) and the less nearly complete referred ilium (Estes and Sanchíz, 1982:fig. 2C, D; unfigured here). These specimens are unique among known North American Cretaceous anuran ilia in having a dorsal crest and, on this basis alone, warrant the continued recognition of P. americanus as a valid anuran taxon. Two minor differences are evident between the two known ilia: (1) the dorsal tubercle is more prominent on UCMP 125830 and (2) UCMP 125827 has a deep pit in the preacetabular area for attachment of the iliacus internus muscle; this pit is absent from the referred ilium. No further examples of this distinctive ilium are available and no other elements have been identified that can be reliably associated with the two ilia. Estes and Sanchíz (1982) tentatively referred the distal ends of two humeri (UCMP 125828 and 125829; Estes and Sanchíz, 1982:fig. 3A, B, respectively) from the holotype locality to P. americanus, but there is no basis for this association.

?"EOPELOBATES" sp. sensu Sanchíz, 1998
(Fig. 12-3)

Horizons, Localities, and Specimens—Lance Formation, two localities: Bushy Tailed Blowout (UCMP V-5711): AMNH 25002, 27205, maxillae; AMNH 22522, ilium; Lull 2 Locality (UCMP V-5620): UCMP 55710, nasal; UCMP 55707, squamosal; UCMP 55710, ilium. Bug Creek Anthills, Hell Creek Formation, Montana: UALVP 40164, frontoparietal. All late Maastrichtian (Lancian) in age.

Remarks—Specimens figured from the above list include an anteriorly incomplete right maxilla (AMNH 25002:Fig. 12-3A, B), an anteriorly incomplete left nasal (UCMP 55710; Fig. 12-3C), a nearly complete right squamosal (UCMP 55707; Fig. 12-3D, E), the anterior part of a right frontoparietal (UALVP 40164; Fig. 12-3F, G), and an incomplete left ilium (UCMP 55712; Fig. 12-3H, I). The nasal and squamosal, along with other Lancian maxillae and ilia that resemble those figured here, previously were interpreted as having come from a pelobatid sensu lato and, based on comparisons with Tertiary species of Eopelobates Parker, were assigned by Estes (1970:315) to ?Eopelobates. Estes and Sanchíz (1982:17) revised this identification to Eopelobates sp., on the strength of resemblances between the Lancian ilia and squamosal with those of the North American Eocene species E. guntheri Estes. By the early 1990s, Eopelobates had become somewhat of a wastebasket taxon. The traditional view of Eopelobates as a Euramerican genus has since been challenged (Henrici, 1994; Sanchíz, 1998). In the most recent review of fossil pelobatids sensu lato, Sanchíz (1998) restricted the name Eopelobates to European Eocene-Pliocene species within the Pelobatinae Bonaparte (sensu Henrici, 1994) and tentatively grouped the North American Maastrichtian-Eocene fossil taxa as "Eopelobates" within the Megophryninae Noble. Extant species of this subfamily are restricted to eastern Asia (Duellman and Trueb, 1986). The status, contents, and affinities of the North American "Eopelobates" have yet to be resolved.

Skull elements listed here have a reticulate ornament that differs from that seen in other North American Campanian and Maastrichtian anuran specimens and can be provisionally associated on this basis. The figured maxilla and, especially, the nasal and squamosal, show some detailed differences in shape and processes in comparison to homologous elements of paracontemporaneous North American anurans. The figured ilium comes from an individual comparable in size to those represented by the cranial elements. This specimen resembles ilia of the North American Oligocene species "Eopelobates" grandis Zweiffel (Sanchíz, 1998:fig. 77A) and differs from other Lancian ilia reported here in lacking a dorsal crest and prominent tubercles and in having the dorsal and ventral acetabular expansions relatively small and more nearly similar in size. These criteria admittedly are a weak basis for associating and assigning the Lancian specimens in question to ?"Eopelobates" sp. To a large extent, my approach here is a pragmatic one that reflects past attempts to deal with these sorts of problematic, but distinctive, specimens (Estes, 1970; Estes and Sanchíz, 1982; Sanchíz, 1998), rather than a conviction that the specimens pertain to conspecific or congeneric individuals. It would be equally valid to identify these specimens as "Anura Indeterminate."

Genus and Species Unnamed A

(Fig. 12-4)

Horizon, Localities, and Voucher Specimens—Dinosaur Park Formation (Judithian), two localities, Alberta: Irvine: UALVP 40180, nasal; UALVP 40181, squamosal; UALVP 40182, 40183, frontoparietals; UALVP 40184, ilium; plus additional, uncatalogued maxillae, squamosals, frontoparietals, and ilia in the collection of the UALVP; Railway Grade: UALVP 40179, maxilla. Oldman or Dinosaur Park Formation, UALVP DB-19, Alberta: UALVP 40177, 40178, maxillae;

Description

A medium-sized Judithian frog is represented by abundant maxillae, rare nasals, squamosals, frontoparietals, and ilia in the collection of the UALVP. Pending more detailed examination of these elements and comparisons with an undescribed paracontemporaneous frog skeleton from the Milk River Formation of Montana and of a new anuran species from the Judith River Formation of Montana currently being described by Richard Blob and colleagues, the following description is brief and serves only to highlight significant features of this unnamed Judithian taxon.

Maxilla (Fig. 12-4A–C)—None of the available maxillae preserve the portion of the bone anterior to the orbital margin. Specimens at hand indicate that the remainder of the bone resembles referred Lancian maxillae of Scotiophryne pustulosa as follows: pars facialis moderate in height; orbital margin shallowly concave and moderately elongate; postorbital region moderately elongate; processus zygomatico-maxillaris low, grooved dorsally for contact with squamosal; pterygoid process a well-developed, medially projecting flange, with roughened dorsal surface for contact with pterygoid; pars palatinum a moderately deep and lingually broad ridge, with flattened lingual and dorsal surfaces; and posterior end of tooth row ends midway between base of pterygoid process and posterior end of bone. The Judithian maxillae are distinctive among maxillae reported here, particularly in comparison with referred maxillae of S. pustulosa in having labial ornament consisting of low, narrow ridges arranged in a loosely reticulate to anastomosing pattern. On some maxillae (Fig. 12-4B) the ridges break up towards the center of the bone into short, isolated ridges and tiny tubercles.

Nasal (Fig. 12-4D)—The figured specimen, UALVP 40180, is an anteriorly and medially incomplete left nasal that dorsally bears ornament similar to that on the maxilla. The processus paraorbitalis is triangular, confluent with the main body of the bone, and pointed distally. Judging by the preserved margins, the nasal was probably rhomboid in outline.

Squamosal (Fig. 12-4E, F)—Available specimens preserve the dorsal part of the bone, which is ornamented externally by fine ridges arranged in an loosely reticulate to anastomosing pattern. The dorsal part of the lamella alaris is narrow, broadly rounded distally, and inclined posterodorsally. A bend along the posterior margin towards the base of the figured specimen (UALVP 40181) implies that the bone was bent midway along its length.

Frontoparietal (Fig. 12-4G–I)—The two figured specimens are UALVP 40182 (Fig. 12-4G, H), the posterior two-thirds of a left frontoparietal, and UALVP 40183 (Fig. 12-4I), the anterior one-third of a right frontoparietal. The two specimens may overlap slightly in their preserved morphologies, but clearly are from slightly different sized individuals. Both specimens dorsally bear ornament similar to that on the maxillae, nasal, and squamosal. The frontoparietals were paired in life, but broadly sutured medially with one another along at least the posterior two-thirds of their length. UALVP 40183 shows that the anterior end of the frontoparietal was somewhat pointed and was not broadly sutured anteriorly with the nasal or sphenethmoid. The more nearly complete specimen, UALVP 40182 reveals the following notable features: the posterior part of the bone is not expanded laterally as in Theatonius; the processus posterior superior extends posteriorly from the posterolateral corner of the bone as an elongate prong; the supraorbital roof is expanded laterally into a broad, triangular flange in the orbital region; the ventral flange on the underside is narrow and, except at its posterior end, extends anteroposteriorly in a straight line; and the incrassatio frontoparietalis is undivided, elongate, and slightly broader posteriorly.

Ilium (Fig. 12-4J, K)—The ilium (UALVP 40184) figured here is from an individual comparable in size to those represented by skull elements listed above. The shaft is slightly compressed laterally and lacks a crest. No obvious areas for attachment of muscles are evident along the shaft or on the dorsal acetabular expansion. The dorsal and ventral acetabular expansions are poorly developed.

Remarks

Voucher specimens listed above are associated based on their modest size and the observation that examples of these kinds of elements are more common in Judithian collections of the UALVP than are homologous specimens of the larger taxon reported below. Cranial elements are further associated on their characteristic ornament. The overall picture that emerges from these Judithian specimens is of a frog that most closely resembles the Lancian Scotiophryne pustulosa in inferred body size and the overall form of maxilla and squamosal. Differences between Judithian specimens and those of S. pustulosa in the pattern of cranial ornament and in the structure of the nasal and ilium indicate that the Judithian specimens pertain to a different taxon.

Uncatalogued, fragmentary maxillae and squamosals from the Milk River Formation in the collection of the UALVP resemble homologous elements of the small

Judithian taxon, but additional study is needed to confirm this observation.

Genus and Species Unnamed B

(Fig. 12-5)

Horizon, Localities, and Specimens—Dinosaur Park Formation (Judithian), four localities, Alberta: Irvine: UALVP 40167, 40169, maxillae; UALVP 40170, nasal; UALVP 40171, 40172, squamosals; UALVP 40173, 40174, frontoparietals; UALVP 40175, ilium; plus additional, uncatalogued maxillae, squamosals, frontoparietals, and ilia in collection of the UALVP; Railway Grade: TMP 74.10.88, ilium; TMP L0086: TMP 86.23.32, frontoparietal; UALVP JMC 111: UALVP 40176, humerus. Dinosaur Park or Oldman formations, unnamed UALVP locality near Sandy Point: UALVP 40168, maxilla.

Description

A larger Judithian anuran is represented by distinctive cranial elements and ilia in the collections of the UALVP and TMP. For the same reasons given in the previous account, the following description is brief and focuses on important features of this unnamed taxon.

Maxilla (Fig. 12-5A–f)—The most nearly complete maxilla (UALVP 40167; Fig. 12-5A, B) is missing the posteriormost end of the bone and is broken anteriorly just in front of the palatine process. The other two figured specimens, UALVP 40168 (Fig. 12-5C, D) and UALVP 40169 (Fig. 12-5E, F) preserve the more anterior part of the bone. The maxillae are ornamented externally with thick, tall ridges that enclose deep lacunae; the latter tend to be in the form of pits in the centre of the maxillae and develop into grooves towards the periphery. The pars facilias is high; the pre- and postorbital regions are of equivalent height and rise well above the level of orbital margin. The lamina anterior remains high along its length and the leading edge is blunt in outline. The palatine process is moderate in size, but the pterygoid process is absent. Instead, the lingual face of the pars facialis in the area usually occupied by the pterygoid process bears thick ridges and grooves for contact with the pterygoid. More dorsally, the processus zygomatico-maxillaris is broadly convex in profile and lacks a dorsal facet for contact with the squamosal. The pars palatinum extends along most of the length of the bone as a lingually thick ridge, broader dorsally than ventrally, and with a gutter-like dorsal surface.

Nasal (Fig. 12-5G)—UALVP 40170 is a nearly complete nasal, with dorsal ornament similar to that on the maxilla. The nasal is triangular in dorsal outline, with an elongate and acuminate processus paraorbitalis. The medial edge is relatively straight, but thick and unelaborated, indicating that the bone probably abutted with its opposite across the midline.

Squamosal (Fig. 12-5H–J)—Figured specimens are from the left side and consist of a large, nearly complete squamosal (UALVP 40171: Fig. 12-5H, I) and a smaller squamosal lacking the ventral part of the bone (UALVP 40172; Fig. 12-5J). Ornament on both specimens resembles that on the maxilla and nasal. In medial and lateral view the lamella alaris is a C-shaped plate, with the concave surface facing posteriorly. The ventral edge of the lamella alaris is smooth and exhibits no evidence of having articulated in life with the maxilla. The processus posterolateralis is an elongate, rod-shaped structure that projects ventromedially off the medial surface of the bone.

Frontoparietal (Fig. 12-5K–M)—The frontoparietal is known from fragments. The three figured fragments come from the anterior, medial, and posterolateral parts (Fig. 12-5K–M, respectively) of the bone. Collectively these demonstrate that when complete the frontoparietals were paired, abutted against one another across the midline at least posteriorly, the anterior end was not in broad contact with more anterior elements, and the posterior part was not expanded laterally to any extent. The supraorbital roof is relatively narrow, more so than in the Judithian taxon reported above. In ventral view (not shown) the flange for contact with the neurocranium is narrow and the incrassatio frontoparietalis is divided into a small circular patch posteriorly and an elongate patch anteriorly.

Ilium (Fig. 12-5N–P)—Ilia are large and robust. The shaft is strongly compressed laterally and a broad trough extends anteroposteriorly along the medial surface. The dorsal acetabular expansion is developed into a high ridge with a horizontal dorsal edge and extends well forward past the level of the acetabular rim. The anterior end of this ridge is demarcated by a groove that curves around the base of the ridge onto the medial face of the shaft. More dorsally the anterior end of the ridge bears the dorsal tubercle. The tubercle is globular in shape, raised and slightly broader than long, and sits on the dorsolateral face of the ridge.

Humerus (Fig. 12-5Q)—The distal end of a large left humerus (UALVP 40176) is notable for having the crista medialis and crista lateralis (i.e., flanges arising off either side of the shaft) similar in height and width.

Remarks

Specimens reported above are associated based on their large size and provenance. Cranial elements additionally can be associated on the strength of the characteristic ornament. Association of the maxillae and squamosal is further supported by the lack of any complementary contact surfaces.

Specimens at hand are large, relative to most other homologous specimens from the Campanian and Maastrichtian of the Western Interior, and suggest a body size at least twice that of Theatonius, Scotiophryne, Palaeobatrachus? occidentalis and of the Judithian taxon reported above. This larger Judithian taxon differs further from other North American Cretaceous anurans in its cranial ornament, structure of the ilium and frontoparietal, and structure and contacts of the maxilla and squamosal. The small maxilla and squamosal (Fig. 12-5E, J, respectively) demonstrate that the characteristic ornament and the shape of the squamosal were established early in growth, and argue against elements of the smaller Judithian taxon being ontogenetic transients of the larger taxon.

Sahni (1972) reported distinct kinds of anuran ilia, humeri, and maxillae from the type area of the Judith River Formation, Montana. The specimens in question are too fragmentary and poorly preserved to be compared meaningfully with other homologous specimens, including those reported above for the two Judithian taxa from Alberta.

Genera and Species Indeterminate

(Fig. 12-6)

Remarks–Collections of Campanian and Maastrichtian anuran elements available to me from the Dinosaur Park, Hell Creek, Lance, Milk River, and, possibly, Oldman formations include numerous other cranial bones, vertebrae, urostyles, ilia, and long bones. These specimens are invariably incomplete and typically provide little new information of note.

Figure 12-6 depicts seven specimens (five maxillae and two ilia) from Bushy Tailed that are worth documenting because they cannot confidently be associated with one another or assigned to any of the taxa reported above. Except for the maxilla AMNH 55711, which was discussed by Estes (1964), none of these specimens has previously been reported. The five maxillae differ from one another in the overall shape of the bone, form of the pterygoid process, pattern of labial ornamentation, and relative posterior extent of the tooth row. Two maxilla warrant particular attention. UCMP 55711 (Fig. 12-6A, B) is unique among anuran maxillae known to me in having a large triangular facet posteriorly in the labial face of the bone. UALVP 40166 (Fig. 12-6I, J) is unique among North American Cretaceous anuran maxillae in having the pars facialis reduced posteriorly to a shallow splinter, the processus frontalis expanded dorsoanteriorly into a broad flange, and the anteroventral edge of the lamina anterior expanded anteriorly into a prong. The two ilia are rather generalized in their construction, except that AMNH 27007 (Fig. 12-6K) has a small, nipple-like tubercle (arrow) placed far posteriorly on the dorsal acetabular expansion, whereas AMNH 22538 (Fig. 12-6L) bears a larger, oval tubercle (arrow) with a flattened lateral face, situated laterodorsally on the shaft and well anterior to the dorsal acetabular expansion.

DISCUSSION

Anuran specimens reported here consist mainly of isolated, distinctive skull elements and ilia that can be associated based on structure, size, relative frequencies, and provenance. With the possible exception of some specimens assigned to "?Eopelobates" sp., these associations appear to be natural and are interpreted as representing different taxa. Variation between homologous elements of the putative fossil taxa is consistent with differences seen among extant anuran genera, suggesting that the fossil taxa are distinct at least at the generic level.

Associations of Lancian elements previously assigned to Paradiscoglossus, Scotiophryne, and Theatonius are generally accepted and these taxa are regarded as valid (i.e., diagnosable) genera. Although Paradiscoglossus and Theatonius are restricted to the Lance Formation and are known from, respectively, ilia and skull bones, these specimens cannot readily be accommodated within a single taxon because the ilia of Paradiscoglossus are from much larger individuals than the individuals represented by skull elements of Theatonius. The two unnamed Judithian taxa are also interpreted as distinct genera, but I defer formally naming and diagnosing these pending more detailed study and comparisons. For reasons discussed in the relevant species account above, the Lancian palaeobatrachid is accepted as a valid taxon, but because its generic allocation is uncertain I follow recent descriptive studies on palaeobatrachids (Sanchíz, 1998; Hossini and Rage, 2000) in questionably retained the species within Palaeobatrachus as P.? occidentalis. The association of Lancian elements under the name ?"Eopelobates" is less secure, although the characteristic cranial ornament and large size of some skull elements suggest that some of the specimens are from conspecific individuals. The six maxillae and two ilia depicted in Figure 12-6 from the Lance Formation are unique specimens; some of these may pertain to previously described taxa for which these elements have not been recognized, but other specimens probably pertain to as yet unrecognized anuran taxa.

While I concur with previous workers (e.g., Estes and Sanchíz, 1982; Evans et al., 1990; Evans and Milner, 1993; Roček and Nessov, 1993; Holman, 1995; Sanchíz, 1998) that isolated anuran ilia and cranial elements are, with some limitations, useful for differentiating among anuran genera and species, at present I am less convinced that these same elements are as informative at the familial level. There are four reasons for my caution. First, anuran systematics currently is in such a state of chaos that there is little consensus on the status and composition for most families, even when only living and, presumably, better understood representatives are considered. To cite a relevant example, the name "Discoglossidae" is currently used in various ways. At one extreme the name is used by Sanchíz (1998) to denote a family containing the traditionally recognized extant genera Alytes Wagler, Barbourula Taylor and Noble, Bombina Oken, and Discoglossus

Otth, plus eight Middle Jurassic–Pliocene genera (Enneabatrachus Evans and Milner, Eodiscoglossus Villalta, Gobiates Špinar and Tatarinov, Kizylkuma Nessov, Latonia Meyer, Paradiscoglossus, Scotiophryne, and Wealdenbatrachus; Wang and Gao [1999] recently named a ninth fossil genus, Callobatrachus). At the other extreme, Cannatella (1985) and Ford and Cannatella (1993) restrict the name Discoglossidae to Discoglossus and Alytes. Others use the familial name in various intermediate ways, by excluding all or some combination of fossil genera (e.g., Clarke, 1988; Roček, 1994). Second, as a result of these differing interpretations of what constitutes a given anuran family, there is no agreement on the diagnostic criteria (i.e., character states) for membership within most families. Three, even when familial diagnoses are presented—Sanchíz's (1998) account for the Discoglossidae is remarkable in providing no familial level diagnosis—these often rely on character states of uncertain polarities or that cannot be determined from the sorts of isolated elements (e.g., maxillae, squamosals, ilia, humeri) that are often are the only source of information for fossil taxa. Finally, of those elements typically available for studies of fossil anurans, none have been surveyed across a broad enough spectrum of taxa to assess the reliability of potentially diagnostic features. This admittedly would be a daunting task, considering that over 4000 species of living anurans (Duellman, 1993) are currently recognized.

For reasons given above, I see no basis for retaining Scotiophryne and Paradiscoglossus in the Discoglossidae sensu lato or ?"Eopelobates" sp. in the Pelobatidae sensu lato (contra Estes and Sanchíz, 1982; Sanchíz, 1998). Nor have I been able to assign either of the unnamed Judithian genera and species to a particular family. The familial position of Theatonius remains uncertain—the taxon exhibits a unique complex of character states that continue to defy its assignment to any known family (Fox, 1976a; Estes and Sanchíz, 1982; Sanchíz, 1998). I recognize that by not assigning these taxa to families, interpretation of these latest Cretaceous taxa in a phylogenetic or biogeographic perspective is more difficult. However unsatisfactory these limitations may be, I feel this conservative approach better and more honestly reflects our current understanding of the higher level affinities of these taxa. As new specimens and information become available, it may be possible to assign these Lancian and Judithian taxa with confidence to particular families and interpret them accordingly.

In contrast, the Lancian taxon Palaeobatrachus? occidentalis can be retained within the Palaeobatrachidae based on character states of the ilium and atlantal complex that, in combination, appear to be diagnostic for the family. Verification of this familial assignment would benefit from the discovery in Lancian horizons of other diagnostic skeletal components, such as the fused and elongate frontoparietals or the synsacrum comprised of fused posterior trunk vertebrae. Palaeobatrachus? occidentalis documents the only North American occurrence for the Palaeobatrachidae and is the second oldest record for the family, the oldest being an indeterminate taxon from the early Campanian of France (Buffetaut et al., 1996). These occurrences support previous suggestions (Estes and Reig, 1973; Estes and Sanchíz, 1982; Duellman and Trueb, 1986) that the Palaeobatrachidae were a Holarctic group during the pre-Tertiary portion of their range.

CONCLUSIONS

My study of anurans from the Campanian and Maastrichtian of the Western Interior is summarized as follows:

(1) Four previously named Lancian taxa are considered valid and revised diagnoses are presented for each: Palaeobatrachus? occidentalis is known from ilia and a fused atlas + first trunk vertebra; Paradiscoglossus americanus is known from ilia; Scotiophryne pustulosa is known from skull bones and ilia, and Theatonius lancensis is known from skull bones.

(2) A small collection of Lancian skull elements and ilia are provisionally associated and identified as belonging to ?"Eopelobates" sp., but it is not certain that these specimens pertain to a single species. Additional Lancian elements of note include six maxillae and two ilia, each of which are unique, but cannot be associated with one another or with any currently recognized Lancian taxon.

(3) Two unnamed Judithian genera and species of uncertain familial position are recognized by distinctive skull and postcranial elements from Alberta. The smaller taxon or a similar one may be represented by fragmentary skull bones from the Aquilan of Alberta, but this is not certain.

(4) Palaeobatrachus? occidentalis is accepted as a member of the Palaeobatrachidae, but its generic status is uncertain. Based on current knowledge, none of the remaining taxa and specimens reported here from the Campanian and Maastrichtian

of the Western Interior can be assigned with confidence to any anuran family.

FIGURE 12-1 Isolated bones of Palaeobatrachus? occidentalis (Estes and Sanchíz) and Scotiophryne pustulosa Estes; late Maastrichtian (Lancian), Montana and Wyoming. Palaeobatrachus? occidentalis (A–H): A–C, UCMP 55704, right ilium, holotype, in (A) lateral, (B) lateral and slightly dorsal, and (C) medial views; (D) UCMP 55705, left ilium, in lateral view; E–H, UALVP 40163, fused atlas and first trunk vertebra, in (E) anterior view, (F) left lateral view, with arrow pointing to foramen at line of fusion between atlas and first trunk vertebra for exit of spinal nerve, and (G) dorsal and (H) ventral views. Provenances: UCMP 55704, 55705, Lance Formation, Wyoming; UALVP 40163, Bug Creek Anthills, Hell Creek Formation, Montana. Scotiophryne pustulosa (I–T); Bug Creek Anthills, Hell Creek Formation, Montana: **I**, **J**, AMNH 26422, left ilium, in (I) lateral and (J) medial views; **K**, UALVP 40155, left ilium; **L**, **M**, UALVP 40157, anterior one-third of left maxilla, in (L) labial and (M) lingual views; **N**, **O**, UALVP 40156, posterior three-quarters of left maxilla, in (N) labial and (O) lingual views; **P**, UALVP 40158, lateroposterior part of left nasal, in dorsal view; **Q**, **R**, UALVP 40159, nearly complete right squamosal, in (Q) lateral and (R) medial views; **S**, **T**, UALVP 40160, anterior end of right frontoparietal, in (S) dorsal and (T) ventral views. Specimens at different scales: top (A–D), middle (E–H), and bottom (I–T) scale bars = 1 mm.

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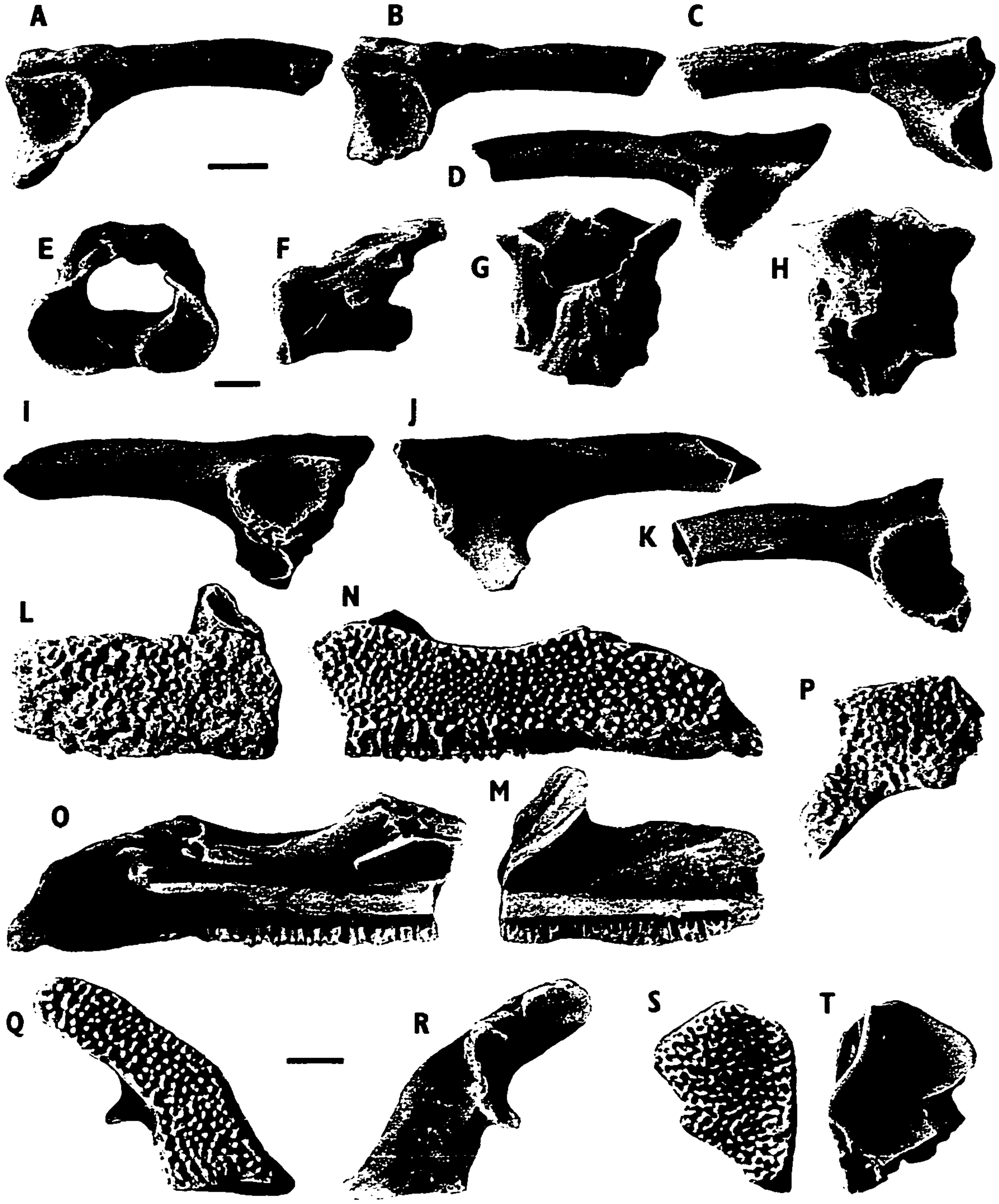

FIGURE 12-2 Isolated bones of Theatonius lancensis Fox and Paradiscoglossus americanus Estes and Sanchíz; late Maastrichtian (Lancian), Lance Formation, Wyoming. Theatonius lancensis (**A–J**): **A–D**, UALVP 12073, nearly complete left maxilla, holotype, in (**A**) labial, (**B**) lingual, (**C**) dorsal, and (**D**) occlusal views; (**E**) UALVP 12075, left maxilla broken in front of orbital margin; (**F**) UALVP 12080, lamella alaris portion of left squamosal; **G, H,** UALVP 12076, left frontoparietal, broken posteriorly, in (**G**) dorsal and (**H**) ventral views; **I, J,** UALVP 12074, nearly complete right frontoparietal, in (**I**) dorsal and (**J**) ventral views. Paradiscoglossus americanus (**K, L**): UCMP 125827, left ilium, holotype, in lateral and medial views. Specimens at different scales: middle left (**A–J**) and bottom center (**K, L**) bars = 1 mm.

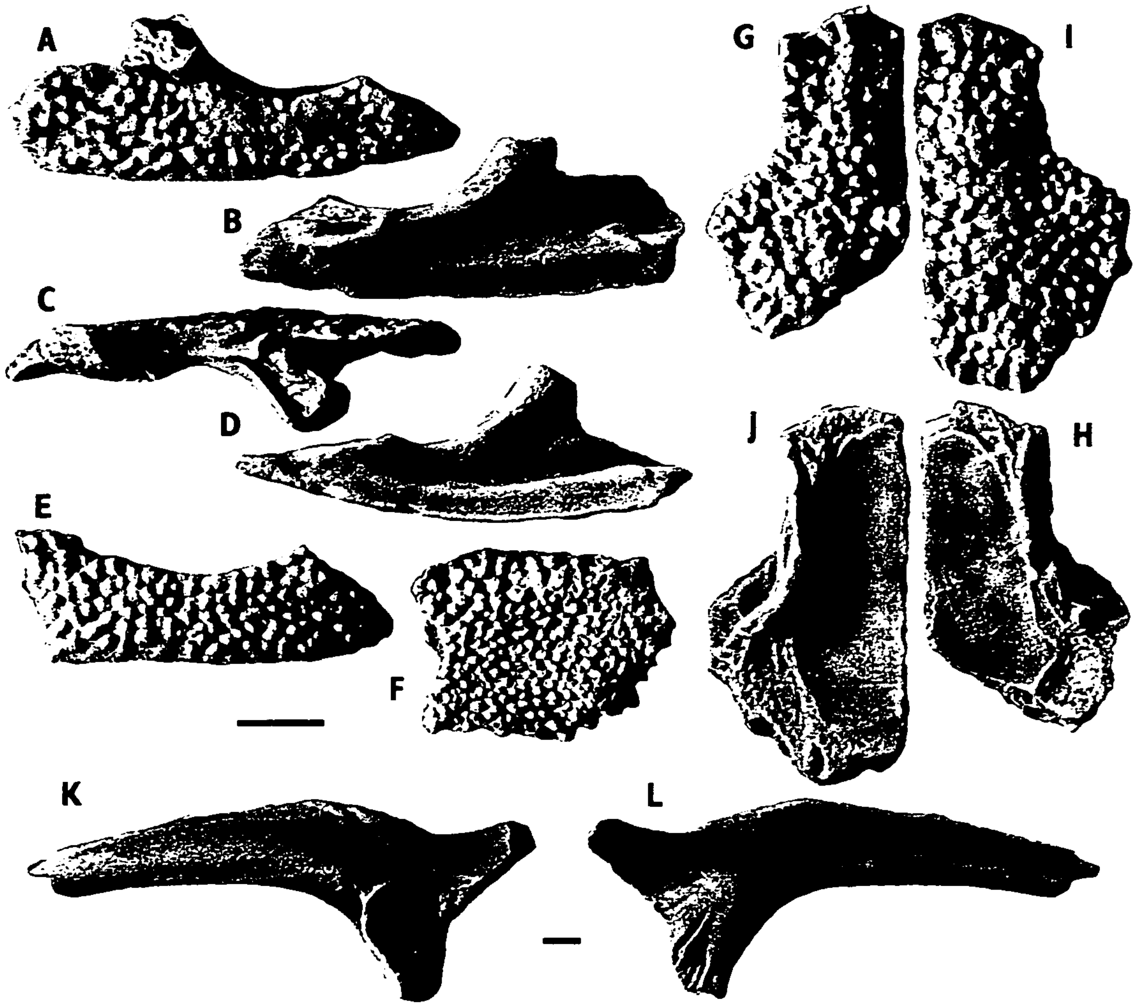
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FIGURE 12-3. Isolated bones of ?"Eopelobates" sp.; late Maastrichtian (Lancian), Wyoming and Montana. **A**, **B**, AMNH 25002, nearly complete right maxilla missing anterior end, in (**A**) labial and (**B**) lingual views; **C**, UCMP 55710, nearly complete left nasal, broken anteriorly, in dorsal view; **D**, **E**, UCMP 55702, nearly complete right squamosal, in (**D**) lateral and (**E**) medial views; **F**, **G**, UALVP 40164, anterior part of right frontoparietal, in (**F**) dorsal and (**G**) ventral views; **H**, **I**, UCMP 55712, left ilium missing distal part of shaft, in (**H**) lateral and (**I**) medial views. Provenances: UALVP 40164, Hell Creek Formation, Montana; all other specimens are from the Lance Formation, Wyoming. Specimens at different scales: top (**A**, **B**), middle right (**C**), middle center (**D**, **E**), and middle right (**F**, **G**), and bottom (**H**, **I**) scale bars = 1 mm.

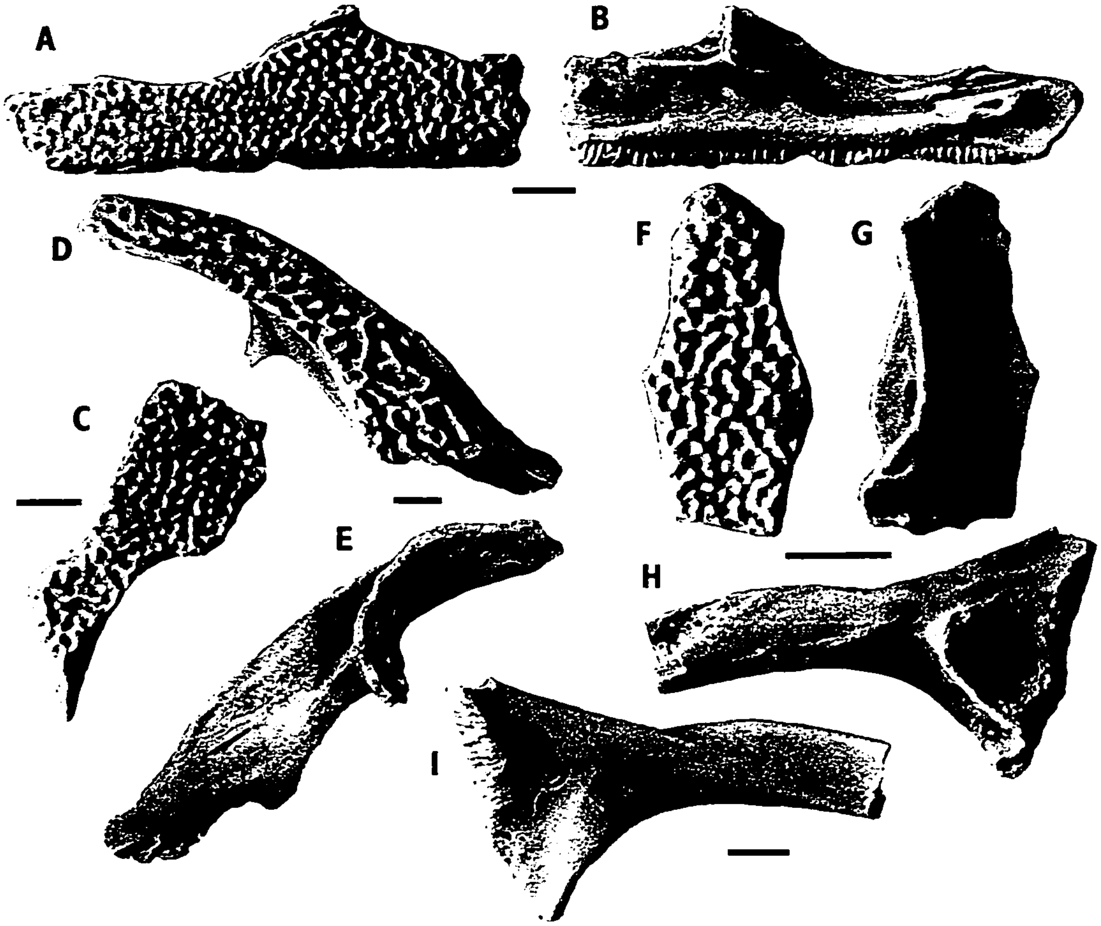
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FIGURE 12-4. Isolated bones of anuran Genus and Species Unnamed A; middle Campanian (Judithian), Dinosaur Park and ?Oldman formations, Alberta. **A**, UALVP 40177, left maxilla broken across anterior part of orbital margin, in labial view; **B**, UALVP 40179, left maxilla broken anteriorly and posteriorly, in labial view; **C**, UALVP 40178, left maxilla, broken across anterior part of orbital margin and missing posterior part of tooth row, in lingual view; **D**, UALVP 40180, posterolateral part of left nasal, in dorsal view; **E**, **F**, UALVP 40181, dorsal part of right squamosal, in (**E**) lateral and (**F**) medial views; **G**, **H**, UALVP 40182, right frontoparietal missing anterior end, in (**G**) dorsal and (**H**) ventral views; **I**, UALVP 40183, anterior end of left frontoparietal, in ventral view; **J**, **K**, UALVP 40184, left ilium, missing distal end of shaft, in (**J**) lateral and (**K**) medial views. Specimens at different scales: bottom (**A–F**, **J**, **K**) and middle right (**G–I**) scale bars = 1 mm.

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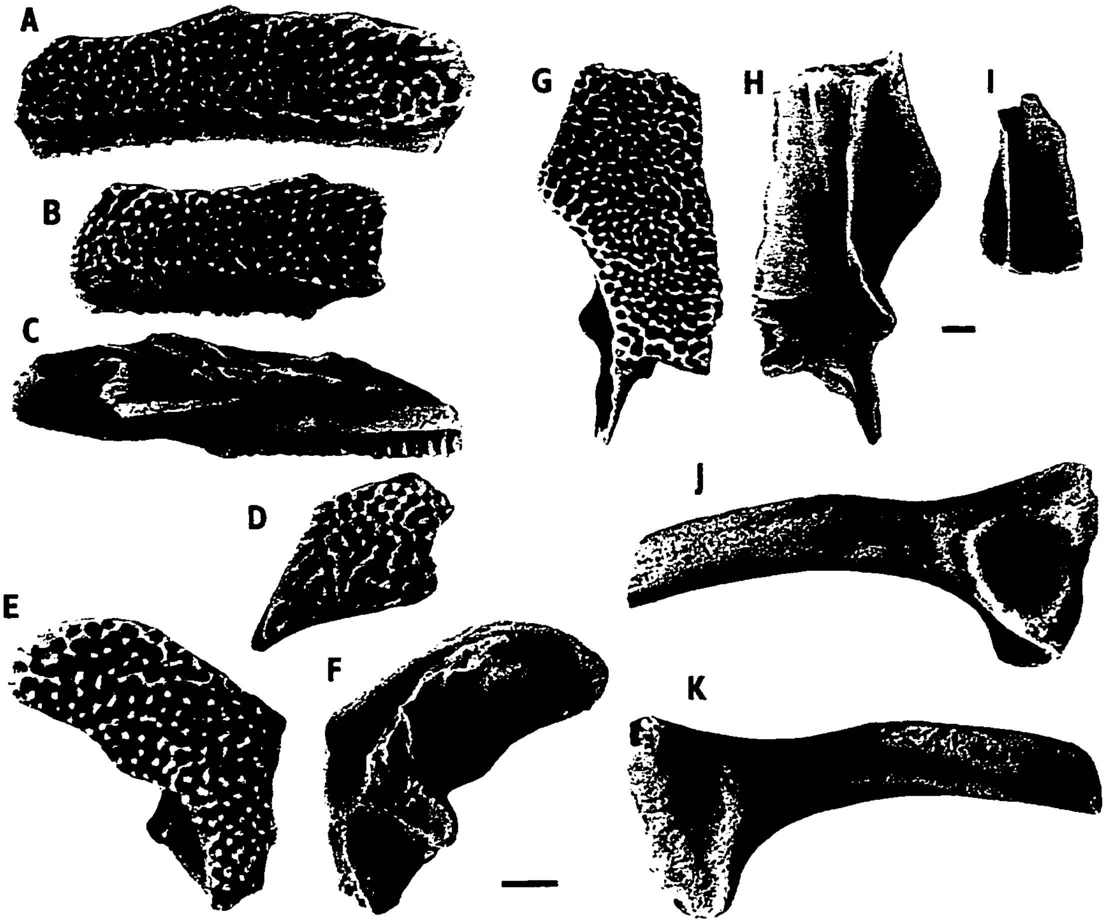

FIGURE 12-5. Isolated bones of anuran Genus and Species Unnamed B; middle Campanian (Judithian), Dinosaur Park and ?Oldman formations, Alberta. **A**, **B**, UALVP 40167, right maxilla missing anterior and posterior ends, in (**A**) labial and (**B**) lingual views; **C**, **D**, UALVP 40168, incomplete right maxilla broken posteriorly below orbital margin and missing anterior part of lamina anterior, in (**C**) labial and (**D**) lingual views; **E**, **F**, UALVP 40169, anterior part of small, right maxilla broken posteriorly across palatine process, in (**E**) labial and (**F**) lingual views; **G**, UALVP 40170, nearly complete left nasal, in dorsal view; **H**, **I**, UALVP 40171, large right squamosal, in (**H**) lateral and (**I**) medial views; **J**, UALVP 40172, incomplete small right squamosal, missing ventral part of processus zygomaticus, in lateral view; **K**, UALVP 40173, anterior part of right frontoparietal, in dorsal view; **L**, TMP 86.23.32, medial part of right frontoparietal, in dorsal view; **M**, UALVP 40174, posterolateral part of left frontoparietal, in dorsal view; **N**, UALVP 40175, proximal part of right ilium, in lateral view; **O**, **P**, TMP 74.10.88, incomplete left ilium, in (**O**) lateral and (**P**) medial views; **Q**, UALVP 40176, distal end of left humerus, in ventral view. Specimens at same scale: scale bar = 1 mm.

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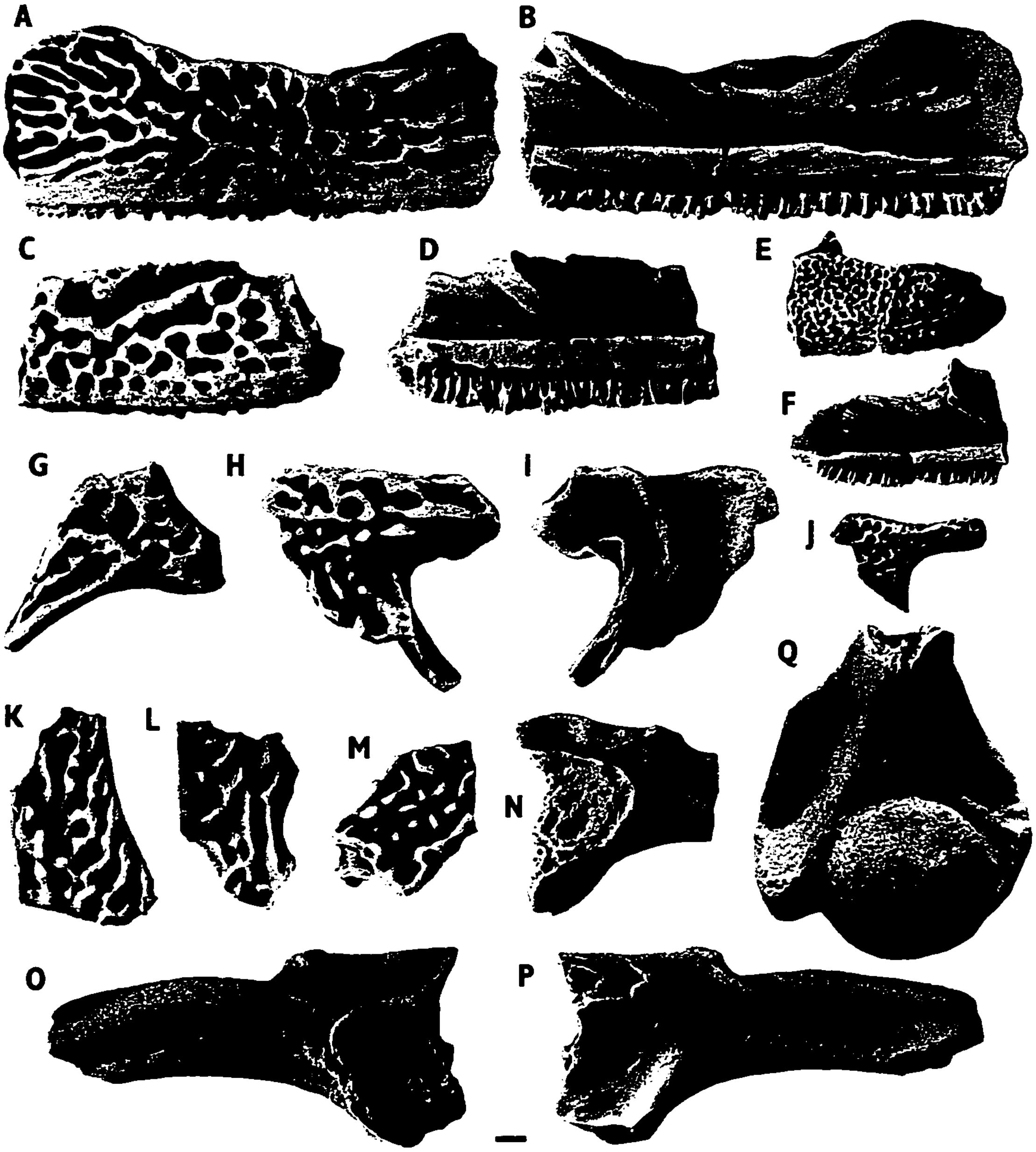
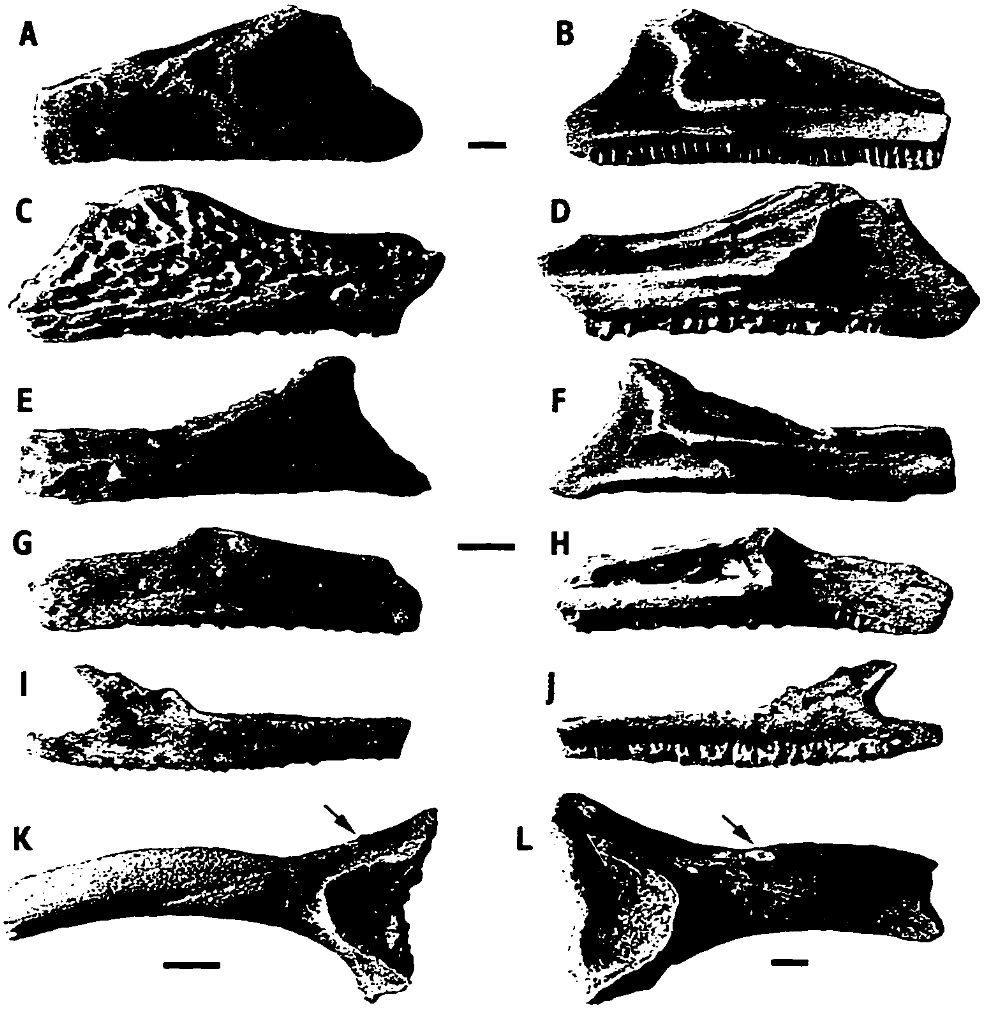


FIGURE 12-6. Maxillae and ilia of anuran Genera and Species Indeterminate; late Maastrichtian (Lancian), Lance Formation, Wyoming. Maxillae (A–L): **A**, **B**, UCMP 55711, posterior part of left maxilla, in (**A**) labial and (**B**) lingual views; **C**, **D**, AMNH 25005, posterior part of right maxilla, in (**C**) labial and (**D**) lingual views; **E**, **F**, UALVP 40165, posterior part of left maxilla, in (**E**) labial and (**F**) lingual views; **G**, **H**, AMNH 29946, posterior part of left maxilla, in (**G**) labial and (**H**) lingual views; **I**, **J**, UALVP 40166, nearly complete left maxilla, missing posteriormost end, in (**I**) labial and (**J**) lingual views. Ilia (**K**, **L**): **K**, AMNH 27007, left ilium, missing distal part of shaft, in lateral view; **L**, AMNH 22538, right ilium, missing distal part of shaft, in lateral view. Specimens at different scales: top (**A**, **B**), center (**C**–**J**), bottom left (**K**), and bottom right (**L**) scale bars = 1 mm.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CHAPTER 13 — GENERAL DISCUSSION AND CONCLUSIONS

My study reveals that lissamphibians were more taxonomically diverse at the genus and species level in the Western Interior during the Campanian and Maastrichtian than was previously recognized (Table 13-1). Three of the four major lissamphibian clades are represented—albanerpetontids, salamanders, and frogs. I recognize twenty species distributed among 17 genera, plus the problematic anuran ?"Eopelobates" sp., which may be a chimera of several species. Eight new species and five new genera are identified: three new species are assignable to established genera, another three new species each belong to new monotypic genera, and two new monotypic Judithian frog genera are informally recognized, but not named. The familial diversity recognized here has decreased from eight to six families because, in contrast to earlier workers (Estes, 1964, 1969, 1970; Estes and Sanchíz, 1982) I do not recognize any representatives of the Discoglossidae sensu lato or Pelobatidae sensu lato among the fossils or taxa included in my study.

Table 13-2 depicts the temporal distribution of lissamphibians during the Aquilan to Lancian NALMAs in the Western Interior. A mixture of temporally long- and short-ranging species is represented. Six species, or slightly more than a third of the species recognized, span two or more Late Cretaceous NALMAs: Albanerpeton nexuosus is known from all four intervals; A. galaktion, Opisthotriton kayi, and Scapherpeton tectum are known from the Aquilan, Judithian, and Lancian; Prodesmodon copei is known from the Judithian, Edmontonian, and Lancian; and Lisserpeton bairdi and Irvinetriton elongatus are known from the Judithian and Lancian. Opisthotriton, Scapherpeton, and Lisserpeton, along with Habrosaurus dilatus, also extend into the Palaeocene. As no taxonomically significant differences are evident among specimens currently available for each taxon from different intervals, it appears that these albanerpetontid and salamander taxa were geologically long-lived species. The remaining species, or slightly less than two-thirds of the recognized species, have more limited temporal distributions and are restricted to single horizons. This latter pattern is particularly evident among the frogs: Lancian and Judithian frog assemblages have no species in common. The Aquilan assemblage may include a taxon similar to the unnamed small bodied Judithian anuran, but the relevant fossils from the Milk River Formation are too poorly preserved to confirm this identification. It is worth noting that of the species restricted to a single horizon, four of these are known from just three or fewer isolated bones: Verdigriserpeton bifurcatus, Esteserpeton robustus, Palaeobatrachus? occidentalis, and Paradiscoglossus americanus.

The Aquilan assemblage, as documented by specimens from the upper Milk River Formation, contains two species of albanerpetontids, three species of salamanders, and at least one indeterminate species of frog. Of these, only the batrachosauroidid Verdigriserpeton bifurcatus is restricted to the Aquilan. Judging by the relative abundance of specimens in the collection of the UALVP, albanerpetontids were the dominant component of the Aquilan assemblage. Albanerpetontids reached their peak diversity in the Judithian with three species. Albanerpetontid remains are rare relative to those of other lissamphibians in collections from Edmontonian and Lancian horizons, suggesting that the family was in decline toward the end of the Cretaceous. The next youngest and only known post-Lancian occurrence for albanerpetontids in North America consists of a small number of isolated elements from several Tiffanian sites in Alberta.

Younger assemblages were dominated by scapherpetontid and batrachosauroidid salamanders, which collectively account for more than a third of the recognized species. Specimens from these two families—especially Opisthotriton, Scapherpeton, and Lisserpeton—typically outnumber those of all other lissamphibians combined at any given Judithian or Lancian site. Both families achieved their maximum diversity during the Lancian.

The taxonomic diversity of the Judithian assemblage falls between that of the Aquilan and Lancian assemblages. Sirenid salamanders make their first appearance in the Judithian, in the form of Habrosaurus prodilatus, a primitive species known only from the Judithian. Three other taxa are restricted to the Judithian: the albanerpetontid Albanerpeton gracilis and the two unnamed monotypic frog genera. Frog specimens currently being described by Richard Blob and colleagues from the type area of the Judith River Formation, Montana, and undescribed articulated and associated skeletons available to me from the Two Medicine Formation, Montana, raise the possibility that additional frog taxa remain to be identified from Judithian horizons. The Judithian also marks the first appearances of three salamanders found in younger assemblages: the batrachosauroidid *Prodesmodon copei* and the scapherpetontids *Lisserpeton bairdi* and *Irvinetriton elongatus*.

Two species known from younger and older horizons are recognized for the Edmontonian: *Albanerpeton nexuosus* and the batrachosauroidid *Prodesmodon*. Given that few productive sites have been identified in deposits of Edmontonian age, the apparent impoverished lissamphibian assemblage from this horizon is best regarded as an artifact.

Late Cretaceous lissamphibian assemblages achieved their maximum diversity during the Lancian, with 15 or 16 species being recognized. Amphiumids make their first appearance, in the form of the primitive genus *Proamphiuma cretacea*. The specialized sirenid *Habrosaurus dilatus*, with its crushing dentition, also appears at this time and extends into the Torrejonian. The new batrachosauroidid *Esteserpeton robustus* is documented by a single characteristic atlas. In contrast, the new scapherpetontid species *Piceoerpeton naylori* is known from several specimens from two formations and represents a range extension for the genus back into the latest Cretaceous. The Lancian is particularly notable for the profusion of frog taxa. At least four taxa are represented and, depending on the identities of elements referred to ?"*Eopelobates*" sp. and the unique maxillae and ilia reported in Chapter 12, more taxa may be represented. An incomplete frog skeleton reported by Cifelli et al. (1999) from the Lancian part of the North Horn Formation may assist in determining associations of some specimens reported here.

In summary, patterns observed in the record of latest Cretaceous lissamphibians in the Western Interior include: (1) albanerpetontids being abundant in the Aquilan and reaching their peak diversity in the Judithian, then declining rapidly thereafter; (2) scapherpetontids and batrachosauroidids becoming increasingly dominant and diverse, with both reaching their maximum taxonomic diversity for any interval in their respective histories during the Lancian; (3) members of living salamander families making their first appearances towards the end of the Cretaceous, with sirenids appearing in the Judithian and amphiumids later in the Lancian; and (4) frogs becoming increasingly diverse, from at least the Judithian to Lancian.

From a paleobiogeographic perspective, Campanian and Maastrichtian lissamphibians in the Western Interior show less affinity with Eurasian groups than previous workers (e.g., Savage, 1973; Estes and Sanchíz, 1982; Duellman and Trueb,

1986) supposed. Albanerpetontids, palaeobatrachid frogs, and batrachosauroidid salamanders are the only families known from both the latest Cretaceous of Europe and the Western Interior. As understood here, the other latest Cretaceous frogs from the Western Interior are best regarded as incertae sedis within the Anura. None of these seem to be closely related to described taxa from elsewhere. Reports of batrachosauroidids and scapherpetontids from the Late Cretaceous of Middle Asia (Nessov, 1981, 1988, 1997) and of sirenids from the Late Cretaceous of Africa and, perhaps, South America (Evans et al., 1996) are rejected. The only unequivocal records for scapherpetontids, sirenids, and amphiumids are in North America, and the earliest occurrences for each family is in the Cretaceous of the Western Interior. Fossil occurrences and the phylogeny proposed here suggest that the Cretaceous evolution of Albanerpeton was centered in the Western Interior, with a Tertiary expansion into Europe. In short, current information implies that lissamphibians in the Western Interior were isolated from outside influences through much of the Late Cretaceous and evolved largely in isolation.

TABLE 13-1. Comparison of lissamphibians recognized from the Campanian and Maastrichtian of the Western Interior in the mid-1980s versus this study. Repeated from Table 1-1; see the latter for further details.

Circa mid-1980s	Current Study
Allocaudata	Allocaudata
Albanerpetontidae	Albanerpetontidae
Albanerpeton nexuosus	*Albanerpeton nexuosus*
Albanerpeton galaktion	*Albanerpeton galaktion*
	Albanerpeton gracilis, sp.nov.
Urodela	Urodela
Amphiumidae	Amphiumidae
Proamphiuma cretacea	*Proamphiuma cretacea*
Sirenidae	Sirenidae
Habrosaurus dilatus	*Habrosaurus dilatus*
	Habrosaurus prodilatus, sp. nov.
Batrachosauroididae	Batrachosauroididae
Opisthotriton kayi	*Opisthotriton kayi*
	"morph I atlantes"
	"morph II atlantes"
Prodesmodon copei	*Prodesmodon copei*
	Esteserpeton robustus, gen. et sp. nov.
Genus & Species Unnamed	*Verdigriserpeton bifurcatus*, gen. et sp. nov.
Scapherpetontidae	Scapherpetontidae
Scapherpeton tectum	*Scapherpeton tectum*
Lisserpeton bairdi	*Lisserpeton bairdi*
Piceoerpeton sp.	*Piceoerpeton naylori*, sp. nov.
	Irvinetriton elongatus, gen. et sp. nov.
Anura	Anura
Palaeobatrachidae	Palaeobatrachidae
Palaeobatrachus occidentalis	*Palaeobatrachus*? *occidentalis*
Discoglossidae *sensu lato*	Family Indeterminate
Scotiophryne pustulosa	*Scotiophryne pustulosa*
Paradiscoglossus americanus	*Paradiscoglossus americanus*
Pelobatidae *sensu lato*	?"*Eopelobates*" sp.
Eopelobates sp.	*Theatonius lancensis*
Incertae Sedis	Genus & Species Unnamed A
Theatonius lancensis	Genus & Species Unnamed B

TABLE 13-2. Chart showing geological distribution of lissamphibians during the Aquilan to Lancian NALMAs in the North American Western Interior as determined by this study. "*Opisthotriton* I and II" denote atlantal morphs referred to the type species (see Chapter 11). An asterisk indicates a taxon that extends into the Palaeocene.

NALMA	ALBANERPETONTIDAE	AMPHIUMIDAE & SIRENIDAE	BATRACHOSAUROIDIDAE	SCAPHERPETONTIDAE	ANURA
LANCIAN	*A. nexuosus* *A. galaktion*	*Proamphiuma* *Habrosaurus dilatus**	*Opisthotriton* I* *Opisthotriton* II* *Prodesmodon* *Esteserpeton*	*Scapherpeton** *Lisserpeton** *Piceoerpeton naylori* *Irvinetriton*	*Palaeobatrachus*? *Scotiophryne* *Theatonius* *Paradiscoglossus* ?"*Eopelobates*" sp.
EDMONTONIAN	*A. nexuosus*		*Prodesmodon*		
JUDITHIAN	*A. nexuosus* *A. galaktion* *A. gracilis*	*Habrosaurus prodilatus*	*Opisthotriton* I *Opisthotriton* II *Prodesmodon*	*Scapherpeton* *Lisserpeton* *Irvinetriton*	Gen. & Sp. Unnamed A Gen. & Sp. Unnamed B
AQUILAN	*A. nexuosus* *A. galaktion*		*Opisthotriton* II *Verdigriserpeton*	*Scapherpeton*	Gen. & Sp. Indet.

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