Albanerpetontid Amphibians from the Upper Cretaceous (Campanian and Maastrichtian) of North America

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ABSTRACT

Three Late Cretaceous albanerpetontids are identified, diagnosed, and described herein based on jaws and frontals from the North American Western Interior: *Albanerpeton nexuosus* Estes, 1981 and *A. galaktion* Fox & Naylor, 1982 (both Campanian and Maastrichtian) and *A. gracilis* n. sp. (middle Campanian). Membership of each in *Albanerpeton* Estes & Hoffstetter, 1976 is founded on diagnostic character states of the frontals and on premaxillary synapomorphies that diagnose less inclusive clades in the genus. *A. nexuosus* is a member of the robust-snouted clade, whereas *A. galaktion* and *A. gracilis* n. sp. belong in the gracile-snouted clade. Species of *Albanerpeton* appear to have evolved largely in isolation through the Late Cretaceous in the Western Interior. Although the three species were broadly sympatric, differences in cranial structure and inferred body size imply that each favored a different ecological niche.

RÉSUMÉ

Albanerpetontidae (Amphibia) du Crétacé Supérieur (Campanien et Maastrichtien) d'Amérique du Nord.

Trois Albanerpetontidae ont été identifiés sur la base de mâchoires et frontaux du Crétacé supérieur de l'Intérieur occidental nord américain ; ils sont décrits et une diagnose est fournie pour chacun d'eux. Il s'agit de deux espèces du Campanien et du Maastrichtien (*Albanerpeton nexuosus* Estes, 1981 et *A. galaktion* Fox & Naylor, 1982) et de *A. gracilis* n. sp. du Campanien moyen. Leur attribution à *Albanerpeton* Estes & Hoffstetter, 1976 est basée sur des états de caractères diagnostiques des frontaux et des synapomorphies des prémaxillaires ; ces caractères diagnosent des clades restreints à l'intérieur du genre. *A. nexuosus* appartient au clade caractérisé par un museau robuste alors que *A. galaktion* et *A. gracilis* n. sp. font partie du clade à museau gracile. Ces espèces d'Albanerpetontidae semblent avoir évolué de façon nettement isolée pendant le Crétacé supérieur dans l'Intérieur occidental. Bien que les trois espèces soient largement sympatriques, des différences dans la structure crânienne ainsi que dans la taille corporelle déduite impliquent qu'elles vivaient dans des niches écologiques différentes.

MOTS CLÉS
Albanerpeton,
Albanerpetontidae,
Campanien,
Crétacé,
Maastrichtien,
Amérique du Nord.

INTRODUCTION

The Albanerpetontidae are Middle Jurassic to Miocene salamander-like tetrapods that are of interest because they are a long lived (*c.* 155 million years) and primarily Laurasian clade of lissamphibians distinct from frogs, salamanders, and caecilians. In North America, albanerpetontids are represented by isolated and occasional articulated bones in Aptian/Albian to Paleocene non-marine deposits in the Western Interior, from southern Alberta and Saskatchewan south into Texas (Estes 1981; Fox & Naylor 1982; Gardner 1999a, b, c). This arguably is the stratigraphically most nearly continuous record for the clade and is important because occurrences of albanerpetontids from elsewhere during this interval are limited to the poorly preserved holotype skeleton of *Celtedens megacephalus* (Costa, 1864) from the lower Albian of Italy (Estes 1981; McGowan & Evans 1995) and isolated, indeterminate skull and postcranial bones from the Cenomanian and Coniacian of Uzbekistan (Nessov 1997; Gardner & Averianov 1998), upper Campanian or lower Maastrichtian of

Spain (Duffaud & Rage 1999), and upper Maastrichtian of Romania (Grigorescu *et al.* 1999). The North American record is particularly important for interpreting the evolution of the type genus *Albanerpeton* Estes & Hoffstetter, 1976 because the oldest occurrences of the genus and all but one of its species are from North America (Gardner 1999a, b, c, d, 2000).

Two species of *Albanerpeton* have been recognized in deposits of Campanian and Maastrichtian age (= Aquilan to Lancian North American Land Mammal ages; see remarks below) in the Western Interior of North America: *A. nexuosus* Estes, 1981 and *A. galaktion* Fox & Naylor, 1982. Estes (1981) named the former species on a distinctive dentary from the upper Maastrichtian (Lancian in age) 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, 1964, a salamander named on a diagnostic atlas and known by additional atlantes and trunk vertebrae from the Lance Formation. On the strength of stratigra-

phical occurrences and morphology, Naylor (1979) convincingly argued that referred jaws of *Prodesmodon* Estes, 1964 pertained instead to an *Albanerpeton*-like taxon, a genus then known only by the type species *A. inexpectatum* Estes & Hoffstetter, 1976 from the Miocene of France. Estes (1981) agreed with Naylor's (1979) findings and erected the new species *A. nexuosus* to accommodate the jaws and femur, he (Estes 1964) originally had referred to *Prodesmodon*. Estes (1981) also reported, without comment, *A. nexuosus* in the upper Maastrichtian (Lancian in age) Hell Creek Formation of Montana, the middle Campanian (Judithian in age) Judith River Formation of Montana and Oldman Formation of Alberta, and the lower Campanian (Aquilan in age) Milk River Formation of Alberta. Fox & Naylor (1982) transferred 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*, both the specific (McGowan 1998) and generic (Rage & 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 & Naylor (1982) for *A. galaktion* sample only a fraction of the specimens available from the formation. An intriguing, but consistently overlooked, aspect of Fox & 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 & 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 & Naylor 1982; Breithaupt 1982; Bryant 1989; McGowan 1998; Duffaud & Rage 1999; Rage & 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 & 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 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.

Specimens reported here come from 16 non-marine formations comprised largely of fluviodeltaic sediments deposited across a broad coastal plain in the North American Western Interior during the Campanian and Maastrichtian (Fig. 1; Table 1). The relative ages of these deposits are commonly expressed using North American Land Mammal ages (NALMAs), which are provincial time units or biochrons based on successions of mammalian assemblages in the Western Interior (see L. S. Russell 1975; Fox 1976; Lillegraven & 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). For osteological terms, measurements, and conventions I follow my previous papers (Gardner & Averianov 1998; Gardner 1999a, b, c, d, 2000a, b).

ABBREVIATIONS

AMNH	American Museum of Natural History, New York;
KUA	Kansas University Archives, University of Kansas, Lawrence;
KUVP	University of Kansas Vertebrate Paleontology collection, Lawrence;
LSUMG	Louisiana State University Museum of Geology, Baton Rouge;
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts;
OMNH	Oklahoma Museum of Natural History, Norman;
RSMNH	Royal Saskatchewan Museum of Natural History, Regina;
RTMP	Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta;
TMM	Texas Memorial Museum, Austin;
UALP	University of Arizona Laboratory of Paleontology, Tucson;
UALVP	University of Alberta Laboratory for Vertebrate Paleontology, Edmonton;
UCM	University of Colorado Museum, Boulder;
UCMP	University of California Museum of Paleontology, Berkeley;
UW	University of Wyoming, Laramie.

IDENTIFICATION AND ASSOCIATION
OF JAWS AND FRONTALS
OF *ALBANERPETON NEXUOSUS*
AND *ALBANERPETON 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 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 2000a) 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. 2)
Estes' figure (1964: fig. 44c; redrawn in Gardner 2000a: fig. 3P) 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. 2A, B) and 49535 (Fig. 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

TABLE 1. — Occurrences of *Albanerpeton nexuosus* Estes, 1981, *A. galaktion* Fox & Naylor, 1982, and *A. gracilis* n. sp. in the Upper Cretaceous (Campanian and Maastrichtian) of the North American Western Interior. Indeterminate albanerpetontids are known from all ten of these formations, plus another six in the Western Interior: Foremost, Scollard, and St. Mary River formations, Alberta; Frenchman Formation, Saskatchewan; Judith River Formation, Montana; and Wahweap Formation, Utah. Absolute dates are from Gradstein *et al.* (1995) and durations of stages and North American Land Mammal ages (NALMAs) are not proportional. Abbreviations: **den**, dentary; **fm**, formation; **fr**, frontals; **mx**, maxilla; **pmx**, premaxilla. An asterisk denotes an element known by just one specimen.

My	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*
71.3		Edmontonian		Fruitland or Kirtland fm, New Mexico *A. nexuosus* den*		
	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		

(Fig. 2D I) and can also be referred to *A. nexuosus*. These dentaries, particularly the 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 & Naylor (1982: 125) for *A. galaktion*. Referred dentaries of *A. nexuosus* from the Milk River Formation (Fig. 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. 2J-M). These conform to Fox & 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
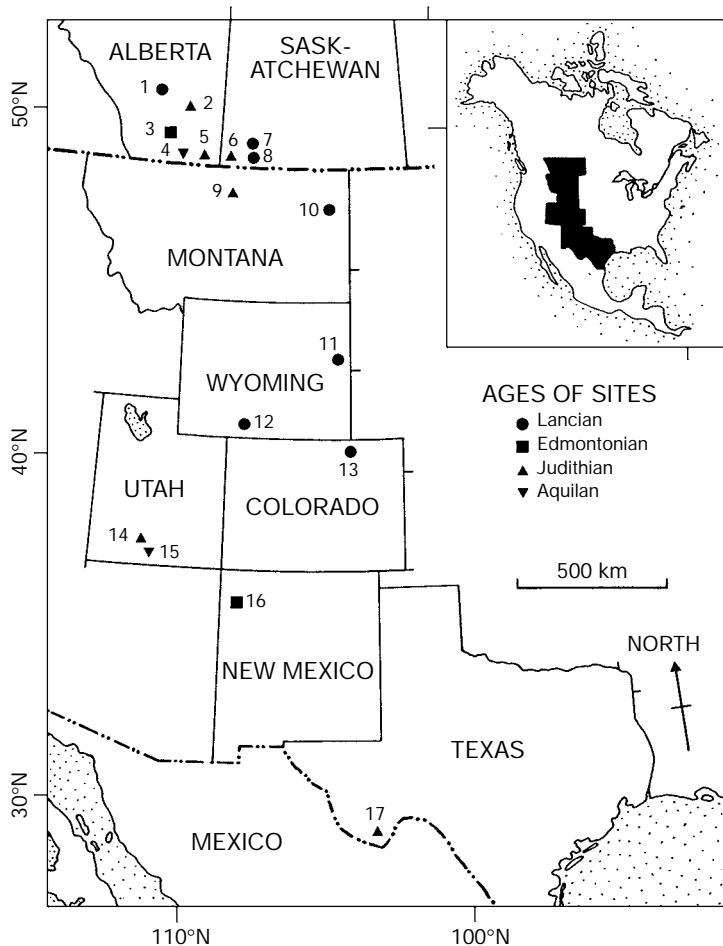
FIG. 1. — Map showing locations of important Upper Cretaceous (Campanian and Maastrichtian) albanerpetontid-bearing sites in the North American Western Interior. Inset map in upper right shows areas (shaded) of provinces in Canada and states in the United States depicted in larger map. Localities and formations: **1**, KUA-1, Red Deer River Valley, Scollard Formation; **2**, RTMP L0406, L0411, and L0413, Oldman Formation, and RTMP L0051, L0054, L0086, L0410 (holotype locality of *Albanerpeton gracilis* n. sp.), 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 & Naylor, 1982), -8, -9, -12, -20, Verdigris Coulee, Deadhorse Coulee Member, Milk River Formation; **5**, RTMP L1124, Foremost Formation, and RTMP 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 (pers. comm. 1999).

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
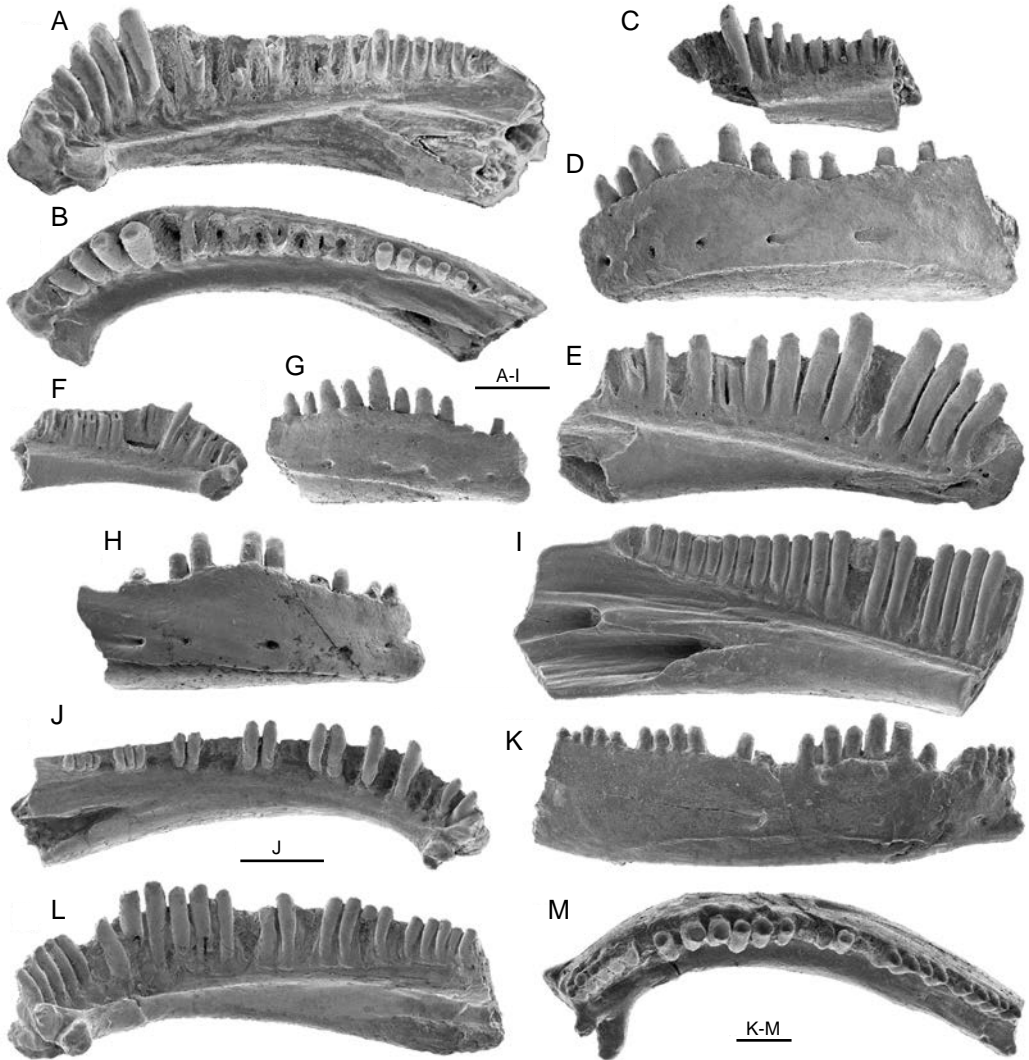
FIG. 2. — Dentaries of *Albanerpeton nexuosus* Estes, 1981 and *A. galaktion* Fox & Naylor, 1982, Campanian and Maastrichtian (Aquilan to Lancian in age), North American Western Interior; **A-I**, *A. nexuosus*; **A, B**, UCMP 49540, topotypic right mandible consisting of incomplete dentary and anterior tip of angular, A, lingual view, B, occlusal view; **C**, UCMP 49535, incomplete topotypic right dentary, lingual view; **D**, **E**, UCM 38714, incomplete left dentary, D, labial view, E, lingual view; **F**, RTMP 96.78.152, anterior part of left dentary, lingual view; **G**, UALVP 16238, anterior part of right dentary, labial view; **H**, UALVP 40014, anterior part of right dentary, labial view; **I**, UALVP 40032, posterior part of left dentary missing posteriormost end of area for attachment of postdentary bones, lingual view; **J-M**, *A. galaktion*; **J**, UALVP 16221, incomplete small, left dentary, lingual view; **K-M**, UALVP 16217, incomplete large, right dentary, K, labial view, L, lingual view, M, occlusal view. Provenances: A-C, UCMP specimens, Lance Formation, Wyoming; D, E, UCM specimen, Laramie Formation, Colorado, all upper Maastrichtian (i.e. Lancian in age); F, RTMP specimen, Oldman Formation, middle Campanian (i.e. Judithian in age), Alberta; G-M, UALVP specimens, Milk River Formation, lower Campanian (i.e. Aquilan in age), Alberta. Scale bars: 1 mm.

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
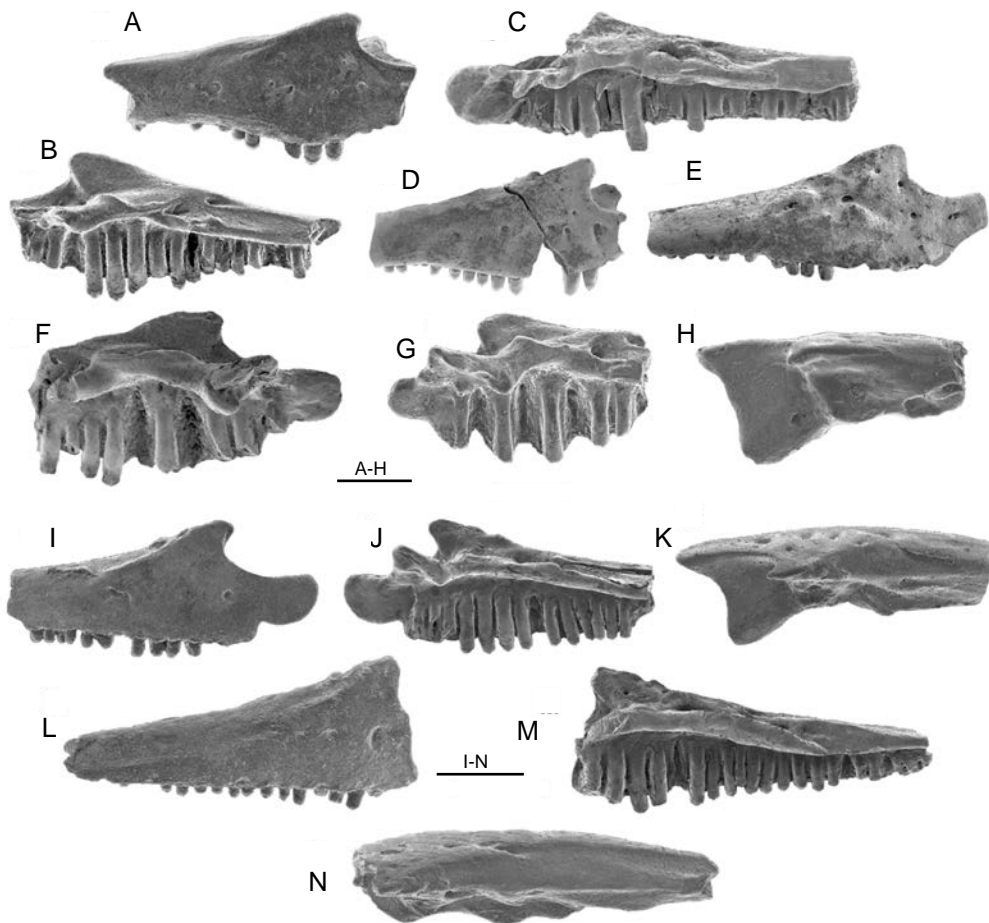
Fig. 3. — Maxillae of *Albanerpeton nexuosus* Estes, 1981 and *A. galaktion* Fox & Naylor, 1982; Campanian and Maastrichtian (Aquilan to Lancian in age), North American Western Interior; **A-H**, *A. nexuosus*; **A**, **B**, UALVP 16242, incomplete right maxilla; A, labial view, B, lingual view; **C**, UALVP 39973, incomplete right maxilla, lingual view; **D**, OMNH 60245, incomplete right maxilla, labial view; **E**, UALVP 39977, incomplete right maxilla, labial view; **F**, OMNH 60239, anterior part of left maxilla, lingual view; **G**, **H**, UALVP 16239, anterior part of right maxilla, G, lingual view, H, dorsal view; **I-N**, *A. galaktion*; **I-K**, UALVP 16240, incomplete right maxilla, I, labial view, J, lingual view, K, dorsal view; **L-N**, UALVP 16241, incomplete right maxilla, L, labial view, M, lingual view, N, dorsal view. Provenances: A-C, E, G-N, UALVP specimens, Milk River Formation, lower Campanian (i.e. Aquilan in age), Alberta; D, OMNH 60245, Kaiparowits Formation, Utah; F, OMNH 60239, Aguja Formation, Texas, both middle Campanian (i.e. Judithian in age). Scale bars: 1 mm.

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. 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,
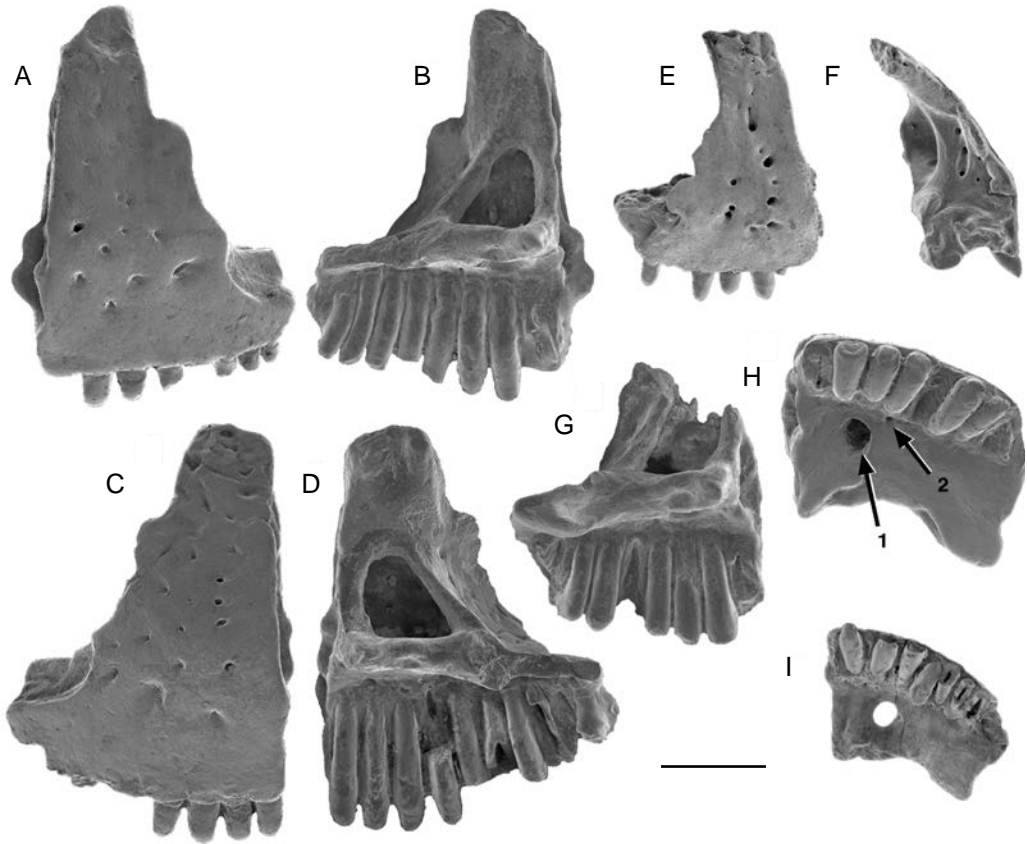
FIG. 4. — Premaxillae of *Albanerpeton galaktion* Fox & Naylor, 1982, Campanian (Aquilan and Judithian in age), North American Western Interior; **A**, **B**, UALVP 16203, holotype, nearly complete left premaxilla; **A**, labial view; **B**, lingual view; **C**, **D**, UALVP 16204, nearly complete right premaxilla; **C**, labial view; **D**, lingual view; **E**, **F**, RTMP 95.177.81, nearly complete right premaxilla; **E**, labial view; **F**, lateral and slightly dorsal view; **G**, **H**, UALVP 16212, left premaxilla missing dorsal part of pars dorsalis; **G**, lingual view; **H**, occlusal view; **I**, RTMP 96.78.124, left premaxilla, occlusal view. Provenances: A-D, G, H, UALVP specimens, Milk River Formation, lower Campanian (i.e. Aquilan in age); E, F, I, RTMP specimens, Oldman Formation, middle Campanian (i.e. Judithian in age), all from Alberta. Arrows: **1**, palatal foramen; **2**, unnamed foramen in junction between pars palatinum and pars dentalis. Scale bar: 1 mm.

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. 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. 3I-N). These features complement those in dentaries that I here refer to *A. galaktion* and argue for assigning the second kind of maxillae in the formation to the
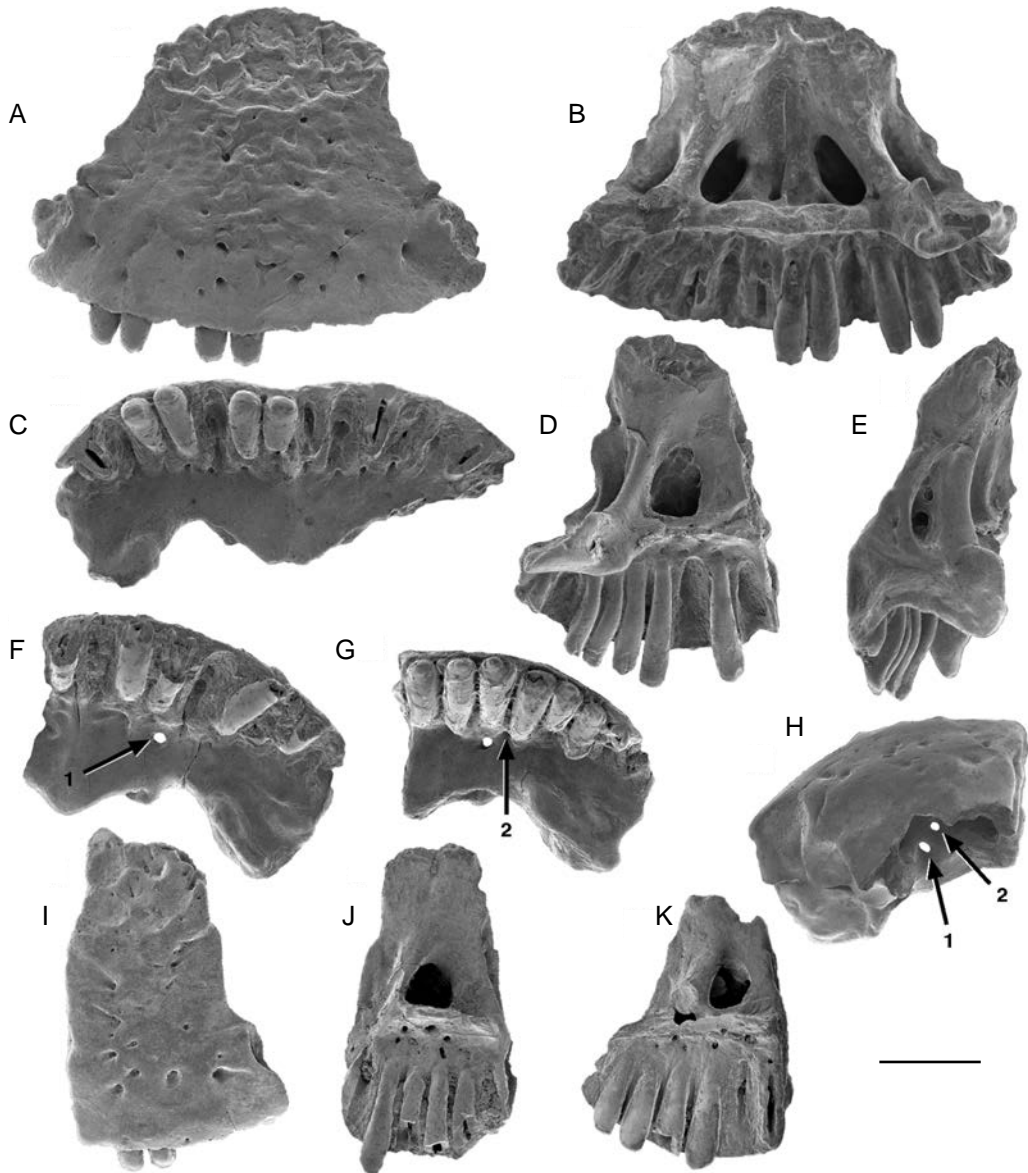
FIG. 5. — Premaxillae of *Albanerpeton nexuosus* Estes, 1981, Campanian and Maastrichtian (Aquilan to Lancian in age), North American Western Interior; **A-C**, UALVP 16206, fused and nearly complete premaxillae; **A**, labial view; **B**, lingual view; **C**, occlusal view; **D**, **E**, UALVP 39955, nearly complete left premaxilla; **D**, lingual view; **E**, lateral and slightly dorsal view; **F**, UALVP 39971, fused premaxillae missing most of right side, occlusal view; **G**, UALVP 39960, left premaxilla, occlusal view; **H**, UALVP 39969, left premaxilla broken transversely across pars dorsalis, dorsal view showing dorsal openings of palatal and unnamed foramina in floor of supra-palatal pit; **I**, OMNH 25345, incomplete left premaxilla, labial view; **J**, OMNH 60238, incomplete left premaxilla, lingual and slightly ventral view; **K**, UCM 38713, incomplete left premaxilla, lingual view. Provenances: A-H, UALVP specimens, Milk River Formation, lower Campanian (i.e. Aquilan in age), Alberta; I, J, OMNH specimens, Aguja Formation, middle Campanian (i.e. Judithian in age), Texas; K, UCM specimen, Laramie Formation, upper Maastrichtian (i.e. Lancian in age), Colorado. Arrows: **1**, palatal foramen; **2**, unnamed foramen in junction between pars palatinum and pars dentalis. Scale bar: 1 mm.

TABLE 2. — Straight line measurements (in mm) for premaxillae of *Albanerpeton nexuosus* Estes, 1981 and *A. galaktion* Fox & Naylor, 1982; Campanian and Maastrichtian (Aquilan to Lancian in age) North American Western Interior. Measurements follow Gardner (1999d: fig. 1a, with LaND and LaNW substituted for, respectively, PfrND and PfrNW) and abbreviations are defined in Table 4. For each entry, first row: number of specimens (left and right sides in fused premaxillae of *A. nexuosus* measured separately); second row: measurement (one specimen) or range of measurements (two or more specimens); third line: mean and standard deviation (three or more specimens).

Species & unit	PmH	PDH	PDW^1	PDW^2	LaND	LaNW	SPH	SPW
A. nexuosus All specimens	9	11	12	18	11	11	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 (Aquilan)	7	9	9	15	9	9	10	16
	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 (Judithian)	2	2	2	2	2	2	2	2
	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 (Lancian)	1	1	1	1	1	1	1	1
	> 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 (Aquilan)	3	3	7	8	3	7	4	10
	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 & Dinosaur Park (Judithian)	2	2	3	6	2	3	2	5
	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
	-	-	0.93 ± 0.14	1.19 ± 0.20	-	0.13 ± 0.03	-	0.72 ± 0.12

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 4; 5; Tables 2; 3)
Fox & Naylor (1982) named *Albanerpeton galaktion* on a nearly complete left premaxilla (UALVP 16203; Fig. 4A, B) and referred ten catalogued premaxillae from the Milk River Formation to the species. Fox & 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. 4) differs from the second (Fig. 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

TABLE 3. — Ratios of straight line measurements for premaxillae of *Albanerpeton nexuosus* Estes, 1981 and *A. galaktion* Fox & Naylor, 1982; Campanian and Maastrichtian (Aquilan to Lancian in age), North American Western Interior. Ratios are defined in Table 4. For each entry, first row: number of specimens (values for left and right sides in fused premaxillae of *A. nexuosus* calculated separately); second row: value (one specimen) or range of values (two or more specimens); third line: mean and standard deviation (three or more specimens).

Species & unit	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 (Aquilan)	9	9	9	9	15
	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 (Judithian)	2	2	2	2	2
	1.17 - 1.25	0.58 - 0.66	0.11 - 0.16	0.34 - 0.34	0.35 - 0.45
	-	-	-	-	-
Laramie (Lancian)	1	0	1	1	1
	> 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 (Aquilan)	3	3	7	3	7
	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 & Dinosaur Park (Judithian)	2	2	3	2	5
	1.40 - 2.10	0.56 - 0.65	0.13 - 0.16	0.26 - 0.29	0.44 - 0.87
	-	-	0.15 ± 0.01	-	0.67 ± 0.14

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 & 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 propor-

tions 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)

Frontals are poorly represented 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. 6A-E) differs from the second (Fig. 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 9) 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 & Naylor, 1982
Family ALBANERPETONTIDAE
Fox & Naylor, 1982

Genus *Albanerpeton* Estes & Hoffstetter, 1976

REMARKS

Elsewhere I have justified my use of the higher level names Allocaudata and Albanerpetontidae (Gardner 1999a), provided revised diagnoses for the Albanerpetontidae and the type genus *Albanerpeton* (Gardner 1999d, 2000a), and presented an outline of my hypothesis of relationships within the genus (Gardner 1999b, c). I currently recognize seven species in *Albanerpeton*. The type species *A. inexpectatum* Estes & Hoffstetter, 1976 (Miocene, France), *A. arthridion* Fox & Naylor, 1982 (uppermost Aptian-middle Albian, Texas and Oklahoma), and *A. cifellii* Gardner, 1999b (upper Turonian, Utah) have been considered in recent papers by myself (Gardner 1999a, b, d, 2000a, b) and others (McGowan 1998; Rage & Hossini 2000). A fourth species represented by jaws and frontals from the upper Paleocene of Alberta will be formally named and described elsewhere.

Each of the three remaining congeners considered below is known by jaws and frontals, and can be assigned to *Albanerpeton* based on the following combination of diagnostic frontal character states (Gardner 2000a): fused frontals triangular-shaped in dorsal or ventral outline; internasal process pointed anteriorly in dorsal or ventral outline; ratio of midline length to width across posterior edge between lateral edge of ventrolateral crests about 1.2 or less; lateral face of internasal process bearing elongate groove for tongue-in-groove contact with nasal; anterolateral process prominent and pointed distally; dorsal and ventral edges of slot for receipt of
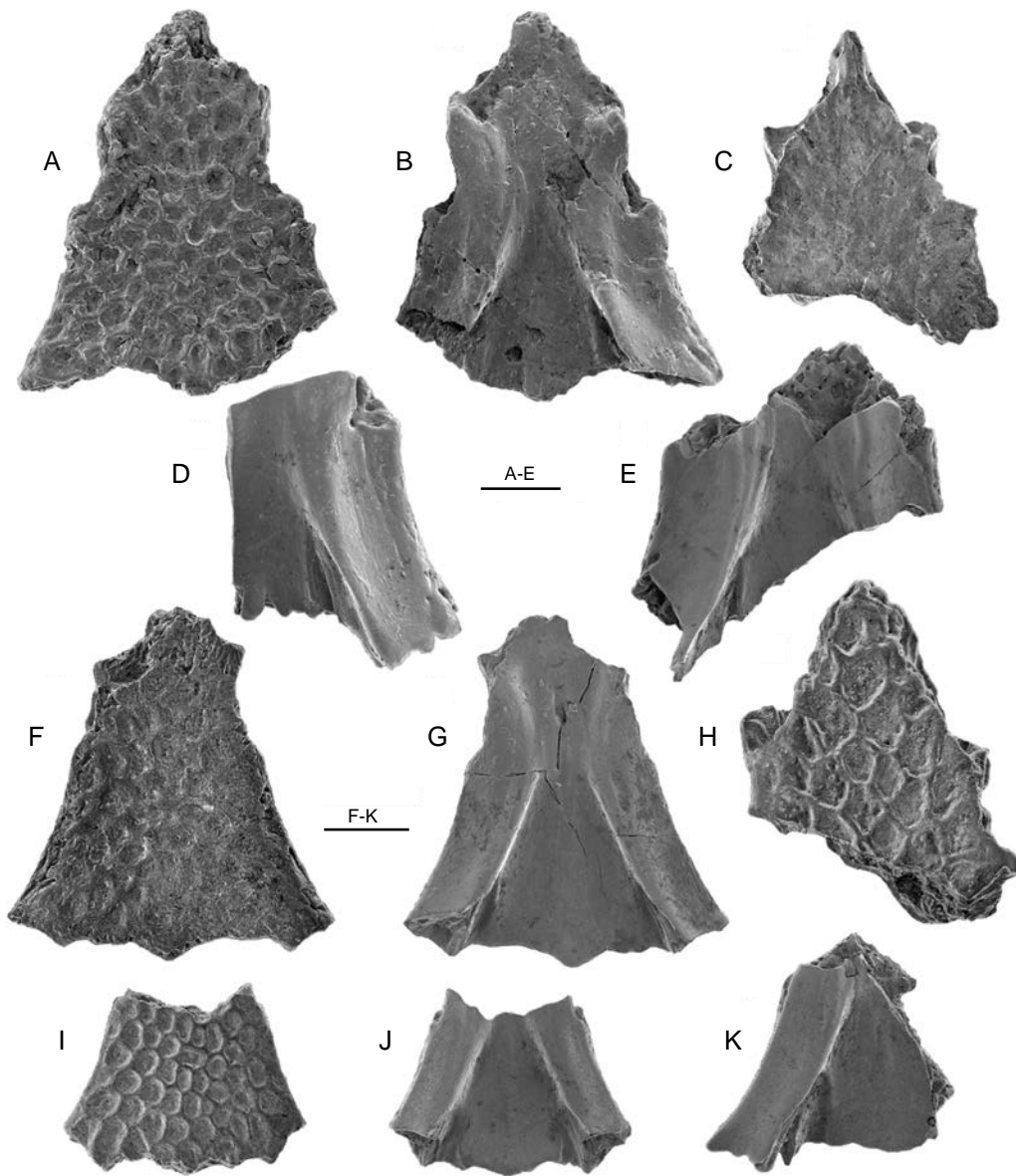
Fig. 6. — Frontals of *Albanerpeton nexuosus* Estes, 1982 and *A. galaktion* Fox & Naylor, 1981, lower Campanian (Aquilan in age), Alberta; **A-E**, *A. nexuosus*; **A**, **B**, UALVP 39996, fused frontals lacking anterior and posterior ends, A, dorsal view, B, ventral view; **C**, UALVP 39983, anterior part of fused frontals, dorsal view; **D**, UALVP 39989, posterior part of left frontal, ventral view; **E**, UALVP 39987, fragmentary fused frontals, ventral view; **F-K**, *A. galaktion*; **F**, **G**, UALVP 16216, fused and incomplete frontals missing anterior end of bone and posterior end of both ventrolateral crests, F, dorsal view, G, ventral view; **H**, UALVP 39946, anterior part of fused frontals, dorsal view; **I**, **J**, UALVP 39945, posterior one-half of fused frontals missing posterior end of both ventrolateral crests, I, dorsal view, J, ventral view; **K**, UALVP 39951, right posterior part of fused frontals, ventral view. All specimens are from the Milk River Formation. Scale bars: 1 mm.

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. Elsewhere I (Gardner 2000a: fig. 1) have depicted reconstructed frontals for the three species based on specimens described below. Each species also exhibits two premaxillary synapomorphies — suprapalatal pit low on pars dorsalis and occupying 4% to no more than 25% of lingual area of pars dorsalis — that are unique among albanerpetontids to a sub-generic clade containing all congeners, except *A. arthridion* (Gardner 1999a, b, c). This unnamed clade consists, in turn, of two less inclusive sister-clades: the robust- and gracile-snouted clades. Each of the species described below belongs to one or the other of these sister-clades.

Albanerpeton nexuosus Estes, 1981
(Figs 2A-I; 3A-H; 5; 6A-E; Tables 2; 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 nexuosus Estes, 1981: 24, fig. 3H-K (original description)
"*Albanerpeton* n. sp. A Estes" Fox & Naylor 1982: 120
"*Albanerpeton* sp. A" Fox & Naylor 1982: table 1
Albanerpeton galaktion Fox & Naylor, 1982: 121-127, figs 2d, e, 3d, e (in part: nine referred, catalogued jaws here transferred to *A. nexuosus*)
Albanerpeton ? *nexuosus* (Estes) McGowan 1998: 191
?*Albanerpeton nexuosus* (Estes) Rage & 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. — Upper Cretaceous (upper Maastrichtian; i.e. Lancian in age) Lance Formation; UCMP V-5620, Niobrara County, Wyoming.

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: RTMP L0406: RTMP 95.177.15, dentary; RTMP L1127: RTMP 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 1). — Upper Cretaceous (Campanian and Maastrichtian), North American Western Interior: lower Campanian (Aquilan in age): Deadhorse Coulee Member, Milk River Formation, Alberta; middle Campanian (Judithian in age): Oldman Formation, Alberta; Kaiparowits Formation, Utah; and Aguja Formation, Texas; upper Campanian or lower Maastrichtian (Edmontonian in age): upper Fruitland Formation or lower Kirtland Formation, New Mexico; upper Maastrichtian (Lancian in age): Hell Creek Formation, Montana; Lance Formation, Wyoming; 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 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 palatine 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 & Naylor (1982:121) for *A. galaktion*. Unless stated otherwise, descriptions below are composites.

Premaxilla (Fig. 5; Tables 2; 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. 5A-C) are solidly fused along the midline. Each fused pair retains a faint median line of fusion lingually and UALVP

16209 (Fox & 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 & 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. 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* (Gardner 1999d). 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 2; 3). The dorsal edge of the process bears well-developed 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. 5B, D) in both absolute and relative terms (Tables 2; 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. 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 & 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. 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. 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 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. 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. 5C, F, G) and bears prominent palatine and maxillary processes with shallow, lingual facets for contact with one or more palatal bones. Medial edges of the palatine processes are solidly fused in the five fused pairs of premaxillae (Fig. 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. 5C) to a short ridge (e.g., UALVP 39971; Fig. 5F). The palatal foramen (Fig. 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 palati-

num at, or slightly inside, the opening of the suprapalatal pit. One or two smaller unnamed foramina (Fig. 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. 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. 5I, J, respectively) from the Aguja Formation and one (UCM 38713; Fig. 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. 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. 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. 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. 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. 3A, D). Damage to the ventral edge of the pars dentalis in some specimens (e.g., UALVP 39973; Fig. 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. 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. 3H) and ventrally bears a transverse ridge, best developed on larger maxillae (Fig. 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. 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. 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. 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. 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. 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 RTMP 96.78.152; Fig. 2C, F, respectively) from elsewhere. No dorsal process is present behind the tooth row (Fig. 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 2A-I; 3A-G; 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. 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. 3C) and 39977 (Fig. 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. 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. 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. 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. 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. 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. 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. 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. 6E) – but the crest is absolutely and

relatively narrower than on comparable-sized frontals of *A. inexpectatum* (Gardner 1999d: pl. 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

Original publication for the name Albanerpeton nexuosus

Estes (1981) first published the name *Albanerpeton nexuosus* on page 24 of the *Encyclopedia of Paleoherpetology*, Part 2, where he provided an adequate account for the species, including the critical designation of the holotype. Yet in that account Estes (1981: 24) cited another 1981 paper (then in press) by himself, in *National Geographic Society Research Reports*, as the original publication for the name *A. nexuosus* (J.-C. Rage, pers. comm. 1999). However, because the latter paper was not published until the following year (Estes 1982) and no holotype was designated, Estes' (1981) account in the *Encyclopedia of Paleoherpetology* remains the first valid publication for the name *A. nexuosus*.

Diagnostic features and affinities of Albanerpeton nexuosus

Estes (1981) and Rage & 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 & Hoffstetter 1976; Estes & Sanchíz 1982; Fox & Naylor 1982; McGowan 1996; McGowan & Ensom 1997; Gardner

1999a, b, d; this study), save for an indeterminate atlas (Seiffert 1969: fig. 1D) from the lower 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 & 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 & Auffenberg, 1958, but now designated as the holotype of *A. arthridion* (Fox & Naylor, 1982). In fact, the pars palatinum on the Albian specimen is broken and largely missing (Fox & Naylor 1982; Gardner 1999a). 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; palatine 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 & 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 & 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 Paleocene 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 1999b, d) 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 & 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 & Hoffstetter 1976: pl. 9; fig. 5; McGowan & 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., 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 *A. 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 *A. nexuosus*. Just two of these can be referred to the species: an incomplete dentary (UW 14584) and maxilla (UW 14582; mis-identified 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 *A. 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 *A. 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 *A. gracilis* n. sp. are all represented.

Albanerpeton galaktion Fox & Naylor, 1982
(Figs 2J-M; 3I-N; 4; 6F-K; Tables 2; 3)

Albanerpeton nexuosus Estes, 1981: 24 (in part: referred jaws from the Milk River Formation)
Albanerpeton galaktion Fox & Naylor, 1982: 121-127, figs 1a, b, d-h; 2-4 (original description)

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 & Naylor 1982: figs 1a, b; 2ac) (Fig. 4A, B).

HOLOTYPE HORIZON AND LOCALITY. — Upper Cretaceous (lower Campanian; i.e. Aquilan in age) Deadhorse Coulee Member, Milk River Formation; UALVP MR-6, Verdigris Coulee, southeastern Alberta.

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: RTMP L0406: RTMP 95.177.81, premaxilla; RTMP L1127: RTMP 96.78.186, premaxilla; RTMP L1128: RTMP 96.78.118, 96.78.184, premaxillae; RTMP L1131: RTMP 96.78.122, premaxilla; RTMP L1137: RTMP 96.78.124, premaxilla.
Kaiparowits Formation. OMNH V6, Utah: OMNH 60326, premaxilla.
Lance Formation. UW V-79032, Wyoming: UW 14593, premaxilla.

DISTRIBUTION (Table 1). — Upper Cretaceous (Campanian and Maastrichtian), North American Western Interior: lower Campanian (Aquilan in age): Deadhorse Coulee Member, Milk River Formation, Alberta: middle Campanian (Judithian in age): Oldman Formation, Alberta; and Kaiparowits Formation, Utah; upper Maastrichtian (Lancian in age): 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 *Albanerpeton gracilis* n. sp. 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 *A. gracilis* n. sp. 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 & 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 & 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 referable to *A. galaktion.* Descriptions below are composites, unless stated otherwise.

Premaxilla (Fig. 4; Tables 2; 3)
Twenty premaxillae are available. The two most nearly complete specimens are the holotype UALVP 16203 (Fig. 4A, B) and UALVP 16204 (Fig. 4C, D). The latter is also the largest specimen, with a height of nearly 3.4 mm. Although the largest available premaxillae of *A. 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 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 2; 3). Labially, the upper one-quarter to one-third of the pars dorsalis bears an indistinct boss, best developed on UALVP 16204 (Fig. 4C) and RTMP 95.177.81

(Fig. 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 4E, specimens such as RTMP 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. 4B, D, G). The suprapalatal pit is large in both absolute (Table 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. 4F) that open inside the suprapalatal pit.

Preserved intact on UALVP 16212 (Fig. 4G, H) and RTMP 96.78.124 (Fig. 4I), the pars palatinum is lingually broad and bears prominent palatine 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. 3I-N)

The two most nearly complete of the seven specimens at hand from the Milk River Formation are UALVP 16240 (Fig. 3I-K) and 16241 (Fig. 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. 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. 2J) and 16217 (Fig. 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 2J-M; 3I, J, L, M; 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. 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. 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 (RTMP 96.78.124; Fig. 4I) has a nearly functional replacement tooth at the fourth locus from the medial edge.

Frontals (Fig. 6F-K)

Nine azygous pairs of frontals are available from the Milk River Formation. UALVP 16216 (Fig. 6F, G), the most nearly complete specimen, is missing most of the anterior end (*contra* McGowan 1998), 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. 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. 6I, J), and 39951 (Fig. 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. 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. 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. 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 (Gardner 1999d).

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 *A. gracilis* n. sp. and allies these species in the less inclusive gracile-snouted clade (Gardner 1999b, c).

Fox & Naylor (1982: 121) diagnosed *A. 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 & Naylor's (1982: 121) statement that *A. 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 & Naylor 1982) are diagnostically useful for albanerpetontids, because the proportions of both structures vary more within and overlap more among species than Fox & Naylor (1982) suspected (see also Gardner 1999a, 2000a).

McGowan (1998) recently presented a revised diagnosis for *A. galaktion* based on four frontal characters. In formulating his diagnosis, McGowan (1998) relied entirely on photographs (Fox & Naylor 1982: fig. 1d, e) of the referred frontals UALVP 16216 (Fig. 6F, G). McGowan (1998) 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 1998) 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 1998). The surface that McGowan (1998) regarded as the outline of the internasal process is actually the broken leading edge of the specimen (Gardner 2000a). UALVP 39946 (Fig. 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 (1998: 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 (1998) claimed; the former condition occurs in all species of *Albanerpeton* and is diagnostic for the genus (Gardner 2000a). Contrary to McGowan (1998), 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 2000a). Emargination of the slot increases with growth (see Gardner 1999d: pl. 2, G-L) and this alone accounts for the shallowly excavated slots in UALVP 16216. McGowan (1998) 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 diffe-

rentiates *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 convincingly 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 1% of surface area of pars dorsalis in non-*Albanerpeton* albanerpetontids and *A. arthridion,* and 4 to 15% 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 (Gardner 1999b, 2000a) and can be expected to have been enlarged in size and, presumably, enhanced in function in *A. galaktion* relative to other albanerpetontids.

Albanerpeton gracilis n. sp.
(Figs 7; 8A-E; Table 4)

"undescribed middle Campanian species" Gardner 1999a: 533
"*Albanerpeton* species B" Gardner 1999d: 63

HOLOTYPE. — RTMP 95.181.70, nearly complete left premaxilla missing palatine process and lateral end of pars dentalis, and having three broken and three intact teeth (Fig. 7A, B).

HOLOTYPE HORIZON AND LOCALITY. — Upper Cretaceous (middle Campanian; i.e. Judithian in age) Dinosaur Park Formation; RTMP L0410, Dinosaur Provincial Park, Alberta.

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

REFERRED SPECIMENS. — **Oldman Formation.** Seven localities, Alberta: RTMP L0406: RTMP 95.177.82, 95.177.83, premaxillae; RTMP 95.177.80, maxilla; RTMP L0411: RTMP 96.1.57, frontals; RTMP L0413: RTMP 95.180.64, premaxilla; RTMP L1127: RTMP 96.78.187-96.78.197, premaxillae; RTMP 96.78.103, dentary; RTMP L1128: RTMP 96.78.135, frontals and incomplete right prefrontal; RTMP L1137: RTMP 96.78.185, premaxilla; RTMP L1141: RTMP 96.78.126, premaxillae.
Dinosaur Park Formation. Eight localities, Alberta: RTMP L0051: RTMP 95.145.67, premaxilla; RTMP L0054: RTMP 86.60.110, frontals; RTMP L0086: RTMP 95.182.22, premaxilla; RTMP L0410 (holotype locality): RTMP 95.181.72, 95.181.73, premaxillae; RTMP 95.181.69, 95.181.71, maxillae; RTMP 95.181.68, dentary; RTMP 86.194.8, 95.181.67, frontals; RTMP L1108: RTMP 95.157.73, maxilla; RTMP L1118: RTMP 95.174.59, maxilla; RTMP L1119: RTMP 95.163.50, premaxilla; RTMP L1120: RTMP 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 1). — Upper Cretaceous (middle Campanian; i.e. Judithian in age), 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% 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.
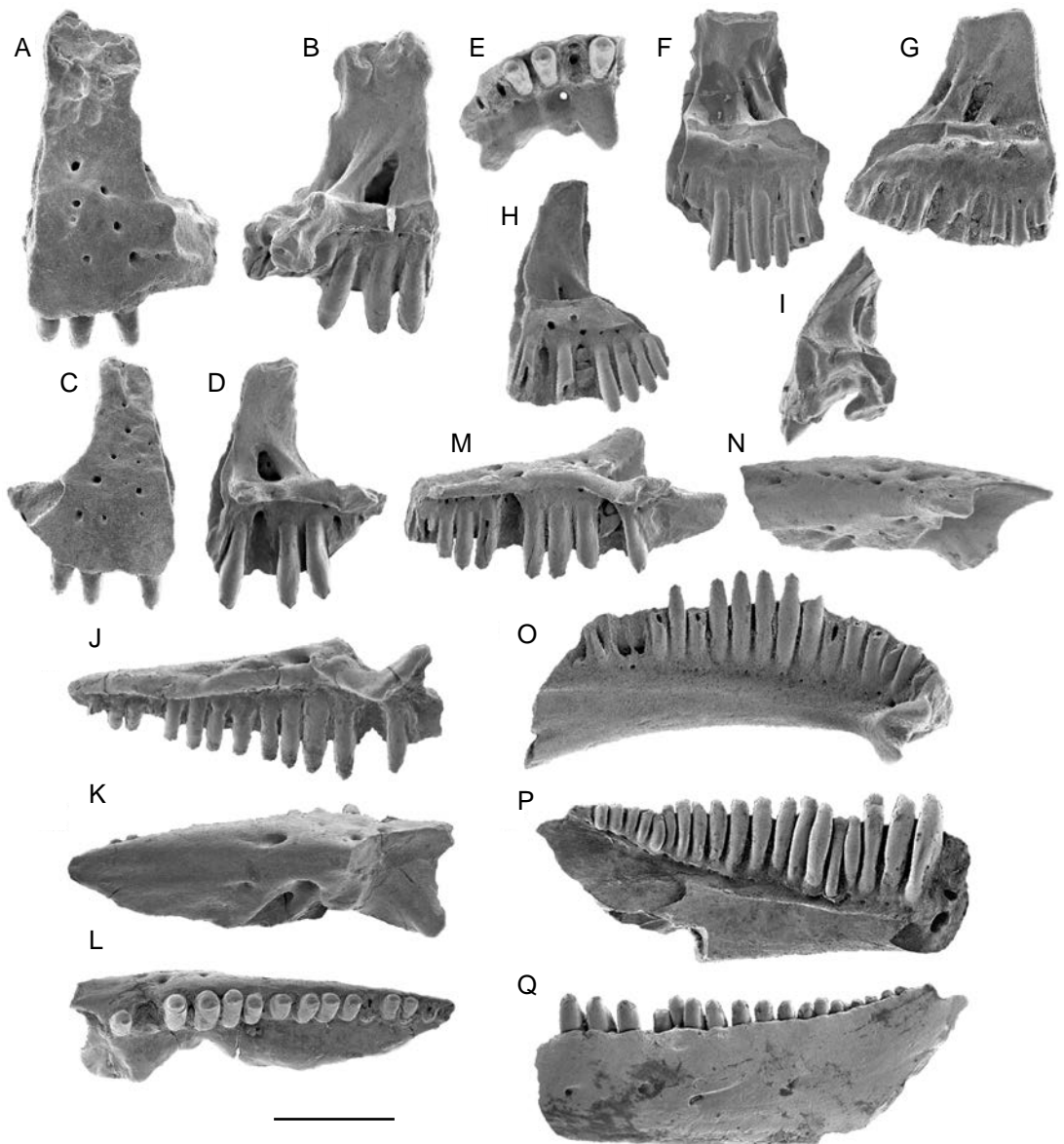
FIG. 7. — Jaws of *Albanerpeton gracilis* n. sp., middle Campanian (Judithian in age), North American Western Interior; **A**, **B**, RTMP 95.181.70 (holotype), incomplete left premaxilla; **A**, labial view; **B**, lingual view; **C-E**, RTMP 96.78.191, nearly complete right premaxilla; **C**, labial view; **D**, lingual view; **E**, occlusal view; **F**, OMNH 60321, incomplete right premaxilla, lingual view; **G**, OMNH 60242, incomplete left premaxilla, lingual view; **H**, RTMP 96.78.196, incomplete right premaxilla, lingual and slightly occlusal view; **I**, RTMP 95.180.64, incomplete left premaxilla, lateral view; **J-L**, RTMP 95.157.73, nearly complete left maxilla; **J**, lingual view; **K**, dorsal view; **L**, occlusal view; **M**, **N**, RTMP 95.177.80, incomplete left maxilla; **M**, lingual view; **N**, dorsal view; **O**, RTMP 96.78.103, anterior part of left dentary, lingual view; **P**, **Q**, RTMP 95.181.68, medial part of left dentary; **P**, labial view; **Q**, lingual view. Provenances: A, B, J-L, P, Q, RTMP specimens, Dinosaur Park; C-E, H, I, M-O, RTMP specimens, Oldman formations, all from Alberta; F, OMNH specimens, Kaiparowits Formation, Utah; G, Aguja Formation, Texas. Scale bar: 1 mm.

TABLE 4. — Straight line measurements (in mm) and ratios of straight line measurements for premaxillae of *Albanerpeton gracilis* n. sp.; middle Campanian (Judithian in age), Oldman and Dinosaur Park formations, Alberta. **Measurement or Ratio**, measurements follow Gardner 1999d: fig. 1a, with LaND and LaNW substituted for, respectively, PfrND and PfrNW; **n**, number of specimens; **R**, range; **x**, mean; **sd**, standard deviation.

Measurement or Ratio	n	R	x and sd
PmH (height of premaxilla)	11	2.17 - 2.82	2.50 ± 0.18
PDH (height of pars dorsalis)	11	1.30 - 1.86	1.50 ± 0.16
PDW[1] (width of pars dorsalis across base of lacrimal notch)	11	0.50 - 1.02	0.72 ± 0.17
PDW[2] (width of pars dorsalis across suprapalatal pit)	18	0.65 - 1.71	0.86 ± 0.15
LaND (depth of lacrimal notch)	10	0.34 - 1.12	0.77 ± 0.22
LaNW (width of lacrimal notch)	11	0.03 - 0.18	0.08 ± 0.05
SPH (height of suprapalatal pit)	18	0.25 - 0.56	0.35 ± 0.07
SPW (maximum width of suprapalatal pit)	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

DESCRIPTION

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

Premaxilla (Fig. 7A-I; Table 4)

With a height of just over 2.8 mm, the holotype (RTMP 95.181.70; Fig. 7A, B) is the largest of the 27 premaxillae at hand. The most nearly complete specimen, RTMP 96.78.91 (Fig. 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 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 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 4) and occupies about four to 10% (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. 7B, D, F-H). RTMP 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 palatine and maxillary processes (Fig. 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 RTMP 95.181.70 and 95.180.64 (Fig. 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 RTMP 95.180.64 is about two-thirds the size of RTMP 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 RTMP 96.78.196 (Fig. 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. 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. 7J-N)

The largest of the nine available specimens, RTMP 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, RTMP 95.157.73 (Fig. 7J-L) and 95.177.80 (Fig. 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. 7O-Q)

Two incomplete dentaries are available: RTMP 96.78.103 (Fig. 7O) preserves about the anterior two-thirds of the bone, whereas RTMP

95.181.68 (Fig. 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. RTMP 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. RTMP 96.78.103 preserves a moderately prominent symphyseal eminence and two intact symphyseal prongs. The remainder of the lingual structure is unremarkable.

Dentition (Fig. 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. 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 (RTMP 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, RTMP 95.174.59 (not figured) and 95.157.73 (Fig. 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 RTMP 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 (RTMP 95.177.80; Fig. 7M) with an in situ replacement crown in the tooth slot at the second locus and in a dentary (RTMP 95.181.68; Fig. 7P) with replacement teeth at the fourth-sixth and fifteenth loci from the broken anterior end of the tooth row.

Frontals (Fig. 8A-E)
Two of the five pairs of fused frontals are nearly complete. RTMP 86.194.8 (Fig. 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. RTMP 96.78.135 (Fig. 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, RTMP 95.181.67 (Fig. 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 RTMP 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
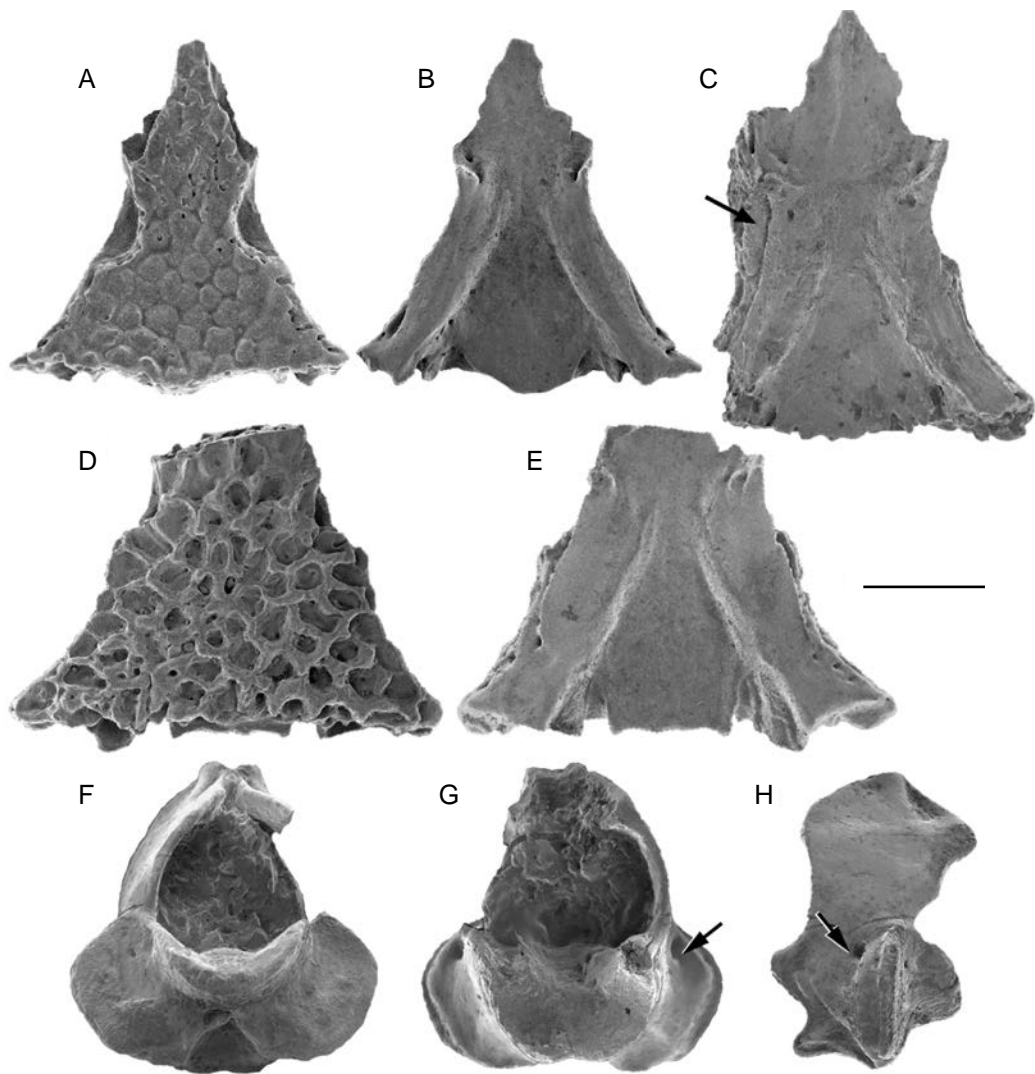
FIG. 8. — Frontals of *Albanerpeton gracilis* n. sp. and atlas of indeterminate albanerpetontid genus and species, Campanian (Judithian and Aquilan in age), Alberta; **A-E**, *A. gracilis* n. sp.; **A**, **B**, RTMP 86.194.8, fused and nearly complete frontals, A, dorsal view, B, ventral view; **C**, RTMP 96.78.135, fused and nearly complete frontals with medial end of right prefrontal (arrow) preserved in articulation, ventral view; **D**, **E**, RTMP 95.181.67, fused frontals missing anterior part, D, dorsal view, E, ventral view; **F-H**, genus and species indeterminate; **F**, **G**, UALVP 16234, nearly complete atlas missing part of left wall of neural arch, F, anterior view, G, posterior view; **H**, right lateral view, with arrows indicating foramen on right side for exit of first spinal nerve. Provenances: A, B, D, E, *A. gracilis* n. sp., Dinosaur Park, C, Oldman formations, middle Campanian (i.e. Judithian in age); F-H, genus and species indeterminate, Milk River Formation, lower Campanian (i.e. Aquilan in age). Scale bar: 1 mm.

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. RTMP 86.194.8 is unusual in having the slot completely open dorsally (Fig. 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 RTMP 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 RTMP 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. 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, RTMP 86.194.8 (Fig. 8B) and 96.1.57 (not figured), the crest resembles that on frontals of *Albanerpeton arthridion* (Gardner 1999a) in being convex ventrally in transverse view. On RTMP 96.78.135 and 95.181.67 (Fig. 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 ($\approx$ 20 *versus* $\approx$ 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 slit- to triangular-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 indet.
(Fig. 8F-H)

HORIZONS, LOCALITIES, AND VOUCHER SPECIMENS. — **Lower Campanian (Aquilan in age) 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 in age) horizons: **Foremost Formation.** RTMP L1124, Alberta: RTMP 96.78.100, lot of four dentaries.
Dinosaur Park Formation. RTMP L0410, Alberta:

RTMP 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.

Upper Campanian-lower Maastrichtian (Edmontonian in age) 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.

Upper Maastrichtian (Lancian in age) 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 & 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 & 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 are limited to a nearly complete atlas (UALVP 16234; Fox & Naylor 1982: fig. 1f-h) (Fig. 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 & Hoffstetter 1976; Estes 1981; Estes & Sanchíz 1982; McGowan 1996; McGowan & Ensom 1997; Gardner 1999a, b) 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 & Naylor (1982). UALVP 16234 differs from referred atlantes of *Albanerpeton inexpectatum* (see Estes & 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 & Hoffstetter 1976; Estes & Sanchíz 1982; McGowan 1996; McGowan & 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 & 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, 1928) 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 & 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 & 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 (RTMP 96.78.144; Peng 1997: pl. 8a, b) resembles albanerpetontid trunk vertebrae in having an amphicoelous centrum and, evidently, unicipital rib-bearers, 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 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 upper Campanian or lower Maastrichtian Laño site in Spain (Duffaud & Rage 1999) and jaws, frontals, and vertebrae from the upper 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 & 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 & 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., D. A. 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 & Averianov 1998) that show no obvious affinities with those of North American taxa, beyond primitive resemblances. Recently I (Gardner 1999a) 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 & 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 (Gardner 1999b, c, unpubl.). 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 (RTMP L0406 and L1127, Oldman Formation, Alberta; OMNH V6, Kaiparowits Formation, Utah) have yielded diagnostic elements of all three congeners. These records indicate that *A. 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 & 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* n. sp. 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* n. sp., both of which lack the osteological novelties of their robust-snouted congeners for strengthening the snout.

CONCLUSION

My survey documents the presence of albanerpetontids in 16 Campanian and Maastrichtian formations in the North American Western Interior. Jaws and frontals from nine of these units are diagnostic at the specific level and permit the identification of three species: *A. nexuosus*, *A. galaktion,* and the new species *A. gracilis.* Assignment of these species to *Albanerpeton* is supported by frontal character states that are diagnostic for the genus, plus premaxillary synapomorphies that diagnose less inclusive clades in the genus.

Skull and postcranial specimens previously described for *A. nexuosus* and *A. galaktion* were incorrectly associated. The topotypic collection for *A. nexuosus* includes dentaries that can be retained in the species, other 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 the range of each species is extended to encompass the Aquilan to Lancian.

The new Judithian species *Albanerpeton gracilis* n. sp. is erected for jaws and frontals from Alberta, Utah, and Texas and is differentiated from its congeners by a unique combination of symplesiomorphies and synapomorphies of the jaws and frontals. *A. gracilis* n. sp. most closely resembles *A. galaktion* and *A. cifellii* in the triangular to slit-like shape of the suprapalatal pit, but primitively lacks the respective premaxillary autapomorphies of the last two species.

Species of *Albanerpeton* appear to have evolved sympatrically during the Late Cretaceous in western North America. *A. nexuosus* is a member of the robust-snouted clade, whereas *A. galaktion* and *A. gracilis* n. sp. belong in the gracile-snouted clade. The origins of both sister-clades antedate the Campanian, as both can be traced back to the early Late Cretaceous. There is no evidence for

immigration of albanerpetontids 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.

While *A. nexuosus, A. galaktion,* and *A. gracilis* n. sp. were broadly sympatric during at least portions of their respective temporal ranges across the Western Interior coastal plain, differences in tooth and premaxillary structure and inferred body size suggest these species favored different ecological niches and need not have competed directly with one another for resources.

REFERENCES

Armstrong-Ziegler J. G. 1978. — An aniliid snake and associated vertebrates from the Campanian of New Mexico. *Journal of Paleontology* 52: 480-483.

Armstrong-Ziegler J. G. 1980. — Amphibia and Reptilia from the Campanian of New Mexico. *Fieldiana Geology,* New Series 4: 1-39.

Breithaupt B. H. 1982. — Paleontology and paleoecology of the Lance Formation (Maastrichtian), east flank of Rock Springs Uplift, Sweetwater County, Wyoming. *Contributions to Geology, University of Wyoming* 21: 123-151.

Bryant L. J. 1989. — Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary boundary in northeastern Montana. *University of California, Publications in Geological Sciences* 134: 1-107.

Carpenter K. 1979. — Vertebrate fauna of the Laramie Formation (Maestrichtian), Weld County, Colorado. *Contributions to Geology, University of Wyoming* 17: 37-49.

Cifelli R. L. 1990. — Cretaceous mammals of southern Utah. IV: Eutherian mammals from the Wahweap (Aquilan) and Kaiparowits (Judithian) formations. *Journal of Vertebrate Paleontology* 10: 346-360.

Clemens W. A., Lillegraven J. A., Lindsay E. H. & Simpson G. G. 1979. — Where, when, and what: a survey of known Mesozoic mammal distribution: 7-58, *in* Lillegraven J. A., Kielan-Jaworowska Z. & Clemens W. A. (eds), *Mesozoic Mammals: The First Two-Thirds of Mammalian History*. University of California Press, Berkeley.

Costa O. G. 1864. — Paleontologia del Regno di Napoli. *Atti dell'Accademia Pontaniana* 8: 1-198.

Denton R. K. Jr. & O'Neill R. C. 1998. — *Parrisia neocesariensis,* a new batrachosauroidid salamander and other amphibians from the Campanian of eastern North America. *Journal of Vertebrate Paleontology* 18: 484-494.

Duffaud S. & Rage J.-C. 1999. — Amphibians from the Upper Cretaceous of Laño (Basque County, Spain). *Estudios del Museo de Ciencias Naturales de Álava* 14 (Núm. esp. 1): 111-120.

Eaton J. G., Cifelli R. L., Hutchison J. H., Kirkland J. I. & Parrish J. M. 1999. — Cretaceous vertebrate faunas from the Kaiparowits Plateau, south-central Utah: 345-353, *in* Gillette D. D. (ed.), Vertebrate Paleontology in Utah, *Utah Geological Survey Miscellaneous Publication* 99 (1).

Estes R. 1964. — Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. *University of California Publications in Geological Sciences* 49: 1-180.

Estes R. 1969. — Prosirenidae, a new family of fossil salamanders. *Nature* 224: 87-88.

Estes R. 1981. — Gymnophiona, Caudata, *in* Wellnhofer P. (ed.), *Encyclopedia of Paleoherpetology*. Part 2. Gustav Fischer Verlag, Stuttgart, 115 p.

Estes R. 1982. — Systematics and paleogeography of some fossil salamanders and frogs. *National Geographic Society Research Reports* 14: 191-210.

Estes R., Berberian P. & Meszoely C. A. M. 1969. — Lower vertebrates from the Late Cretaceous Hell Creek Formation, McCone County, Montana. *Breviora* 337: 1-33.

Estes R. & Hoffstetter R. 1976. — Les Urodèles du Miocène de La Grive-Saint-Alban (Isère, France). *Bulletin du Muséum national d'Histoire naturelle,* 3e Série, n° 398, 57: 297-343.

Estes R. & Sanchíz B. 1982. — Early Cretaceous lower vertebrates from Galve (Teruel), Spain. *Journal of Vertebrate Paleontology* 2: 21-39.

Fox R. C. 1976. — Upper Cretaceous terrestrial vertebrate stratigraphy of the Gobi Desert (Mongolian People's Republic) and western North America, *in* Stelck C. R. & Chatterton B. D. E. (eds), Western and Arctic Canadian Biostratigraphy, *Geological Association of Canada Special Paper* 18: 577-594.

Fox R. C. 1989. — The Wounded Knee local fauna and mammalian evolution near the Cretaceous-Tertiary boundary, Saskatchewan, Canada. *Palaeontographica* 208 (A): 11-59.

Fox R. C. & Naylor B. G. 1982. — A reconsideration of the relationships of the fossil amphibian *Albanerpeton. Canadian Journal of Earth Sciences* 19: 118-128.

Francis E. T. B. 1934. — *The Anatomy of the Salamander.* Clarendon Press, Oxford, 381 p., 25 pls.

Gao K. & Fox R. C. 1996. — Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bulletin of Carnegie Museum of Natural History* 33: 1-107.

Gardner J. D. 1999a. — The amphibian *Albanerpeton arthridion* and the Aptian-Albian biogeography of albanerpetontids. *Palaeontology* 42: 529-544.

Gardner J. D. 1999b. — New albanerpetontid amphibians from the Albian to Coniacian of Utah, USA — bridging the gap. *Journal of Vertebrate Paleontology* 19: 632-638.

Gardner J. D. 1999c. — Current research on albanerpetontid amphibians: a North American perspective. *Canadian Association of Herpetologists Bulletin* 13: 12-14.

Gardner J. D. 1999d. — Redescription of the geologically youngest albanerpetontid (?Lissamphibia): *Albanerpeton inexpectatum* Estes & Hoffstetter, 1976, from the middle Miocene of France. *Annales de Paléontologie* 85 : 57-84.

Gardner J. D. 2000a. — Revised taxonomy of albanerpetontid amphibians. *Acta Palaeontologica Polonica* 45: 55-70.

Gardner J. D. 2000b. — Comments on the anterior region of the skull in the Albanerpetontidae (Temnospondyli; Lissamphibia). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2000: 1-14.

Gardner J. D. & Averianov A. O. 1998. — Albanerpetontid amphibians from Middle Asia. *Acta Palaeontologica Polonica* 43: 453-467.

Gilmore C. W. 1928. — Fossil lizards of North America. *National Academy of Sciences, Memoir* 22: 1-201.

Goin C. J. & Auffenberg W. 1958. — New salamanders of the family Sirenidae from the Cretaceous of North America. *Fieldiana Geology* 10: 449-459.

Gradstein F. M., Agterberg F. P., Ogg J. G., Hardenbol J., Van Veen P. Thierry J. & Huang Z. 1995. — A Triassic, Jurassic and Cretaceous time scale, *in* Berggren W. A., Kent D. V., Aubry M.-P. & Hardenbol J. (eds), Geochronology, Time Scales and Global Stratigraphic Correlation, *Society of Economic Paleontologists and Mineralogists, Special Publication* 54: 95-126.

Grigorescu D., Venczel M., Csiki Z. & Limberea R. 1999. — New latest Cretaceous microvertebrate fossil assemblages from the Hateg Basin (Romania). *Geologie en Mijnbouw* 78: 301-314.

Haeckel E. 1866. — *Generelle Morphologie der Organismen*, 2 volumes. Reimer, Berlin.

Hairston N. G. 1987. — *Community Ecology and Salamander Guilds.* Cambridge University Press, New York, 230 p.

Jaeger R. G. & Forester D. C. 1993. — Social behavior of plethodontid salamanders. *Herpetologica* 49: 163-275.

Kauffman E. G. & Caldwell W. G. E. 1993. — The Western Interior Basin in time and space, *in* Caldwell W. G. E. & Kauffman E. G. (eds), Evolution of the Western Interior Basin, *Geological Association of Canada, Special Paper* 39: 1-30.

Langston W. Jr., Standhardt B. & Stevens M. 1989. — Fossil vertebrate collecting in the Big Bend: history and retrospective: 11-21, *in* Busbey A. B. III & Lehman T. H. (eds), *Vertebrate Paleontology, Biostratigraphy and Depositional Environments, Latest Cretaceous and Tertiary, Big Bend Area, Texas.* Guidebook, Field Trip Numbers 1A, B and C, 49th Annual Meeting of the Society of Vertebrate Paleontology, Austin, Texas.

Lillegraven J. A. 1972. — Preliminary report on Late Cretaceous mammals from the El Gallo Formation, Baja California del Norte. *Natural History Museum of Los Angeles Contributions to Science* 232: 1-11.

Lillegraven J. A. 1976. — A new genus of therian mammal from the Late Cretaceous "El Gallo Formation", Baja California, Mexico. *Journal of Paleontology* 50: 437-443.

Lillegraven J. A. & McKenna M. C. 1986. — Fossil mammals from the "Mesaverde" Formation (Late Cretaceous, Judithian) of the Bighorn and Wind River basins, Wyoming, with definitions of Late Cretaceous North American Land-mammal "ages". *American Museum Novitiates* 2840: 1-68.

Lynch J. F. 1985. — The feeding ecology of *Aneides flavipunctatus* and sympatric plethodontid salamanders in northwestern California. *Journal of Herpetology* 19: 328-352.

Mathis A., Jaeger R. G., Keen W. H., Ducey P. K., Walls S. C. & Buchanan B. W. 1997. — Aggression and territoriality by salamanders and a comparison with the territorial behaviour of frogs: 633-676, *in* Heatwole H. & Sullivan B. (eds), *Amphibian Biology.* Vol. 3: Social Behaviour. Surrey Beatty and Sons, Chipping Norton, Australia.

McGowan G. J. 1996. — Albanerpetontid amphibians from the Jurassic (Bathonian) of southern England, *in* Morales M. (ed.), The Continental Jurassic. *Bulletin of the Museum of Northern Arizona* 60: 227-234.

McGowan G. J. 1998. — Frontals as diagnostic indicators in fossil albanerpetontid amphibians. *Bulletin of the National Science Museum* 24 (C): 185-194.

McGowan G. J. & Evans S. E. 1995. — Albanerpetontid amphibians from the Cretaceous of Spain. *Nature* 373: 143-145.

McGowan G. J. & Ensom P. C. 1997. — Albanerpetontid amphibians from the Lower Cretaceous of the Isle of Purbeck, Dorset. *Proceedings of the Dorset Natural History and Archaeological Society* 118: 113-117.

Naylor B. G. 1979. — The Cretaceous salamander *Prodesmodon* (Amphibia: Caudata). *Herpetologica* 35: 11-20.

Nessov L. A. 1997. — *Cretaceous Nonmarine Vertebrates of Northern Eurasia*. Institute of Earth's Crust, University of Saint Petersburg, Saint Petersburg, 218 p. (in Russian with English abstract).

Peng J. 1997. — *Palaeoecology of Vertebrate Assemblages from the Upper Cretaceous Judith River Group (Campanian) of Southeastern Alberta, Canada*. Ph.D. thesis, University of Calgary, Calgary, Canada, 312 p.

Rage J.-C. & Hossini S. 2000. — Les amphibiens du Miocène moyen de Sansan (Gers, France), *in* Ginsburg L. (ed), La faune Myocène de Sansan et son environnement, *Mémoires du Muséum national d'Histoire naturelle* 183 : 177-217.

Rowe T., Cifelli R. L., Lehman T. M. & Weil A. 1992. — The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos Texas. *Journal of Vertebrate Paleontology* 12: 472-493.

Russell D. A. 1993. — The role of Central Asia in dinosaurian biogeography. *Canadian Journal of Earth Sciences* 30: 2002-2012.

Russell L. S. 1975. — Mammalian faunal succession in the Cretaceous System of western North America, *in* Caldwell W. G. E. (ed.), The Cretaceous System in the Western Interior of North America. *Geological Association of Canada Special Paper* 13: 137-161.

Sahni A. 1972. — The vertebrate fauna of the Judith River Formation, Montana. *Bulletin of the American Museum of Natural History* 147: 321-412.

Sankey J. T. 1998. — *Vertebrate Paleontology and Magnetostratigraphy of the Upper Aguja Formation (Late Campanian), Talley Mountain Area, Big Bend National Park, Texas.* Ph.D. thesis, Louisiana State University and Agricultural and Mechanical College, Baton Rouge, États-Unis, 251 p.

Seiffert J. 1969. — Urodelen-Atlas aus dem obersten Bajocien von SE-Aveyron (Südfrankreich). *Paläontologische Zeitschrift* 43: 32-36.

Sereno P. C. 1997. — The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences* 25: 435-489.

Smith A. G., Smith D. G. & Funnell B. M. 1994. — *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge University Press, New York, 99 p.

Staub N. L. 1993. — Intraspecific agnostic behavior of the salamander *Aneides flavipunctatus* (Amphibia: Plethodontidae) with comparisons to other plethodontid species. *Herpetologica* 49: 271-282.

Standhardt B. R. 1986. — *Vertebrate Paleontology of the Cretaceous/Tertiary Transition of Big Bend National Park*. Ph.D. thesis, Louisiana State University and Agricultural and Mechanical College, Baton Rouge, États-Unis, 299 p.

Storer J. E. 1993. — Additions to the mammalian palaeofauna of Saskatchewan. *Modern Geology* 18: 475-487.