# THE AMPHIBIAN *ALBANERPETON ARTHRIDION* AND THE APTIAN–ALBIAN BIOGEOGRAPHY OF ALBANERPETONTIDS

*by* JAMES D. GARDNER

ABSTRACT. *Albanerpeton arthridion* is rediagnosed and redescribed based on jaws, frontals, atlantes and humeri from the Lower Cretaceous (uppermost Aptian–middle Albian), Antlers Formation of Oklahoma and Texas, USA. Frontals described herein for the first time for *A. arthridion* confirm that the species belongs in the type genus *Albanerpeton*, making it the geologically oldest reported member of the genus. *A. arthridion* is interpreted as the most primitive species of *Albanerpeton* and to have been relatively small. Reduced body size is proposed to be derived and to have developed at least twice within the genus. *A. arthridion* and an indeterminate species reported herein, the latter known by fragmentary jaws from the paracontemporaneous Cloverly Formation, Wyoming, USA, are the geologically oldest records of unequivocal albanerpetontids in North America. These occurrences provide a minimum age of latest Aptian for the establishment of albanerpetontids on the continent and indicate that the Western Interior Seaway, which opened in the latest Albian, would not initially have prevented the movement of albanerpetontids across the continent.

THE Albanerpetontidae are salamander-like, probable lissamphibians characterized by apomorphies such as a mortise and tenon intermandibular joint, fused frontals and highly modified first three vertebrae (Fox and Naylor 1982; Milner 1988; McGowan and Evans 1995; McGowan 1998). Albanerpetontids are known by isolated bones and rare skeletons from the Middle Jurassic–Miocene of Laurasia (Estes and Hoffstetter 1976; Estes 1981; Fox and Naylor 1982; Nessov 1988, 1997; Evans and Milner 1994; Milner 1994; McGowan and Evans 1995; Gardner and Averianov 1998) and have recently been reported from the Lower Cretaceous of North Africa (Broschinski and Sigogneau-Russell 1996, p. 149). Two albanerpetontid genera are presently recognized (McGowan and Evans 1995; Gardner and Averianov 1998) based on differences in the construction and contacts of the fused frontals (McGowan and Evans 1995; Gardner in press): the type genus *Albanerpeton* Estes and Hoffstetter, 1976 (*sensu* McGowan and Evans 1995), from the Aptian–Paleocene of western North America and Miocene of France (Estes and Hoffstetter 1976; Estes 1981; Fox and Naylor 1982; Gardner 1996); and *Celtedens* McGowan and Evans, 1995, an exclusively European genus that has been reported from the Bathonian–Albian (McGowan and Evans 1995; McGowan 1996; McGowan and Ensom 1997).

*Albanerpeton arthridion* Fox and Naylor, 1982 is of interest because it is the geologically oldest member of the type genus and the oldest diagnosable North American albanerpetontid species. Fox and Naylor (1982) described *A. arthridion* based on the incomplete holotype premaxilla and three referred dentaries from outcrops of the upper Antlers Formation (early–mid Albian in age) exposed at Greenwood Canyon, Texas, USA. These four jaws, along with isolated trunk vertebrae and an atlas from the Antlers Formation, had earlier been referred by Estes (1969, 1981) to *Prosiren elinorae* Goin and Auffenberg, 1958, a prosirenid salamander named on a trunk vertebra from the same formation. No other fossils have since been described for *A. arthridion*. In the absence of more diagnostic specimens, concerns have been raised about the validity of the species (McGowan 1994) and its generic affinities (Rage and Hossini in press). Herein I report on collections of cranial and postcranial bones of *A. arthridion* from the Antlers Formation of Texas and Oklahoma that provide critical new information about the osteology and relationships of this hitherto poorly known species. Material from Oklahoma also extends the range of *A. arthridion* down into the uppermost Aptian. I further report on paracontemporaneous albanerpetontid jaws from the Cloverly Formation of Wyoming and comment on the identity of a supposed *Albanerpeton-*
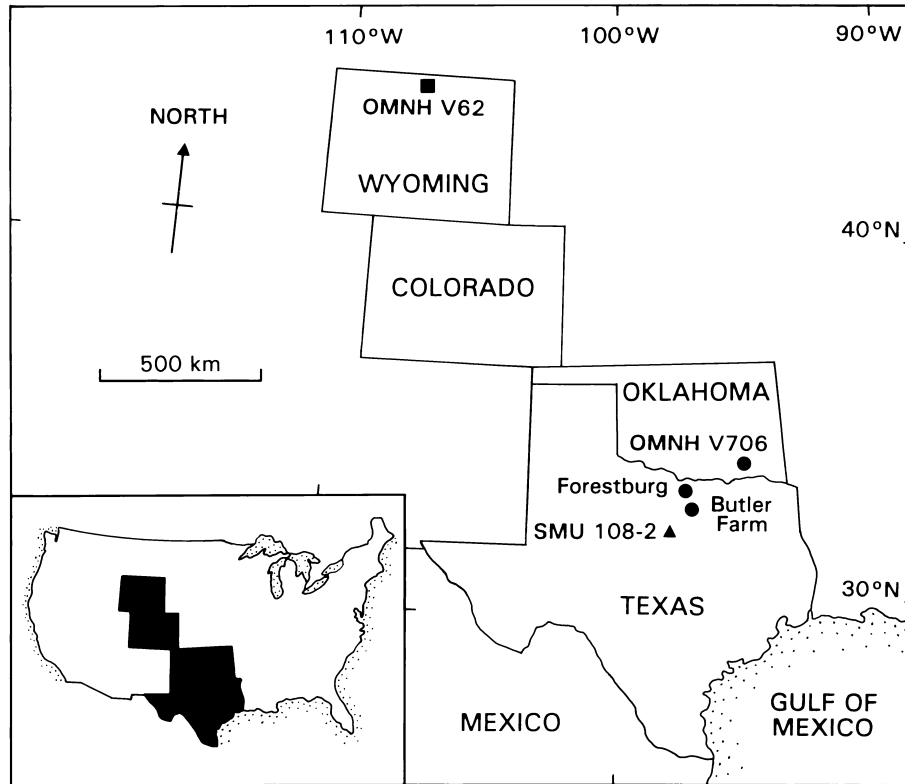
TEXT-FIG. 1. Map of the western USA showing Lower Cretaceous (Aptian–Albian) localities mentioned in the text. Symbols: square, Cloverly Formation; circle, Antlers Formation; and triangle, Paluxy Formation.

like atlas (Winkler *et al*. 1990) from the Paluxy Formation of Texas. Fossils from the Antlers and Cloverly formations are the oldest records (Aptian–Albian) of albanerpetontids in North America. In the final section of this paper, I examine the biogeographical implications of these occurrences.

Fossils described herein were collected in the western United States from microvertebrate sites in the Cloverly, Antlers and Paluxy formations (Text-fig. 1). These formations consist of terrigenous sediments deposited during the Aptian–mid Albian on broad alluvial plains (Fisher and Rodda 1967; Caughey 1977; Hobday *et al*. 1981; Winslow and Heller 1987) and have yielded diverse non-marine vertebrate assemblages (Ostrom 1970; Winkler *et al*. 1989, 1990; Cifelli *et al*. 1997).

Osteological terms, measurements and conventions used herein follow Gardner (in press) for jaws, frontals and atlantes; osteological terms for the humerus follow Francis (1934). Head–body length in herpetological studies is typically described as the snout–vent length (SVL), a straight line measurement between the tip of the snout and the anterior or, more rarely, posterior edge of the cloaca (Peters 1964, p. 324). Because the cloaca is rarely preserved in fossils, palaeontologists typically use a skeletal marker, such as the pelvic girdle or sacrum, as a proxy for the position of the cloaca. A more appropriate term for a measurement made in this way is snout–pelvis length (SPL) which, for my purposes here, I define as the straight line distance between the tip of the snout and the midpoint of the pelvis. The distinction between the two head–body values is important, as evidenced by Blob's (1998) survey of extant lizards in which he showed that SPL routinely underestimates SVL. Blob (1998) also discusses some implications of underestimating actual SVL and difficulties associated with using pelvic markers.

*Institutional abbreviations*. FMNH, Field Museum of Natural History, Chicago, Illinois, USA; OMNH, Oklahoma

Museum of Natural History, Norman, Oklahoma, USA; and SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas, USA.

## SYSTEMATIC PALAEONTOLOGY

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

Genus ALBANERPETON Estes and Hoffstetter, 1976

*Remarks*. In accordance with the Linnaean system of classification I continue to use the ordinal name Allocaudata, even though this name and the familial name Albanerpetontidae are redundant. Elsewhere, I (Gardner in press) have presented a revised diagnosis for *Albanerpeton*. I recognize seven species in the genus: the type species *A. inexpectatum* Estes and Hoffstetter, 1976 from the middle and ?lower Miocene of France (Estes and Hoffstetter 1976; Estes 1981; Gardner in press; Rage and Hossini in press); *A. nexuosus* Estes, 1981 and *A. galaktion* Fox and Naylor, 1982, both from the Campanian–Maastrichtian of western North America (Estes 1964, 1981; Fox and Naylor 1982; Gardner 1996); *A. arthridion* Fox and Naylor, 1982 from the uppermost Aptian–middle Albian of Texas and Oklahoma; and three undescribed species, one each from the upper Turonian, middle Campanian and upper Paleocene of western North America. Redescriptions of *A. nexuosus*, *A. galaktion* and formal descriptions of the three unnamed congeners are in preparation, and will be presented elsewhere. *Albanerpeton* is the only albanerpetontid genus known from North America.

### *Albanerpeton arthridion* Fox and Naylor, 1982

Text-figures 2–4

v* 1969    *Prosiren elinorae* Goin and Auffenberg; Estes, p. 87, fig. 2a–j [*non* Goin and Auffenberg 1958].
v* 1981    *Prosiren elinorae* Goin and Auffenberg; Estes, p. 18 [*non* Goin and Auffenberg 1958].
v* 1982    *Albanerpeton arthridion* Fox and Naylor, p. 120–121, fig. 1c [premaxilla and dentaries referred to *P. elinorae* by Estes 1969, 1981].
  in press    *Albanerpeton*? *arthridion* (Fox and Naylor) [?Rage and Hossini in press].

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

*Type horizon and locality*. Upper unit (*sensu* Fisher and Rodda 1967), Antlers Formation; Turtle Gully, Greenwood Canyon, Montague County, north-central Texas, USA (Text-fig. 1); lower–middle Albian (Winkler *et al*. 1989, 1990; Jacobs *et al*. 1991). Patterson (1956) and Winkler *et al*. (1989) described the Greenwood Canyon locality.

*Referred specimens*. Upper unit, Antlers Formation; Forestburg localities, Montague County, north-central Texas (Text-fig. 1); lower–middle Albian: Turtle Gully, Greenwood Canyon: FMNH PR806–PR807, dentaries; Triconodont Gully, Greenwood Canyon: FMNH PR2025, premaxilla; FMNH PR2046–PR2050, dentaries; FMNH PR2026–PR2027, fused frontals; unrecorded gully, Greenwood Canyon: FMNH PR1891, dentary; unrecorded Forestburg locality(ies): FMNH PR2023–PR2024, premaxillae; FMNH PR2031–PR2045, PR2051, dentaries. Upper unit, Antlers Formation; Butler Farm locality, Wise County, north-central Texas (Text-fig. 1); lower–middle Albian (Slaughter 1965; Winkler *et al*. 1989): SMU 61041, humerus. Middle unit (*sensu* Fisher and Rodda 1967), Antlers Formation; OMNH locality V706, Atoka County, south-eastern Oklahoma (Text-fig. 1); uppermost Aptian–lowermost Albian (Cifelli *et al*. 1997): OMNH 32344, 33282, 33287, 34067, premaxillae; OMNH 33284, 34072, maxillae; OMNH 32337, 32340–32342, 32348, 32350, 32362, 32365, 32368, 33283, 33285–33286, 33336–33337, 33339, 33342, 33344–33345, 33347, 34056, 34058–34066, 34068–34071, dentaries; OMNH 32397–32400, fused frontals; OMNH 32371–32372, atlantal centra; OMNH 33516, humerus. I follow Winkler *et al*. (1989) in using the name 'Forestburg' for three localities – Greenwood Canyon and two unnamed localities – reported by Patterson (1956) in the upper unit of the Antlers Formation near Forestburg, Montague County, Texas.
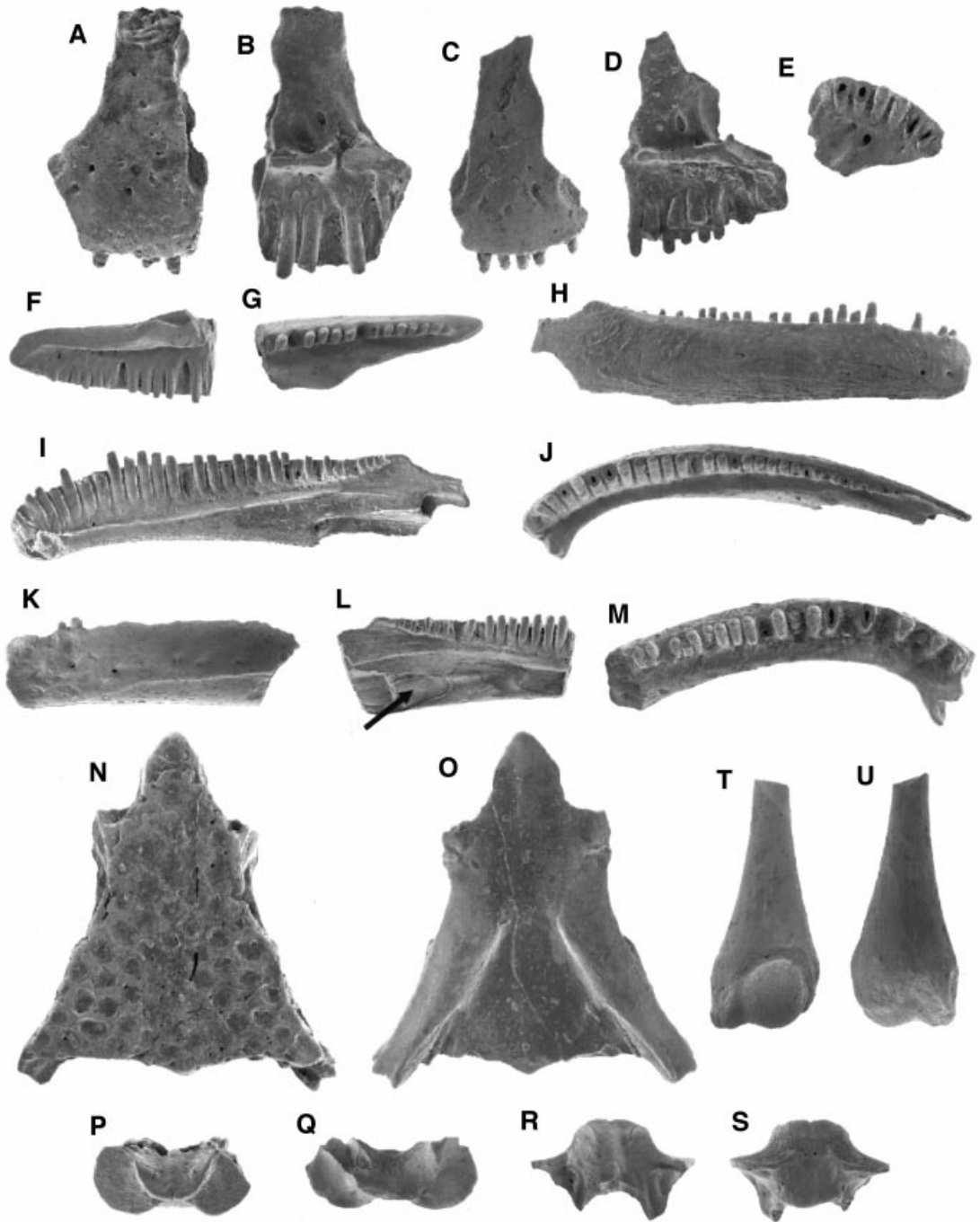
TEXT-FIG. 2. *Albanerpeton arthridion* Fox and Naylor, 1982; Lower Cretaceous (uppermost Aptian–middle Albian), Antlers Formation, Texas and Oklahoma, USA. A–B, FMNH PR805; holotype; right premaxilla, labial and lingual views; ×25. C, OMNH 33287; left premaxilla, labial view; ×25. D, FMNH PR2023; right premaxilla, lingual view;

*Distribution*. Middle and upper units, Antlers Formation; Texas and Oklahoma, USA; uppermost Aptian–middle Albian.

*Revised, differential diagnosis*. Species of *Albanerpeton* with no recognized autapomorphies. Differs from congeners in having premaxilla primitively retaining suprapalatal pit that is small, occupying about 0·01 of lingual area of pars dorsalis, and located well dorsal to pars palatinum. Among congeners, differs further from *A. galaktion*, unnamed upper Turonian species and unnamed middle Campanian species in primitively retaining suprapalatal pit that is oval in lingual outline and from *A. inexpectatum*, *A. nexuosus* and unnamed upper Paleocene species in having premaxilla primitively unfused medially, relatively gracile in build and bearing pars dorsalis that is relatively taller and not strongly sutured with nasal. Resembles unnamed upper Paleocene congener in one derived feature, estimated SPL less than about 40 mm, but differs further in having premaxilla primitively retaining boss on pars dorsalis and, evidently, a prominent palatine process on pars palatinum.

*Description*

Unless explicitly stated otherwise, descriptions below are composites.

*Premaxilla* (Text-figs 2A–E, 3A–C). The eight premaxillae at hand are incomplete, but collectively they document most of this element's morphology. Premaxillae are delicate and tiny. The largest specimen, the holotype (Text-figs 2A–B, 3A–B), is only *c*. 1·6 mm high. The pars dorsalis is complete on FMNH PR805 and nearly complete on OMNH 33287 (Text-fig. 2C) and FMNH PR2023 (Text-fig. 2D). On each specimen, the process is tall and narrow (Table 1). The dorsal edge of the pars dorsalis on FMNH PR805 is smooth, indicating that this surface abutted against the anterior end of the nasal. The prefrontal notch on FMNH PR805 and OMNH 33287 is relatively narrow and deep (Table 1). All eight premaxillae are unfused. In several specimens, including the holotype, the medial flange extends down the medial edge of the pars dorsalis and on to the upper part of the medial edge of the pars dentalis, but in FMNH PR2025 (not figured) and OMNH 33287 the flange is restricted to the basal part of the pars dorsalis and uppermost part of the pars dentalis (cf. Text-fig. 2A, C). Labially, the dorsal part of the pars dentalis and ventral two-thirds of the pars dorsalis are perforated with scattered, tiny external nutritive foramina. The dorsal one-third of the pars dorsalis on the holotype bears a low boss that is ornamented with indistinct, anastomosing ridges. The presence of a boss cannot be determined for the remaining specimens, because these all lack the dorsal end of the pars dorsalis.

Opening in the lingual face of the pars dorsalis, the suprapalatal pit lies slightly greater than half the distance from the medial edge of the process and well dorsal to the pars palatinum. The pit is ovoid to elliptical in lingual outline and remarkably tiny (Table 1), occupying in the holotype about 0·01 of the area of the pars dorsalis. The pit is bounded laterally by a labiolingually low internal strut and medially by a less prominent internal strut. Both struts arise just dorsal to the dorsal margin of the suprapalatal pit and extend ventrolaterally down the internal face of the pars dorsalis. The base of neither strut extends any significant distance lingually onto the dorsal surface of the pars palatinum. Several premaxilla, including FMNH PR805 (see Estes 1969, fig. 2e) have a tiny, sediment-infilled foramen in the lateral face of the more lateral internal strut.

The pars palatinum is most nearly complete in FMNH PR2023 (Text-fig. 2D). This and other referred premaxillae show that the pars palatinum is as well developed as in other albanerpetontids (*contra* Estes 1981). FMNH PR2024 (Text-figs 2E, 3C) preserves the base of an evidently well-developed and lingually directed palatine process. FMNH PR2023 preserves a broad maxillary process that is smooth dorsally and bears along its lingual edge a low dorsal rim. The palatal foramen is tiny (i.e. foramen diameter one-half to one-third the diameter of the bases of the more medial of the premaxillary teeth) and sub-circular in occlusal outline. The foramen opens dorsally in the junction between the

×25. E, FMNH PR2024; left premaxilla, occlusal view; ×25. F–G, OMNH 32284; posterior two-thirds of left maxilla, lingual and occlusal views; ×20. H–J, FMNH PR806; right dentary, labial, lingual and occlusal views; ×20. K, FMNH PR2046; anterior part of left dentary, labial view; ×20. L, FMNH PR2036; posterior part of left dentary with anterior end of angular (arrow) in articulation, lingual view; ×20. M, FMNH PR1891; anterior half of left dentary, occlusal view; ×20. N–O, FMNH PR2026; fused frontals, dorsal and ventral views; ×20. P, OMNH 32371; atlantal centrum, anterior view; ×20. Q–S, OMNH 32372; atlantal centrum, posterior, dorsal and ventral views; ×20. T–U, OMNH 33516; distal half of left humerus, ventral and dorsal views; ×20. Specimens in figures A–B, D–E, H–O are from the Forestburg localities, Texas; other specimens are from OMNH locality V706, Oklahoma.
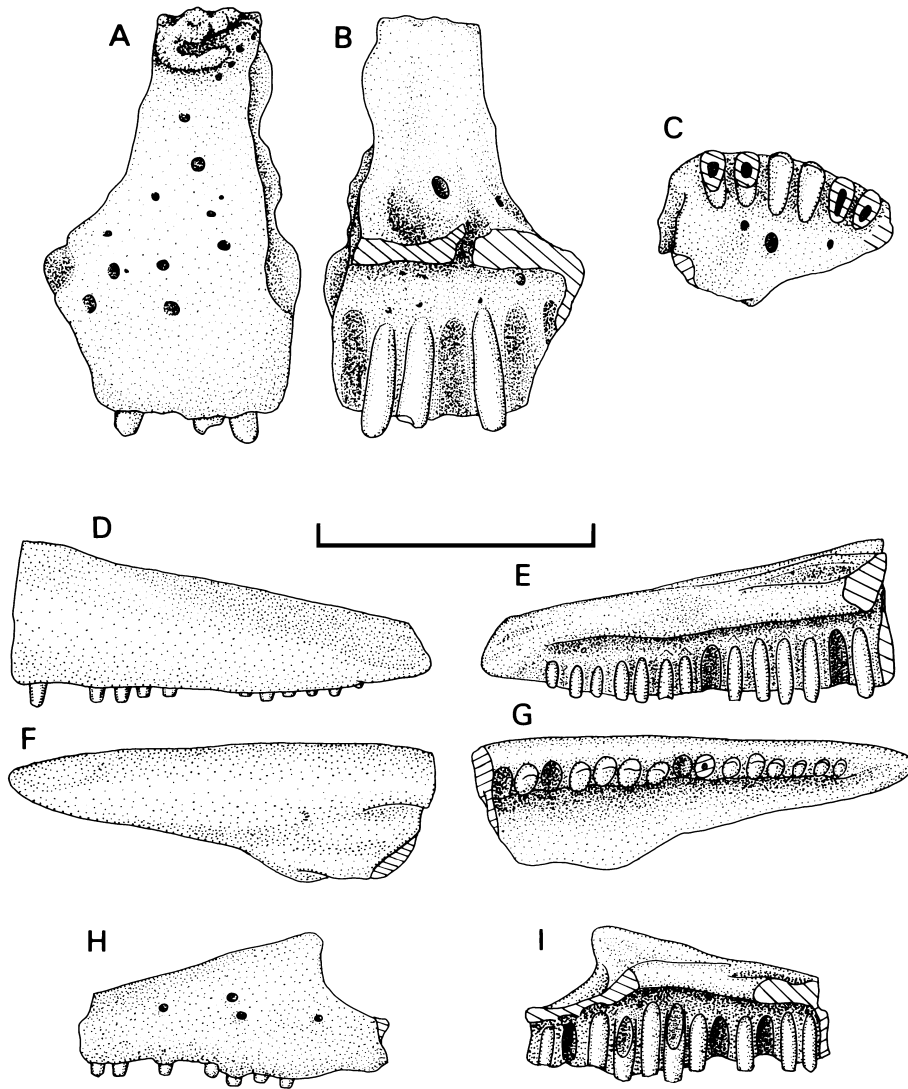
TABLE 1. Straight line measurements and ratios for premaxillae of *Albanerpeton arthridion* Fox and Naylor, 1982; Lower Cretaceous (uppermost Aptian–middle Albian) Antlers Formation, Texas and Oklahoma, USA. Measurements are linear values (see Gardner in press, fig. 2); 'value' is measurement or ratio for one specimen; 'N' is number of specimens; 'Range' is for two or more specimens; 'x̄' and 'SD' are, respectively, mean and standard deviation of measurements or ratios for three or more specimens.

| Measurement or Ratio | Value | N | Range | x̄ and SD |
|---|---|---|---|---|
| PmH (height of premaxilla; mm) | 1·63 | 1 | – | – |
| PDH (height of pars dorsalis; mm) | 0·96 | 1 | – | – |
| PDW$^1$ (width of pars dorsalis across base of prefrontal notch; mm) | – | 2 | 0·48–0·50 | – |
| PDW$^2$ (width of pars dorsalis across suprapalatal pit; mm) | – | 7 | 0·41–0·53 | 0·48 ± 0·04 |
| PfrND (depth of prefrontal notch; mm) | 0·43 | 1 | – | – |
| PfrNW (width of prefrontal notch; mm) | – | 2 | 0·07–0·16 | – |
| SPH (height of suprapalatal pit; mm) | – | 7 | 0·07–0·12 | 0·08 ± 0·02 |
| SPW (maximum width of suprapalatal pit; mm) | – | 7 | 0·05–0·07 | 0·06 ± 0·02 |
| PDH:PDW$^2$ (relative height of pars dorsalis) | 1·8 | 1 | – | – |
| PfrND:PDH (relative depth of prefrontal notch) | 0·45 | 1 | – | – |
| PfrNW:PDW$^1$ (relative width of prefrontal notch) | – | 2 | 0·15–0·33 | – |
| SPH:PDH (relative height of suprapalatal pit) | 0·08 | 1 | – | – |
| SPW:PDW$^2$ (relative width of suprapalatal pit) | – | 7 | 0·10–0·15 | 0·13 ± 0·02 |

dorsal surface of the pars palatinum and the lingual face of the pars dorsalis, between the bases of the internal struts, well ventral and slightly lateral to the suprapalatal pit. Ventrally, the palatal foramen opens about one-third of the distance lingually across the pars palatinum, in line with the third to fourth loci. The canal connecting the dorsal and ventral openings of the palatal foramen is exposed in the broken face of the pars palatinum on the holotype and clearly extends dorsoventrally through the shelf (Text-figs 2B, 3B). One or two smaller foramina open more labially in the junction between the ventral surface of the pars palatinum and the pars dentalis. I have not been able to identify the dorsal openings of these more labial foramina, but homologous foramina in other albanerpetontid premaxillae open dorsally in the floor of the suprapalatal pit (Gardner in press).

*Maxilla* (Text-figs 2F–G, 3D–I). Previously unknown for *Albanerpeton arthridion*, two incomplete maxillae are now available from OMNH locality V706. OMNH 33284 (Text-figs 2F–G, 3D–G) is the posterior two-thirds of a left maxilla that is broken transversely between the internal narial opening and posteriormost part of the nasal process. OMNH 34072 (Text-fig. 3H–I) is a less nearly complete right maxilla. The latter specimen is broken posteriorly just behind the internal narial margin and anteriorly it is missing the premaxillary dorsal process, the anterior end of the premaxillary lateral process and, possibly, the anteriormost end of the tooth row. OMNH 33284 and 34072 are delicate, small and when complete would have been no longer than *c*. 2·5 mm and 1·8 mm, respectively. Both specimens are unornamented labially, except for four tiny external nutritive foramina on OMNH 34072. The pars facialis is low and tapers posteriorly. OMNH 34072 preserves an intact nasal process that is triangular in labial outline. The posterior edge of the process and adjacent part of the pars facialis are bevelled where the maxilla was overlapped dorsally and slightly labially by the lacrimal. The posterior end of the maxilla is complete in OMNH 33284 and labiodorsally has a shallow facet for contact with the anterior end of the jugal. Both specimens show that the pars palatinum is broad lingually, with a shallow trough dorsolingually for articulation with an unknown palatal bone. OMNH 33284 further shows that the pars palatinum tapers posteriorly. More nearly intact in OMNH 34072, the internal narial margin is shallowly concave in dorsal outline and spans at least five tooth positions. The ventral margin of the pars dentalis is straight in lingual or labial view, although breakage in OMNH 34072 creates the impression that the margin was shallowly convex ventrally. The anterior end of the tooth row in OMNH 34072 extends at least two loci anterior to the leading edge of the base of the nasal process.

*Dentary* (Text-fig. 2H–M). None of the 57 dentaries is complete. Each specimen is delicate, slender and small. The most nearly complete of these, FMNH PR806 (Estes 1969, fig. 2g, i–j; Text-fig. 2H–J), has an intact tooth row, but

TEXT-FIG. 3. *Albanerpeton arthridion* Fox and Naylor, 1982; Lower Cretaceous (uppermost Aptian–middle Albian), Antlers Formation, Texas and Oklahoma, USA. A–B, FMNH PR805; holotype; Forestburg (Greenwood Canyon) locality, Texas; right premaxilla, labial and lingual views. C, FMNH PR2024; unrecorded Forestburg locality, Texas; left premaxilla, occlusal view with labial margin to top of page. D–G, OMNH 33284, OMNH locality V706, Oklahoma; posterior two-thirds of left maxilla, labial, lingual, dorsal and occlusal views. H–I, OMNH 34072; OMNH locality V706, Oklahoma; anterior third of right maxilla, broken anteriorly, labial and lingual views. Scale bar represents 1 mm. Cross hatches denote broken surfaces.

lacks the posteriormost end of the bone and the ventral edge of the area for attachment of the postdentary bones. FMNH PR806 is 4·3 mm long; the other specimens were comparable in size when complete. The dorsal margin of the dental parapet is horizontal and essentially straight in labial view. The labial face is smooth, except for a row of up to six small external nutritive foramina that extends along the anterior one-half to two-thirds of the bone. Ventrally and ventrolaterally is an anteroposteriorly elongate scar, bounded laterally by a low rim or groove (Text-fig. 2K), for attachment of the intermandibularis muscles. This scar is indistinct on some specimens, including the three dentaries

that Fox and Naylor (1982) described. The symphyseal eminence is moderately well developed. Nine dentaries preserve intact symphyseal prongs: five of the six right dentaries, including FMNH PR806, each bear a single symphyseal prong; the other right dentary and each of the three left dentaries have a pair of symphyseal prongs. As in other albanerpetontids, the subdental shelf deepens posteriorly, the Meckelian canal is closed anteriorly and the posterior third of the dentary bears scars for attachment of the postdentary bones. The dorsal edge of the dentary behind the tooth row lacks a dorsally directed process. Several dentaries preserve the anterior tip of the angular *in situ* within the opening for the Meckelian canal (Text-fig. 2L).

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

*Frontals* (Text-figs 2N–O, 4). Previously unknown for *Albanerpeton arthridion*, six pairs of frontals are now available. The two pairs, FMNH PR2026 (Text-figs 2N–O, 4) and FMNH PR2027 (not figured), from Greenwood Canyon are nearly complete and measure *c.* 2·6 mm and 2·4 mm in midline length, respectively. The four pairs of frontals from OMNH locality V706 are fragmentary, but when complete would have been about the same size as FMNH PR2026 and PR2027. Frontals are solidly fused along the midline, although several retain a faint median line of fusion ventrally. FMNH PR2026 and PR2027 are *c.* 1·2 times longer than wide and, in dorsal outline, resemble an anteroposteriorly elongate isosceles triangle. The internasal and anterolateral processes and the slots for receipt of the nasal anteriorly and prefrontal posteriorly are well developed. The internasal process is anteriorly acute in dorsal outline, with the length subequal to the width, and has a groove along the lateral face for contact with the medial edge of the nasal. Posterior to the anterolateral process, the lateral wall of the frontal extends posterolaterally at *c.* 15° from the midline. The dorsal and ventral edges of the more posterior slot are shallowly excavated medially and the orbital margin is shallowly concave in dorsal or ventral view. The posterior edge of the frontal roof is shallowly emarginated to either side of the midline and the posterior face is smooth, indicating that the frontal roof abutted against the paired parietals. The dorsal surface is indented with shallow, broad pits that are polygonal in dorsal outline. These pits are enclosed by low, round-topped ridges that coalesce to form a reticulate pattern. On some frontals, such as FMNH PR2026, the pits are shallower and more irregular in outline across the anterior third of the frontals.

Ventrally, the anterolateral process bears a shallow facet, evidently for articulation with the underlying neurocranium. Just posterior and medial to this facet, a tiny unnamed foramen penetrates the ventral surface of the bone. The ventrolateral crest is relatively narrow in ventral view, i.e. ratio of width across crest, behind slot for prefrontal, versus width across posterior edge of frontals, between medial edge of each crest, is *c.* 0·4 in FMNH PR2026 and 0·3 in PR2027. In transverse view, the crest is developed into a thick, ventrally convex rim, the ventrolateral face of which is shallowly bevelled along the orbital margin. The crest projects beyond the posterior edge of the frontal where, in life, the posterior end of the crest underlapped the parietal and medially received an anteriorly projecting tab from the parietal.

*Atlas* (Text-fig. 2P–S). OMNH 32371 (Text-fig. 2P) and 32372 (Text-fig. 2Q–S) are from OMNH locality V706. These are the only vertebrae known for *Albanerpeton arthridion*. Neither centrum preserves the neural arch, although from the broken bases of the neural arch walls it is evident that an arch was present. Both centra are *c.* 1·3 mm wide across the outer edges of the anterior cotyles and *c.* 0·7 mm long between the anterior edge of the odontoid process and the ventral edge of the posterior cotyle. The specimens resemble other albanerpetontid altantes (see Seiffert 1969; Estes and Hoffstetter 1976; Estes 1981; Estes and Sanchíz 1982; Fox and Naylor 1982; McGowan 1996, 1998) as follows: centrum short; articular surface for contact with skull continuous across anterior cotyles and ventral surface of odontoid process; anterior cotyles kidney-shaped in anterior outline, with anterior face shallowly concave; odontoid
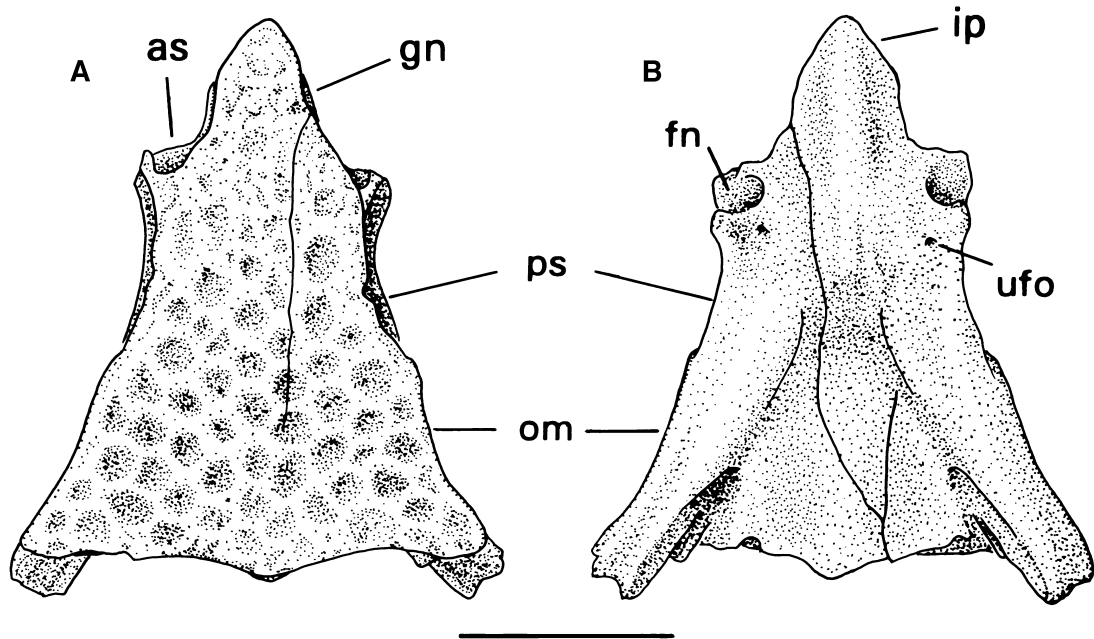
TEXT-FIG. 4. *Albanerpeton arthridion* Fox and Naylor, 1982; Lower Cretaceous (lower–middle Albian) Greenwood Canyon locality, Antlers Formation, Texas, USA. A–B, FMNH PR2026; fused frontals, dorsal and ventral views. Scale bar represents 1 mm. Abbreviations: as, anterior slot for receipt of nasal; fn, facet for contact with neurocranium; gn, groove along lateral face of internasal process for tongue-in-groove contact with medial edge of nasal; ip, internasal process; ps, posterior slot for receipt of prefrontal; om, orbital margin; ufo, unnamed foramen.

process gutter-like in anterior view, broad and lateral edges confluent to either side with dorsal margin of anterior cotyles; deep notch beneath odontoid process separates medial edges of anterior cotyles; and posterior cotyle having dorsal and ventral edges deeply excavated anteriorly. Much of the posterior cotyle is broken on OMNH 32371, but OMNH 32372 preserves the characteristic, faint tripartite facets for articulation with the axis. Both centra lack an open notochordal pit. In this respect they resemble all other described albanerpetontid atlantes, except for an indeterminate centrum (see Seiffert 1969, fig. 1D) from the Middle Jurassic of France. A small foramen, of uncertain function, opens low on the posterior surface of the anterior cotyle. On either side and just behind the posterior face of the anterior cotyle, the broken base of the neural arch exposes a narrow groove extending transversely between the neural canal and the lateral surface of the bone. This groove is particularly well exposed on the right side of OMNH 32372 (Text-fig. 2R). Comparisons with rare albanerpetontid atlantes from elsewhere that preserve a complete or nearly complete neural arch (see Estes and Hoffstetter 1976, pl. 6, fig. 14; Fox and Naylor 1982, fig. 1h) suggest that, when intact, the neural arch on OMNH 32371 and 32372 would have enclosed the groove dorsally to form a foramen. The position of this foramen argues for it being the homologue of the spinal foramen in salamanders (see Edwards 1976). A spinal foramen occurs in all North American Cretaceous albanerpetontid atlantes that I have seen (Gardner in press) and at least one atlas of *Albanerpeton inexpectatum* (Estes and Hoffstetter 1976, pl. 6, fig. 14; Gardner in press). According to McGowan (1998), however, the foramen is absent in other atlantes of *A. inexpectatum* and referred atlantes of *Celtedens*.

*Humerus* (Text-fig. 2T–U). The distal ends of two humeri are available: one left (OMNH 33516; Gardner and Averianov 1998, fig. 4A; Text-fig. 2T–U) from OMNH locality V706 and one right (SMU 61041; Estes 1969, fig. 2a–b) from Butler Farm. The latter specimen was originally referred by Estes (1969, 1981) to *Prosiren elinorae*. Both humeri resemble the incomplete left humerus in the holotype skeleton of *Celtedens megacephalus* (Costa, 1864), referred humeri of *Albanerpeton inexpectatum* (see Estes and Hoffstetter 1976, pl. 9, figs 6–7) and indeterminate European Cretaceous humeri (see Estes and Sanchíz 1982, fig. 5J; McGowan and Ensom 1997, fig. 2b; Duffaud and Rage in press, fig. 1) as follows: shaft elongate, slender and in line with radial condyle; distal end about twice as wide in ventral

view as diameter of shaft; radial condyle developed into a prominent, hemispherical ball; ulnar condyle markedly smaller than radial condyle; and epicondylus lateralis humeri virtually absent. OMNH 33516 and SMU 61041 differ from referred humeri of *A. inexpectatum* and the humerus in the holotype skeleton of *C. megacephalus* in being smaller and from some of the humeri described by Estes and Sanchíz (1982) from the Spanish Barremian and by McGowan and Ensom (1997) from the English Berriasian in having a completely ossified radial condyle.

*Remarks.* Albanerpetontid elements described above can be associated based on their structure, small size and provenance. These indicate that only one species, namely *Albanerpeton arthridion*, can be identified in the Antlers Formation. Fox and Naylor's (1982) generic assignment of *A. arthridion* is upheld by referred frontals that exhibit the three diagnostic character states for *Albanerpeton*: (1) fused frontals triangular in dorsal or ventral outline (more nearly rectangular or hourglass-shaped in *Celtedens*); (2) internasal process pointed in dorsal or ventral outline (bulbous in *Celtedens*); and (3) lateral face of internasal process has anteroposteriorly elongate groove for tongue-in-groove contact with medial edge of nasal (internasal process lacks groove and, instead, dorsally overlaps medial edge of nasal in *Celtedens*). As discussed below, two of the three premaxillary characters previously used to differentiate *A. arthridion* from its congeners are unreliable for this purpose.

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

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

    Despite the problems outlined above, in my opinion, the premaxilla remains the most diagnostically informative element for *Albanerpeton arthridion*, as it does for other species in the genus. Although I have not been able to identify any autapomorphies or unique combinations of synapomorphies for *A. arthridion*, the species can be reliably differentiated from all congeners by two primitive character states of the suprapalatal pit: (1) pit occupies about 0·01 of lingual surface area of pars dorsalis (pit occupies 0·04 to nearly 0·25 of pars dorsalis in other congeners) and (2) pit located high on lingual face of pars dorsalis, well dorsal to pars palatinum (pit opens lower on pars dorsalis, often with ventral edge of pit confluent with dorsal surface of pars palatinum in other congeners). The suprapalatal pit is relatively invariant within albanerpetontid species, but considerable interspecific variation is evident in the position, shape and relative size of the pit (Gardner in press). I consider this variation to be taxonomically and phylogenetically useful at the specific level. Judging by its structure and associated foramina, the suprapalatal pit probably housed a gland (Fox and Naylor 1982). Such a gland presumably was involved in olfaction, feeding or both.

*Albanerpeton arthridion* also lacks other derived character states of the premaxilla (e.g. premaxillae fused medially; boss enlarged or absent; suprapalatal pit triangular or slit-shaped in lingual outline) and frontals (e.g. ventrolateral crest relatively broader and flatter or concave in transverse view) that are present, in some combination, in all geologically younger congeners. Many of the premaxillary character states that I interpret as primitive for the genus also occur in isolated premaxillae that others have referred to the sister genus *Celtedens* (see McGowan 1996, fig. 1; McGowan and Ensom 1997, fig. 1c). This distribution of character states argues for *A. arthridion* being the most basal of the species currently included within *Albanerpeton*.

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

Examination of the holotype skeleton of *Celtedens megacephalus* and measurements taken from McGowan and Evans' photograph (1995, fig. 1a) of the holotype skeleton of *C. ibericus* indicate that the fused frontals in both specimens are about one-tenth the SPL. Applying this ratio to FMNH PR2026, the largest and most nearly complete of the six pairs of frontals at hand for *A. arthridion*, I estimate a SPL of only about 30 mm. This approaches the lower limit of body size (measured as SVL) for tailed amphibians (see Clarke 1996, tables 1–2 and references therein). The unnamed *Albanerpeton* species from the upper Paleocene of Alberta is known by jaws and a pair of frontals that are not much larger than those of *A. arthridion*, suggesting that the former species is also relatively small. However, derived premaxillary character states (e.g. premaxillae fused; pars dorsalis short; boss absent) in the Paleocene species argue against a close relationship between the two congeners. This implies that small body size (i.e. SPL less than about 40 mm) developed at least twice within *Albanerpeton*. This trend is not surprising, considering that reduced body size has arisen independently, and occasionally repeatedly, in many lineages of extant lissamphibians (see review by Clarke 1996). Clarke (1996) noted that small body size conveys several advantages to extant amphibians, most notably allowing a greater range of microhabitats and variety of prey to be exploited. Individuals of *A. arthridion* probably enjoyed similar benefits by virtue of their small size.

<center>Genus and Species indet.</center>

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

*Horizon and locality.* Unit V of Ostrom (1970), lower part of Cloverly Formation; OMNH locality V62, Bighorn County, Wyoming (Text-fig. 1); Aptian–Albian (Ostrom 1970; Jacobs *et al.* 1991; Chen and Lubin 1997). Jacobs *et al.* (1991) suggested that the Cloverly Formation may be slightly younger than fossiliferous horizons of the Antlers and Paluxy formations in Texas, but this is uncertain.

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

Order CAUDATA Scopoli, 1777?

Family, Genus and Species indet.

1990    Caudata?, gen. et sp. indet.; Winkler *et al.*, table 1.

*Material.* SMU 72153, atlantal centrum lacking neural arch.

*Horizon and locality.* Base of Paluxy Formation; SMU locality 108-2, Erath County, north-central Texas (Text-fig. 1); lower–middle Albian (Winkler *et al.* 1990).

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

## THE EARLY BIOGEOGRAPHY OF NORTH AMERICAN ALBANERPETONTIDS

As discussed by Gardner and Averianov (1998), deciphering the biogeographical history of the Albanerpetontidae is hampered by the group's limited fossil record. The oldest occurrences of albanerpetontids are in the Jurassic of western Europe, and consist of the following: an indeterminate centrum (Seiffert 1969; Estes and Hoffstetter 1976; Estes, 1981) from the lower Bathonian (Kriwet *et al.* 1997) of France; isolated elements, including some referred by McGowan (1996) to *Celtedens*, from upper Bathonian sites in England (Evans and Milner 1994); and undescribed elements, including diagnostic *Celtedens* frontals (McGowan 1996), from Kimmeridgian or Oxfordian sites in Portugal (e.g. Estes 1981; Milner 1994; McGowan 1996). Early Cretaceous albanerpetontids are represented in Europe by isolated bones of *Celtedens* from the Berriasian of England (McGowan and Ensom 1997), two skeletons of *C. ibericus* (McGowan and Evans 1995) and indeterminate skull and postcranial bones (Estes 1981; Estes and Sanchíz 1982) from Barremian sites in Spain, and the holotype skeleton of *C. megacephalus* from the Albian (Bravi 1994) of Italy (D'Erasmo 1914; Estes 1981). The oldest reliable records elsewhere in the Old World are undescribed elements from the Berriasian of Morocco (Broschinski and Sigogneau-Russell 1996; A. Broschinski, pers. comm. 1997; J.-C. Rage, pers. comm. 1998) and indeterminate dentaries from the Cenomanian of Uzbekistan (Gardner and Averianov 1998). Nessov's (1988) report of a Middle Jurassic (Callovian) albanerpetontid frontal from Kirghizia cannot be confirmed because the specimen was never described or figured and it has not subsequently been located (Gardner and Averianov 1998).

The oldest North American albanerpetontid fossils come from the Cloverly and Antlers formations (this study). These specimens provide a minimum age of latest Aptian for the establishment of albanerpetontids in North America. Given the presence of older (i.e. Bathonian–Barremian) albanerpetontids in the Old World and the distribution of landmasses during this time (Smith *et al.* 1994), I suspect that albanerpetontids were in North America substantially before the latest Aptian, but no fossils are presently known from the continent that confirm that this was the case. Fossil occurrences and palaeogeographical reconstructions
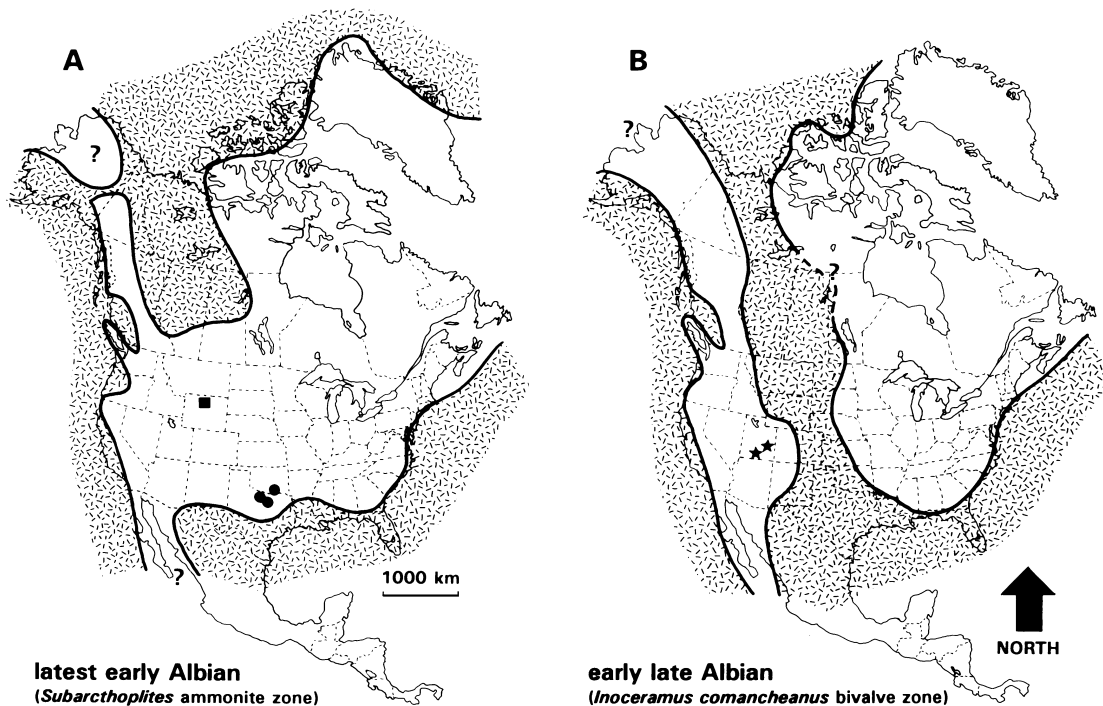
TEXT-FIG. 5. Palaeogeographical maps of North America during the late Early Cretaceous (modified from Williams and Stelck 1975, text-figs 2–3) showing the opening of the Western Interior Seaway and pre-Campanian occurrences of albanerpetontids on the continent. A, latest early Albian. B, early late Albian. Symbols: square, Cloverly Formation (Aptian–Albian), Wyoming; circle, Antlers Formation (uppermost Aptian–middle Albian), Texas and Oklahoma; and star, upper part (uppermost Albian–lowermost Cenomanian) of Cedar Mountain Formation and middle part (Turonian–Coniacian) of Straight Cliffs Formation, both in Utah.

(Gardner and Averianov 1998, fig. 5) suggest four possible scenarios for the establishment of albaner-petontids in North America: (1) dispersal from Asia; (2) dispersal from Europe; (3) albanerpetontids were present on the proto-North American continent before the break-up of Laurasia and subsequent isolation of North America; or (4) some combination of these. The Asian dispersal scenario is weakened by the fact that the oldest unequivocal albanerpetontid fossils (Cenomanian) from Asia postdate the establishment of the Bering Land Bridge in the Albian (Gardner and Averianov 1998), whilst the oldest North American occurrences (this study) antedate the establishment of the land bridge. The remaining scenarios are somewhat better supported by the available evidence, but none can be favoured at present.

Regardless of when or how albanerpetontids became established in North America, fossils from the Cloverly and Antlers formations demonstrate that these amphibians were on the continent before (Text-fig. 5A) the Western Interior Seaway opened briefly in the early late Albian (Text-fig. 5B) and then continuously from about the latest Albian–mid Maastrichtian (Williams and Stelck 1975; Kauffman and Caldwell 1993). This timing is significant, because it means that the seaway, which effectively divided North America into eastern and western subcontinents for most of the Late Cretaceous, would not initially have been a barrier to the east–west movement of albanerpetontids across the continent. The record of non-marine Cretaceous microvertebrates to the east of the Western Interior Seaway is sparse and lissamphibians are known only from the Campanian age Ellisdale locality in New Jersey, USA (Denton and O'Neill 1998). The apparent lack of diagnostic albanerpetontid fossils at this locality is surprising, considering that the Ellisdale lissamphibian assemblage otherwise resembles contemporaneous, albaner-petontid rich-assemblages in the Western Interior.

CONCLUSIONS

Albanerpetontid fossils reported herein from the Lower Cretaceous (Aptian–Albian) Antlers Formation of Texas and Oklahoma and the Cloverly Formation of Wyoming, USA, are the geologically oldest records of this poorly known group in North America. On the basis of moderate-sized collections from the Antlers Formation, *Albanerpeton arthridion* is argued to be a valid species of *Albanerpeton* and the basalmost species in the genus. Fossils from the Antlers and Cloverly formations establish the presence of albanerpetontids in North America by at least the latest Aptian, well before the opening of the Western Interior Seaway. As this date almost certainly underestimates the antiquity of albanerpetontids on the continent, further insights into the early history of North American albanerpetontids await the discovery of fossils that are contemporaneous with, or antedate, geologically older occurrences in Europe.

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