

MONOPHYLY AND INTRA-GENERIC RELATIONSHIPS OF *ALBANERPETON* (LISSAMPHIBIA; ALBANERPETONTIDAE)

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ABSTRACT—The first phylogenetic analysis of the Euramerican Early Cretaceous–Miocene genus *Albanerpeton* is presented based on 16 characters of the jaws, frontals, and inferred body size scored for the seven recognized species in the genus and three other albanerpetontid taxa. Monophyly of *Albanerpeton* is corroborated and nested sets of synapomorphies yield the following hypothesized relationships: *A. arthridion* ((*A. cifellii* + *A. galaktion* + *A. gracilis*) (*A. nexuosus* (unnamed late Paleocene species + *A. inexpectatum*))). Osteological modifications identified in *Albanerpeton* initially involve the frontals, then shift largely to the jaws. Many of these changes are interpreted to be associated with broadening the head and strengthening the snout and jaws, presumably for feeding and burrowing. The first half or more (latest Aptian/earliest Albian to late Paleocene) of the known record for *Albanerpeton* and six of the seven species are restricted to the North American Western Interior. These occurrences and the phylogenetic framework proposed here suggest that the evolutionary history of *Albanerpeton* was centered in the Western Interior of North America.

INTRODUCTION

The Albanerpetontidae Fox and Naylor are a clade of Middle Jurassic to Miocene salamander-like lissamphibians with a primarily Laurasian distribution. Several recent phylogenetic analyses nest albanerpetontids within the Lissamphibia Haeckel, crownward of gymnophionans and as the sister-taxon of salientians and caudates (McGowan and Evans, 1995; Gardner, 2001). As currently recognized the family includes the Euramerican type genus *Albanerpeton* Estes and Hoffstetter, the European Late Jurassic and Early Cretaceous *Celtesdens* McGowan and Evans, and unnamed taxa and indeterminate specimens from the Middle Jurassic to Late Cretaceous of North America, Europe, Asia, and North Africa (e.g., Estes and Hoffstetter, 1976; McGowan and Evans, 1995; McGowan, 1998; Gardner and Averianov, 1998; Sigogneau-Russell et al., 1998; Gardner, 1999a, 2000a). *Albanerpeton* is the better known of the two named genera and includes seven species (Gardner, 2000a) with a biogeographically interesting distribution: the type species is recorded from the Miocene of France (Estes and Hoffstetter, 1976; Estes, 1981; Gardner, 1999a; Rage and Hossini, 2000), Austria (Sanchíz, 1998), and Germany (Böhme, 1999), whereas the remaining six species range from the Early Cretaceous to Paleocene of the North American Western Interior (Estes, 1981; Fox and Naylor, 1982; Gardner, 1999a, b, c, 2000b). Relationships within *Albanerpeton* have not previously been considered in any detail, largely because until recently only four species were recognized, none of these were particularly well known, and few systematically informative characters had been identified. The phylogeny of *Albanerpeton* can now be examined as a consequence of recent redescriptions and reinterpretations of the four named congeners, the identification of additional characters and three new congeners (Gardner, 1999a, b, c, 2000a, b), and new information (McGowan and Evans, 1995; McGowan, 1996, 1998; McGowan and Ensom, 1997; Gardner and Averianov, 1998; Gardner, 2000a), some of which is unpublished, on other albanerpetontid taxa and fossils. Here I assess the status and internal relationships of *Albanerpeton* and use this phylogenetic framework to interpret the evolutionary history of the genus.

Osteological terms and measurements follow my previous papers (Gardner, 1999a, b, c, 2000a, b, c; Gardner and Averianov, 1998); see also Figure 1.

Institutional Abbreviations—**DORCM**, Dorset County Museum, Dorchester, England; **FMNH**, Field Museum of Natural History, Chicago, USA; **LH**, Las Hoyas collection, Museo de Cuenca, Cuenca, Spain; **MNHN.LGA**, La Grive-St. Alban collection, Muséum National d’Histoire Naturelle, Paris, France; **MNHN.MCM** Anoual collection, Muséum National d’Histoire Naturelle, Paris, France; **MNP**, Museo di Paleontologia dell’Università di Napoli, Naples, Italy; **NHM**, Natural History Museum, London, England; **OMNH**, Oklahoma Museum of Natural History, Norman, USA; **UALVP**, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Canada; **UCL**, University College London, England; **UCM**, University of Colorado Museum, Boulder, USA; and **UCMP**, University of California Museum of Paleontology, Berkeley, USA.

Taxa, Specimens, and Literature Examined—*Albanerpeton*: *A. inexpectatum* Estes and Hoffstetter, type species, jaws and frontals listed by Gardner (1999a); *A. arthridion* Fox and Naylor, jaws and frontals listed by Gardner (1999b); *A. cifellii* Gardner, holotype premaxilla described by Gardner (1999c); *A. galaktion* Fox and Naylor, *A. gracilis* Gardner, and *A. nexuosus* Estes, jaws and frontals listed by Gardner (2000b); and “Paskapoo species” (unnamed *Albanerpeton* sp.), undescribed jaws and frontals in collection of UALVP. *Celtesdens*: *C. megacephalus* (Costa), type species, holotype skeleton (MNP 542); *C. ibericus* McGowan and Evans, based on McGowan and Evans’ (1995) preliminary description of holotype skeleton (LH 6020); and *Celtesdens* sp., jaws and frontals from Purbeck (Berriasian), England, in collections of DORCM and UCL, including specimens listed by McGowan and Ensom (1997) and Gardner (2000a). “Kirtlington species:” jaws and frontals in collections of NHM and UCL, including specimens listed by McGowan (1996) and Gardner (2000a). “Anoual species:” undescribed jaws and frontals in collection of MNHN.MCM.

PHYLOGENETIC ANALYSIS

Assumptions and General Procedure

For the purposes of this study, the following assumptions are made: (1) the Albanerpetontidae are a monophyletic clade diagnosed by apomorphies such as crowns on marginal teeth labiolingually compressed and faintly tricuspid, unique mortise and tenon style intermandibular joint, mandibular–skull joint

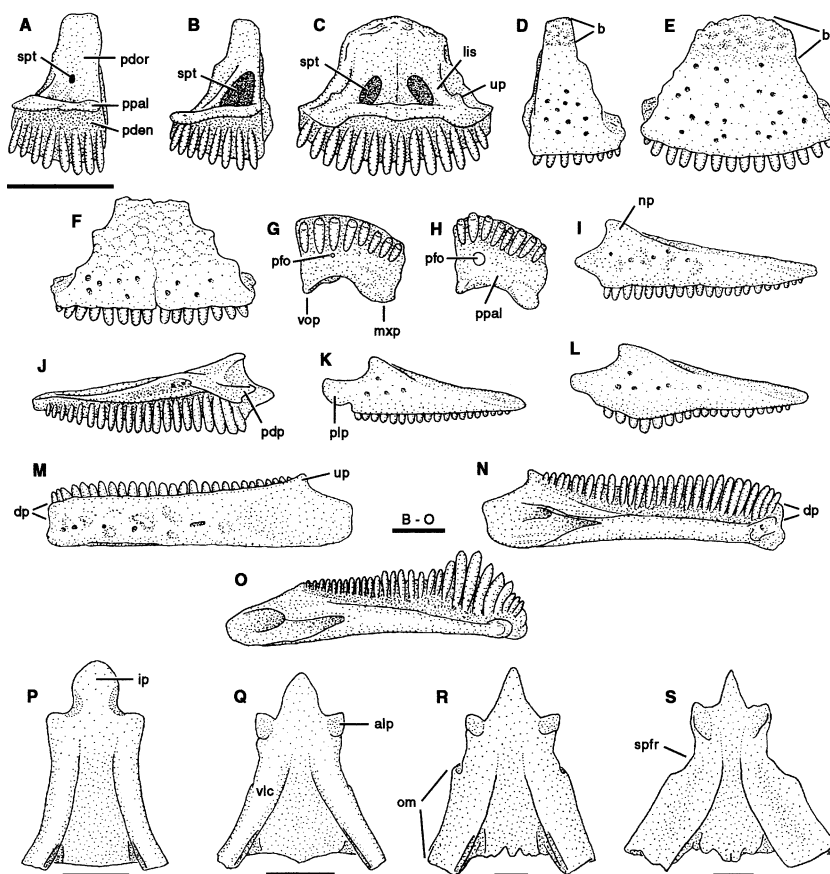


FIGURE 1. Representative jaws and azygous frontals of albanerpetontids. Premaxillae in lingual view (A–C): A, *Albanerpeton arthridion* Fox and Naylor, left premaxilla based on FMNH PR805 (holotype), FMNH PR2023, and OMNH 33287; B, *A. galaktion* Fox and Naylor, left premaxilla based on UALVP 16203 (holotype), 16204, and 16212; C, *A. nexuosus* Estes, fused premaxillae based on UALVP 16206 and 39971. Premaxillae in labial view (D–F): D, *A. galaktion*, left premaxilla based on UALVP 16203 (holotype), 16204, and 16212; E, *A. nexuosus*, fused premaxillae based on UALVP 16206 and 39971; F, *A. inexpectatum* Estes and Hoffstetter, fused premaxillae based on MNHN.LGA 1210 and 1211. Left premaxillae in occlusal view (G, H): G, *A. nexuosus*, based on UALVP 39960; H, *A. galaktion*, based on UALVP 16203 (holotype), 16204, and 16212. Left maxillae (I–L): I, J, *Albanerpeton inexpectatum*, based on MNHN.LGA 1213 and 1232, in (I) labial and (J) lingual views; K, *A. galaktion*, based on UALVP 16240 and 16241, in labial view; L, *A. nexuosus*, based on OMNH 60245 and UALVP 16242, 16239, and 39973, in labial view. Left dentaries (M–O): M, N, *Albanerpeton inexpectatum*, based on MNHN.LGA 1201, 1244, and 1248, in (M) labial and (N) lingual views; O, *A. nexuosus*, based on UALVP 40014, UCM 38714, and UCMP 49540 and 49547 (holotype), in lingual view. Fused frontals, all in ventral view (P–S): P, *Celtedens* sp. indet., based on DORCM GS35; Q, *A. arthridion*, based on FMNH PR2026 and PR2027; R, *A. nexuosus*, based on UALVP 39983, 39987, 39989, and 39996; S, *A. inexpectatum*, based on MNHN.LGA 1222. **Abbreviations:** alp, anterolateral process; b, boss; dp, dental parapet; ip, internasal process; lis, lateral internal strut; mxp, maxillary process; np, nasal process; om, orbital margin; pden, pars dentalis; pdor, pars dorsalis; pdp, premaxillary dorsal process; pfo, palatal foramen; plp, premaxillary lateral process; ppal, pars palatinum; spfr, slot for receipt of prefrontal; spt, suprapalatal pit; up, unnamed process; vlc, ventrolateral crest; and vop, vomerine process. Scale bars equal 1 mm. Elements in figures A–C, G–S modified from Gardner (2000a:figs. 1–3).

nearly vertical in orientation, frontals solidly fused and have a prominent internasal process anteriorly and pair of slots to either side for receipt of nasal and prefrontal, and first three vertebrae modified in a unique manner (Fox and Naylor, 1982; Milner, 1988; McGowan and Evans, 1995; Gardner, 2000a, 2001); (2) the Albanerpetontidae nest within the Lissamphibia, as the sister-taxon of frogs + salamanders (McGowan and Evans, 1995; Gardner, 2001); and (3) the Lissamphibia are crown-clade temnospondyls (Milner, 1988, 1993; McGowan and Evans, 1995; Gardner, 2001).

To assess monophyly and internal relationships of *Albanerpeton*, the branch-and-bound algorithm in PAUP 3.1.1 (Swoford, 1993) was used to analyze 16 characters scored for the seven species of *Albanerpeton* and three non-*Albanerpeton* albanerpetontids (Table 1). Another nine characters (6, 8, 12–14, and 16–19) are useful for diagnosing individual species of *Albanerpeton*, but were excluded from searches because these

characters are uninformative for assessing monophyly of *Albanerpeton* and relationships in the genus. PAUP 3.1.1 was also used to map character state distributions, perform bootstrap and decay analyses, and compute consensus trees and generate tree statistics. The ingroup (i.e., *Albanerpeton*) was not constrained to be monophyletic and the geologically oldest outgroup taxon, the “Kirtlington albanerpetontid,” was used to root the network. Using either of the other two non-*Albanerpeton* taxa to root the network did not alter topologies within *Albanerpeton*.

Terminal Taxa

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

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

	0000 12345	0001 67890	1111 12345	1112 67890	2222 12345	percent missing
Kirtlington species	0?0??	?0?00	00000	00110	00110	20
Anoual species	01000	00000	00?00	??110	00000	12
<i>Celtedens</i>	000??	?0?00	0????	0000?	00000	36
<i>Albanerpeton arthridion</i>	00000	00000	0000?	00000	11001	4
<i>Albanerpeton gracilis</i>	00000	00011	10000	00001	11000	0
<i>Albanerpeton galaktion</i>	00000	00012	10010	?0000	11010	4
<i>Albanerpeton cifellii</i>	00020	00011	1000?	?????	?????	44
<i>Albanerpeton nexuosus</i>	11110	10111	01001	00110	11110	0
<i>Albanerpeton inexpectatum</i>	11111	91211	00001	11001	12120	4
Paskapoo species	11111	91011	00101	00001	1?101	8

least one of the outgroups. *Celtedens* includes two named species, both known from skeletons: the type species *C. megacephalus* (early Albian, Italy) and *C. ibericus* (early Barremian, Spain) (Estes, 1981; McGowan and Evans, 1995). The genus is also represented by isolated elements—some of which may represent additional species—from other Lower Cretaceous and Upper Jurassic sites in Europe (McGowan, 1998; Gardner, 2000a). *Celtedens* is the only supraspecific taxon included in my analysis and monophyly of the genus is supported by the peculiar bulbous shaped internasal process on the fused frontals (Gardner, 2000a). The other two outgroup taxa are currently being studied in collaboration with S. E. Evans and D. Sigogneau-Russell, and will be formally described elsewhere: the “Kirtlington albanerpetontid” is represented by isolated bones from the Middle Jurassic (late Bathonian) of Kirtlington, England (McGowan, 1996, 1998; Gardner, 2000a), whereas the “Anoual albanerpetontid” is from the basal Cretaceous (Berriasian) of Anoual, Morocco (Sigogneau-Russell et al., 1998) and is represented by undescribed jaws and frontals. This pair of unnamed taxa can justifiably be employed as separate outgroups because they differ in details of jaw and frontal construction from each other and from *Albanerpeton* and *Celtedens*; see Gardner (2000a) for further comments on the generic identity of the Kirtlington albanerpetontid.

Species of *Albanerpeton* are known from isolated and rare articulated bones. Seven congeners are currently recognized (Gardner, 2000a): the type species *A. inexpectatum*, early and middle Miocene, Austria, Germany, and France; *A. arthridion*, latest Aptian/earliest Albian–middle Albian, Texas and Oklahoma, USA; *A. cifellii*, late Turonian, Utah, USA; *A. nexuosus* and *A. galaktion*, both Campanian and Maastrichtian, and *A. gracilis*, middle Campanian, all from the North American Western Interior; and an unnamed late Paleocene species, here called the “Paskapoo species,” from Alberta, Canada. A dentary and fused pair of premaxillae from the latest Albian/earliest Cenomanian of Utah resemble those of the younger *A. nexuosus*, but both specimens are too incomplete to be identified more precisely (Gardner, 1999c). Neither specimen provides any new osteological information and, for this reason, they are excluded from the analysis; however, these specimens are useful for establishing minimum times of origin for several less inclusive clades in the genus.

Character Analysis

This analysis uses 12 binary and four multistate informative characters, for a total of 20 derived states. Fifteen of these characters and the nine uninformative characters (eight binary and one multistate) describe attributes of the premaxilla, maxilla, dentary, and frontals. Examples of each of these elements are available for all but one of the terminal taxa. The exception is

Albanerpeton cifellii, which is known only by its distinctive holotype premaxilla (Gardner, 1999c). The sole non-osteological character (25) describes body size. Scoring decisions for species of *Albanerpeton* and the Kirtlington and Anoual albanerpetontids rely on firsthand study of specimens. Scoring decisions for *Celtedens* are composites based partly on McGowan and Evans’ (1995) preliminary description and figures of skeletons of *C. ibericus* and my examination of the poorly preserved holotype skeleton of *C. megacephalus*, but largely on examination of isolated skull elements (see McGowan and Ensom, 1997; Gardner, 2000a) of an indeterminate congener from the Early Cretaceous (Berriasian) of Purbeck, England.

Twenty-two characters were polarized against the three non-*Albanerpeton* albanerpetontid outgroups, using the outgroup comparison method (Watrous and Wheeler, 1981; Maddison et al., 1984; Bryant, 1991). Eleven of these characters can be scored for all three outgroup taxa—polarity decisions using outgroup comparisons are unequivocal for nine of these characters (1, 3, 7, 9–11, 21, 22, and 25) and rely on the consensus of two out of three outgroup taxa for two characters (23 and 24). The other 11 characters assessed using the outgroup comparison method cannot be scored for all three outgroups; in these cases, polarity decisions are founded on two outgroups for six characters (12, 14–17, 20) and one outgroup for five characters (4–6, 8, 13). Where polarities could not be decisively resolved (character 2) or were potentially misleading (characters 18 and 19) when assessed against the non-*Albanerpeton* albanerpetontid outgroups, the condition in *A. arthridion* was interpreted as being primitive for the genus. The latter approach is one of two variations of the paleontological method for character state polarization (Bryant, 1991, 1997), which operates under the assumption that the geologically oldest member of the ingroup, in this case *A. arthridion*, exhibits the plesiomorphic condition for characters. Polarity decisions for three characters (18, 19, and 21) also benefited from outgroup comparisons with non-albanerpetontid temnospondyls.

All characters were run as unweighted and most as unordered. Two multistate characters (10 and 22) were run as ordered because states in each character are interpreted as forming a linear transformation series. Running these characters as unordered did not change the topologies or lengths of the shortest trees.

Character Descriptions

Figure 1 depicts relevant character states of jaws and frontals.

Premaxilla (characters 1–14)

1. Build—0, gracile; 1, robust. Although admittedly subjective and perhaps influenced by body size and ontogeny, these two qualitative states nonetheless are useful for describing dif-

ferences in the relative build or construction of the premaxilla. This and the next three characters may be linked among species of *Albanerpeton*.

2. Height of Premaxillary Pars Dorsalis Relative to Width of Process Across Suprapalatal Pit—0, “high,” ratio of height versus width greater than about 1.55; 1, “low,” ratio of height versus width less than about 1.55. The pars dorsalis (=“alary process” of some authors) is a plate-like process that extends dorsally and slightly posteriorly from the main body of the premaxilla. The process articulates dorsally with the nasal and laterodorsally with the lacrimal, and contributes lateroventrally to the rim of the external narial opening. Outgroup comparisons are equivocal for interpreting polarities because the pars dorsalis is low in the Anoual species and, judging by McGowan and Evans’ photograph (1995:fig. 1b) of the holotype skeleton of *C. ibericus*, high in *Celtedens*. The latter state is judged here as being primitive for *Albanerpeton* because this is the condition in *A. arthridion*.

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

4. Pattern of Premaxillary-Nasal Contact—0, premaxillary pars dorsalis minimally overlaps and abuts against or weakly sutures with anterior end of nasal; 1, premaxillary pars dorsalis minimally overlaps and strongly sutures with anterior end of nasal; 2, anterior end of nasal fits into lingual facet on premaxillary pars dorsalis and is braced ventrolaterally by expanded dorsal end of lateral internal strut. Although nasals remain unknown for *Albanerpeton*, the three patterns of premaxillary-nasal contact described above can be inferred from the structure of the dorsal end of the premaxillary pars dorsalis. Two independently derived states are recognized: the premaxilla and nasal are strongly sutured along their complementary margins in *A. inexpectatum*, *A. nexuosus*, and the Paskapoo species, whereas the more complex overlapping and buttressed pattern is unique to *A. cifellii*.

5. Presence of Boss—0, present; 1, absent. The premaxillary boss is a raised bony patch or swelling on the dorsal part of the labial face of the pars dorsalis. The boss is present in all Cretaceous species of *Albanerpeton*, but is absent from both Tertiary congeners. Premaxillae of *A. gracilis* show that the boss appears ontogenetically (Gardner, 2000b) and this may have been true for other species.

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

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

8. Pattern of Labial Ornament—0, discontinuous, anastomosing ridges and irregular pits; 1, continuous ridges enclosing polygonal pits; 2, pustulate. Premaxillary ornament in albanerpetontids typically consists of irregular pits and ridges. The sec-

ond and third states are unique to, respectively, *Albanerpeton nexuosus* and *A. inexpectatum*.

9. Vertical Position of Suprapalatal Pit on Premaxillary Pars Dorsalis—0, “high,” with ventral edge of pit well above dorsal face of pars palatinum; 1, “low,” with ventral edge of pit just above or, more typically, continuous with dorsal face of pars palatinum. Albanerpetontid premaxillae are characterized by a pocket, called the suprapalatal pit, that opens in the lingual face of the pars dorsalis. The suprapalatal pit lies relatively high on the pars dorsalis in all non-*Albanerpeton* albanerpetontids and *A. arthridion*, but low in geologically younger species of *Albanerpeton*. In some referred premaxillae of *A. inexpectatum* a foramen opens lingually in the ventromedial corner of the pars dorsalis (Gardner, 1999a), thereby displacing the suprapalatal pit dorsally to mimic the primitive state.

10. Size of Suprapalatal Pit Relative to Lingual Surface Area of Premaxillary Pars Dorsalis—0, “small,” about 1%; 1, “moderate,” about 4–15%; 2, “large,” about 20–25%. The relative size of the suprapalatal pit is described by three states that form a linear transformation series leading to increased size of the pit. The strikingly enlarged suprapalatal pit in *A. galaktion* is unique among albanerpetontids and is probably linked with enlargement of the palatal foramen (character 14).

11. Lingual Outline of Suprapalatal Pit—0, oval; 1, triangular to slit shaped. The suprapalatal pit is oval in lingual outline in most albanerpetontids, but varies from triangular to slit-shaped in *Albanerpeton cifellii*, *A. gracilis*, and *A. galaktion*.

12. Form of Dorsal Process on Lingual Edge of Maxillary Process on Pars Palatinum—0, low, isolated ridge; 1, high flange, continuous labially with base of lateral internal strut. The lingual edge of the maxillary process on albanerpetontid premaxillae bears an unnamed dorsal process that typically is developed as a low, isolated ridge. This process abutted against the lingual edge of the premaxillary dorsal process on the maxilla which, in life, dorsally overlapped onto the maxillary process on the premaxilla. *Albanerpeton nexuosus* is unique in having the unnamed process developed into a high, labiolingually compressed, and dorsally convex flange that is continuous with a low ridge extending labiomediaally across the dorsal face of the pars palatinum to the base of the lateral internal strut.

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

14. Diameter of Palatal Foramen Relative to Diameter of Base of Any One of the More Medial Premaxillary Teeth—0, “small,” diameter of palatal foramen subequal to or, typically, considerably less than basal diameter of tooth; 1, “large,” diameter of foramen greater than about one and one-third basal diameter of tooth. The palatal foramen is an opening that extends through the pars palatinum, about midway along the labiolingual length of the shelf and between the vomerine and maxillary processes. The dorsal opening of the foramen is intimately associated with the suprapalatal pit. The palatal foramen is relatively small in most albanerpetontids, but it is markedly enlarged in *Albanerpeton galaktion*.

Maxilla and Dentary (characters 15–20)

15. Length of Premaxillary Lateral Process on Maxilla Relative to Height of Process at Base—0, “long,” length greater than height; 1, “short,” length subequal to or less than height. The premaxillary lateral process on the maxilla extends anteriorly from the pars dentalis to labially overlap and fit into a complementary facet on the pars dentalis of the premaxilla. The process is primitively long in albanerpetontids, but it is

relatively shorter in *Albanerpeton inexpectatum*, *A. nexuosus*, and the Paskapoo species.

16. Presence of Dorsal Process Behind Tooth Row on Dentary—0, absent; 1, present. In most albanerpetontids the dorsal edge of the dentary above the area for attachment of the postdentary bones descends posteroventrally from the posterior end of the tooth row. In *Albanerpeton inexpectatum* a small, triangular process projects dorsally from behind the tooth row to labially overlap the coronoid process on the prearticular.

17. Presence of Labial Ornament on Maxilla and Dentary, in Large Specimens—0, absent; 1, present. The labial surfaces of the maxilla and dentary are typically smooth in albanerpetontids. On large maxillae and dentaries of *Albanerpeton inexpectatum* the labial surface is sparsely ornamented with pustules and short, anastomosing ridges.

18. Labial or Lingual Profile of Occlusal Margins of Maxilla and Dentary—0, occlusal margins essentially straight; 1, occlusal margins strongly convex or angular, with pars dentalis on maxilla and dental parapet on dentary deepest adjacent to tallest teeth, becoming shallower anterior and posterior from this region. The profile of the occlusal margins of the maxilla and dentary are described using two states. Although an essentially straight occlusal margin occurs in just one of the three non-*Albanerpeton* albanerpetontid outgroups, this condition is here regarded as primitive for *Albanerpeton* because it occurs in the geologically oldest congener, *A. arthridion*, and most closely resembles the condition for temnospondyls in general. Within *Albanerpeton* a more convex or angular occlusal margin, with the apex directed occlusally, is unique to *A. nexuosus*.

19. Size Heterodonty of Teeth on Maxilla and Dentary—0, weakly heterodont; 1, strongly heterodont. Teeth vary in relative size along the maxilla and dentary in albanerpetontids: teeth are longest about a third of the distance along the row from the anterior end, and become smaller anterior and posterior from this region. These teeth generally are weakly heterodont in size, with the largest teeth only slightly longer relative to nearby teeth in the row. This condition occurs in only one of the three outgroups, but is regarded here as primitive for *Albanerpeton* because it is the condition in *A. arthridion* and most other temnospondyls. The Anoual and Kirtlington species and *Albanerpeton nexuosus* differ in having the maxillary and dentary teeth more strongly heterodont in size, with the longest teeth about a fifth to a quarter again as long compared to nearby teeth.

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

20. Position of Anterior End of Maxillary Tooth Row Relative to Point of Maximum Indentation Along Leading Edge of Nasal Process—0, anterior to; 1, approximately in line. In albanerpetontids the leading edge of the nasal process, which is a triangular process located dorsoanteriorly on the maxilla, is posteriorly concave in lingual outline. The anterior end of the maxillary tooth row generally lies several loci forward of a line extending ventrally from the point of maximum indentation along the leading edge of the nasal process. In *Albanerpeton inexpectatum*, *A. gracilis*, and the Paskapoo species the anterior end of the tooth row instead lies more posteriorly, approximately in line with the point of maximum indentation along the leading edge of the nasal process.

Frontals (characters 21–24)

21. Dorsal or Ventral Outline of Fused Frontals—0, bell- or hourglass-shaped; 1, triangular. The fused frontals are approximately hourglass- or bell-shaped in non-*Albanerpeton* albanerpetontids, but are more nearly triangular in *Albanerpeton*. The outline of the fused frontals in non-*Albanerpeton* albanerpetontids more closely resembles the condition in gymnophionans and non-lissamphibian temnospondyls—making allowances for the fact that frontals are paired in these taxa, rather than fused—and thus can be regarded as primitive for albanerpetontids.

22. Midline Length of Fused Frontals Relative to Width Across Posterior Edge of Bone, Between Lateral Edges of Ventrolateral Crests, in Large Specimens—0, “long,” ratio of length versus width greater than about 1.2; 1, “moderate,” ratio of length versus width between about 1.2 and 1.1; 2, “short,” ratio of length versus width equal to or less than about 1.0. Variation in the relative proportions of frontals are described using three states that form a linear transformation series leading to relatively shorter frontals. The intermediate state characterizes most *Albanerpeton* species, whereas the more derived state is restricted to *A. inexpectatum*. Frontals available for *A. inexpectatum* from La Grive-St. Alban, France, show that the bone becomes relatively shorter with growth (Gardner, 1999a); as such, estimates of relative frontal length for a given species ideally should be made from the largest available frontals.

23. Proportions of Internasal Process—0, “broad,” width subequal to length; 1, “narrow,” width less than length. The internasal process projects anteriorly from the midline of the fused frontals and partially separates the paired nasals in albanerpetontids (Gardner, 2000c). A broad internasal process is judged as primitive for *Albanerpeton*, because this state occurs in *A. arthridion* and two of the three non-*Albanerpeton* outgroups. The Kirtlington species, *A. inexpectatum*, *A. nexuosus*, and the Paskapoo species have a relatively narrower internasal process.

24. Form of Ventrolateral Crest, in Large Specimens—0, narrow and convex ventrally in transverse profile, with ventral face convex to slightly bevelled ventrolaterally; 1, narrow and triangular in transverse profile, with ventral face flat to shallowly concave; 2, wide and triangular in transverse view, with ventral face deeply concave. Located on the underside of the frontals, the ventrolateral crest is a prominent ridge that extends alongside the lateral edge of the bone and projects posteriorly to underlap the parietals. The form of the ventrolateral crest is described here using three states that reflect variation in the relative width of the crest, outline of the crest in transverse view, and shape of the ventral face along the orbital margin. The width of the crest is described in relative terms, using the ratio of the width of the crest immediately behind the slot for receipt of the prefrontal versus the width across the posterior edge of the fused frontals between the medial edges of the ventrolateral crests. The crest is relatively narrow (ratio less than about 0.40) in large individuals of most albanerpetontids, except for *Albanerpeton inexpectatum* in which the crest is relatively wider (ratio greater than about 0.45). Considering that the ventrolateral crest becomes more bevelled and relatively wider with growth in at least some species of *Albanerpeton* (Gardner, 1999a, 2000b), this character should ideally be scored from the largest available specimens.

Body Size

25. Estimated, Maximum Snout–Pelvic Length—0, “large,” greater than about 50 mm; 1, “small,” less than about 40 mm. Body size in albanerpetontids is here described using the snout–pelvic length (sensu Gardner, 1999b). This value can

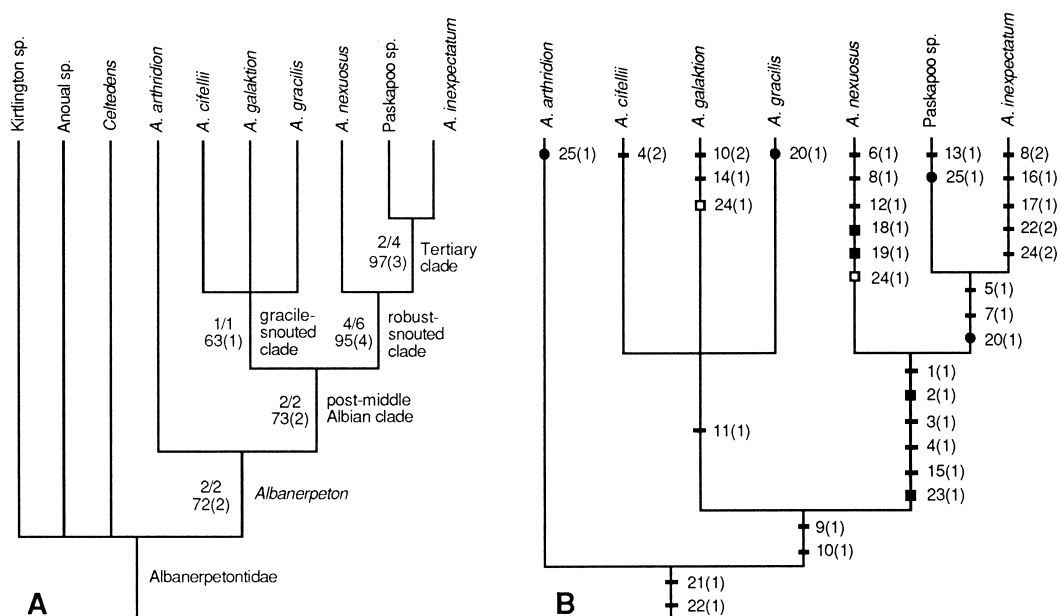


FIGURE 2. Strict consensus of six shortest trees based on 16 informative characters scored for three outgroup taxa and seven species of *Albanerpeton*. **A**, strict consensus tree showing names and indices of support for clades. Indices of support to left of node: upper values are number of unambiguous synapomorphies/total number of synapomorphies; lower values are bootstrap value (%) for 2,000 replicates and, in brackets, decay index (steps). **B**, strict consensus tree, with outgroups deleted, showing distribution of apomorphies for all 25 characters within *Albanerpeton* as mapped by the DELTRAN character state optimization and the most conservative, preferred arrangement of apomorphies within the gracile-snouted clade. The ACCTRAN optimization differs only in shifting character state 22(2) stemward to the more inclusive node for the Tertiary clade. Figure 3 depicts alternative arrangements for apomorphies in the gracile-snouted clade. Symbols for apomorphies are: horizontal bar, unique apomorphy; solid circle, convergent within *Albanerpeton*; solid square, convergent with one or more non-*Albanerpeton* albanerpetontids; and open square, convergent within *Albanerpeton* and with a non-*Albanerpeton* albanerpetontid. Tree statistics (uninformative characters excluded): tree length = 26 steps; CI = 0.769, HI = 0.231, and RI = 0.818.

be measured directly from skeletons, but more commonly it is estimated from the midline length of frontals assuming a ratio of about 10:1 between snout–pelvic length and frontal length (Gardner, 1999b). This character is admittedly problematic, in part, because snout–pelvic length can be measured directly from only a few skeletons and, in part, because any measure of absolute size requires a large sample in order to estimate the upper size limit with any confidence. Despite these limitations, maximum body size warrants consideration because this measurement varies considerably within *Albanerpeton*. Further, such differences are potentially important for interpreting the paleobiology of species (Gardner, 1999b, 2000b). In absolute terms albanerpetontids were relatively small animals and most taxa appear to have maximum inferred snout–pelvic lengths of about 50 mm to, perhaps as much as, 70 mm; maximum inferred body sizes for species in this range form a continuum. Frontals currently available for *A. arthridion* and the Paskapoo species indicate that these taxa were smaller, with maximum estimated snout–pelvic lengths less than about 40 mm.

RESULTS

The branch-and-bound search yielded six shortest trees of 26 steps. Figure 2 depicts the strict consensus of these trees. Each of the shortest trees recovers a monophyletic *Albanerpeton* and the same four less inclusive clades within the genus. There are two sources of topological variation among the shortest trees. The first involves the inferred relationship between *Albanerpeton* and *Celtdens*: these are identified as sister-taxa in three trees, whereas the other three trees identify only an unresolved polychotomy among the three outgroups and *Albanerpeton*. Although the relationship between *Albanerpeton* and *Celtdens* is interesting and worthy of future study, it is irrelevant for assessing monophyly and relationships in *Albanerpeton*. The only significant variation concerns the unresolved relationships among the three members (*A. galaktion*, *A. gracilis*, and *A. cifellii*) of the gracile-snouted clade.

The synapomorphies and support for each of the five clades of interest are discussed below. Figure 2A and Table 2 show

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

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

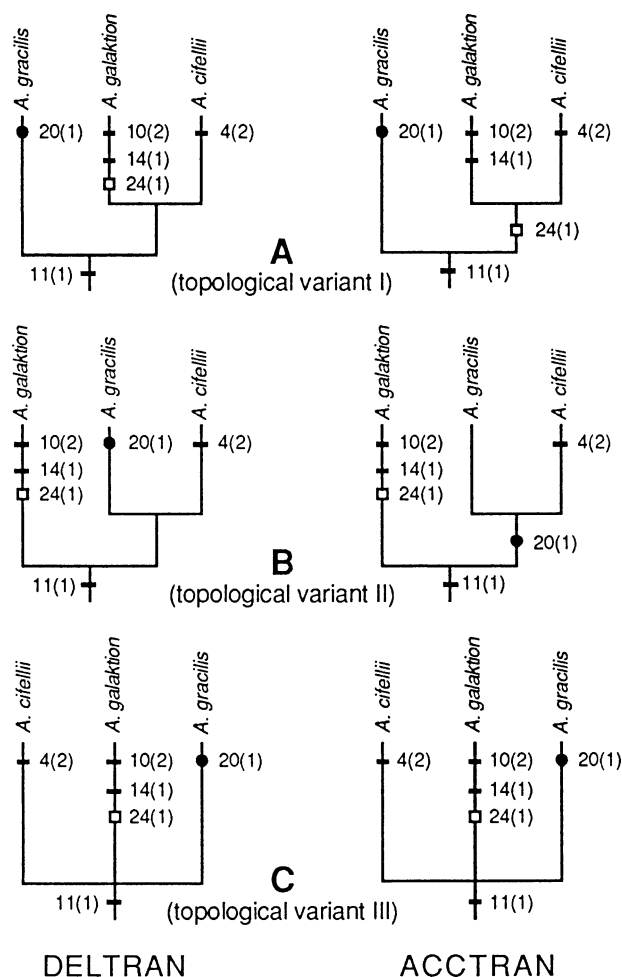


FIGURE 3. The three topological variants recovered in the gracile-snouted clade and distribution of apomorphies as mapped by DELTRAN (left) and ACCTAN (right) character state optimizations. **A**, topological variant I: *Albanerpeton gracilis* (*A. galaktion* + *A. cifellii*). **B**, topological variant II: *A. galaktion* (*A. gracilis* + *A. cifellii*). **C**, topological variant III: *A. galaktion* + *A. gracilis* + *A. cifellii*. Each topological variant is recovered in two trees. The hypothesized sister-pair relationships in the first two topological variants are each founded on one convergence identified only by ACCTAN and involve a character that cannot be scored for *A. cifellii*. The unresolved trichotomy identified in the third topological variant is the most conservative and preferred arrangement.

that levels of support for these clades vary, with bootstrap values of 63 to 97% and decay values of one to four steps. Figure 2B reports the distribution of apomorphies within *Albanerpeton*; Figure 3 presents the same information for topological variants in the less inclusive gracile-snouted clade.

Albanerpeton: *A. arthridion* (Robust-snouted Clade + Gracile-snouted Clade)

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

Post-Middle Albian Clade: Robust-snouted Clade + Gracile-snouted Clade

A less inclusive clade containing all species of *Albanerpeton* except *A. arthridion* is diagnosed by having the suprapalatal pit

low on the premaxillary pars dorsalis [9(1)] and occupying at least four percent of the area of the pars dorsalis [10(1)]. Support for this clade is also modest. The clade has the third lowest bootstrap value (73%) and collapses after two additional steps.

Gracile-Snouted Clade: *Albanerpeton galaktion* + *A. gracilis* + *A. cifellii*

Members of the gracile-snouted clade are united by a unique triangular to slit-shaped suprapalatal pit [11(1)]. This is the weakest supported clade in the analysis, with both the lowest bootstrap (63%) and decay (one step) values. Three topological variants, of two trees each, are recovered (Fig. 3). The first two variants postulate a sister-pair relationship between *Albanerpeton cifellii* and either *A. galaktion*, based on the narrow and triangular ventrolateral crest [24(1)], or *A. gracilis*, based on the more posterior position of the anterior end of the maxillary tooth row [20(1)] (Fig. 3A and B, respectively). Neither arrangement is defensible, because each hinges upon a character state that cannot be scored for *A. cifellii* and is postulated to be synapomorphic for the sister-pair only by the ACCTAN optimization. Within the gracile-snouted clade the DELTRAN optimization more conservatively restricts character 24(1) to *A. galaktion* and character 20(1) to *A. gracilis*. In the third topological variant (Fig. 3C) relationships among *A. cifellii*, *A. galaktion*, and *A. gracilis* are unresolved; this is the most conservative and preferred arrangement.

Robust-Snouted Clade: *Albanerpeton nexuosus* (*A. inexpectatum* + Paskapoo Species)

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

Tertiary Clade: *Albanerpeton inexpectatum* + Paskapoo Species

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

DISCUSSION

Monophyly of *Albanerpeton* and Taxonomic Implications

The analysis presented here corroborates the monophyly of *Albanerpeton*. The strength of this corroboration is admittedly

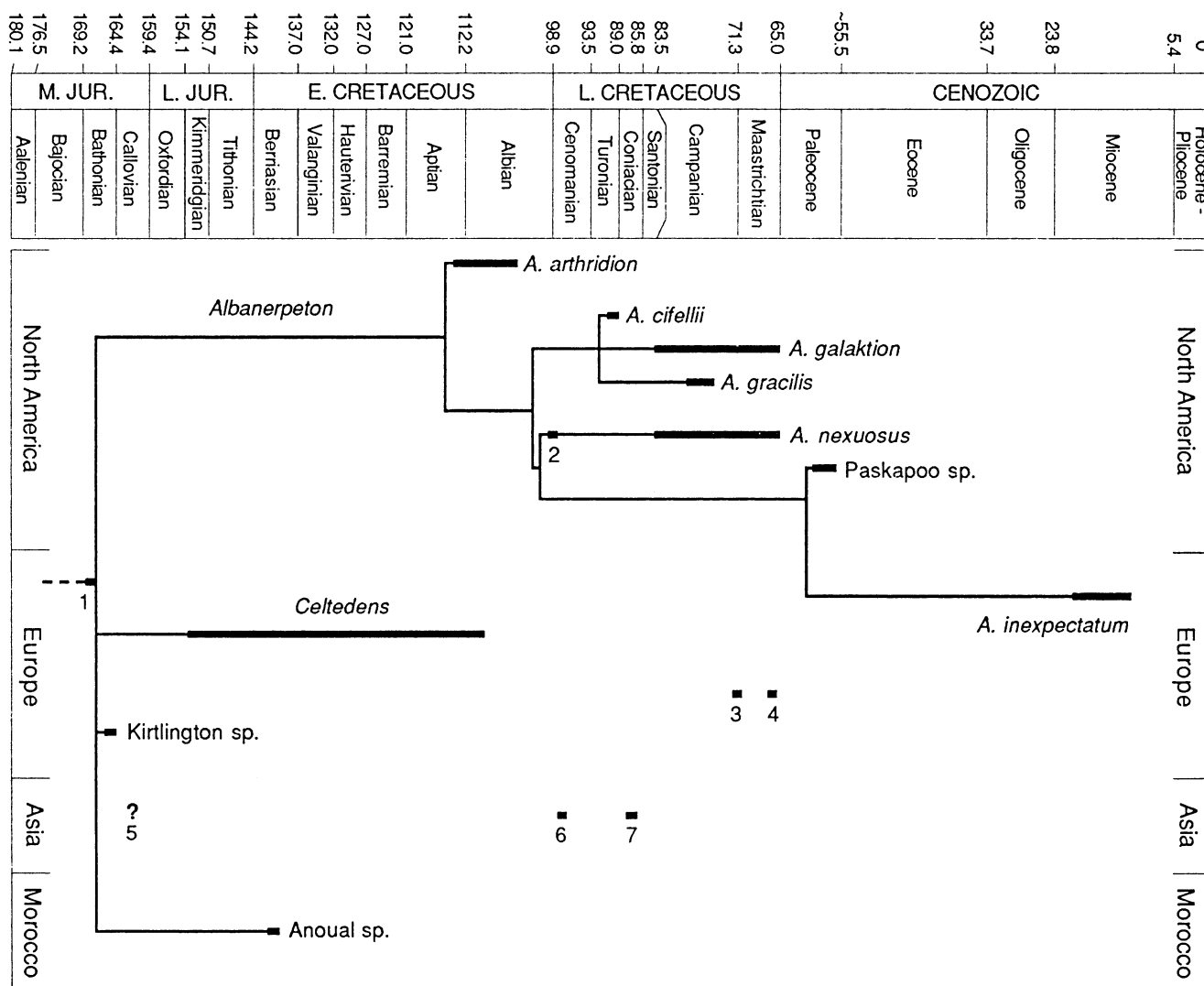


FIGURE 4. Strict consensus tree showing stratigraphical and geographical ranges of terminal taxa, estimated divergence times, and notable occurrences of other albanerpetontids (1–7; see Appendix 1). Absolute ages are from Gradstein et al. (1995) and Berggren et al. (1995).

moderate, as evidenced by bootstrap and decay values of 72% and two steps, respectively. Nevertheless, alternative arrangements that recover a paraphyletic *Albanerpeton* are far less well supported: the most common topology of this sort identified by the decay analysis (*Anoual* species + *Celtedens* + *A. arthridion*) requires two more steps and is recovered in just 11% of the 81 trees, whereas the arrangement identified by the bootstrap analysis (same clade + species in the gracile-snouted clade) is recovered in only 17% of 2,000 bootstrap replicates. Although indices for support of the genus are moderate, both of the synapomorphies identified for *Albanerpeton* are unique within the Albanerpetontidae to the genus and one—frontals triangular in outline—appears to be unique at a more inclusive level among temnospondyls as a whole. Six other frontal character states collectively differentiate *Albanerpeton* from other albanerpetontids (Gardner, 2000a), but were not included here because they are uninformative for assessing relationships within the genus: internasal process pointed in dorsal or ventral outline; lateral face of internasal process indented by anteroposteriorly elongate groove for tongue-in-groove contact with medial edge of nasal; anterolateral process prominent and pointed distally; dorsal and ventral edges of slot for receipt of pre-

frontal excavated medially; anterior end of orbital margin located approximately in line with, or posterior to, anteroposterior midpoint of frontals; and orbital margin uniformly shallowly concave to nearly straight along entire length in dorsal or ventral outline. A pointed internasal process is primitive for albanerpetontids based on comparisons with other temnospondyls, but further work is needed to clarify polarities and distributions of the other five character states within the Albanerpetontidae; some of these character states may prove to be apomorphic for *Albanerpeton*.

As recognized here, *Albanerpeton* extends from the latest Aptian/earliest Albian to late middle Miocene (MN 7+8) or about 100 million years according to time scales for the Mesozoic (Gradstein et al., 1995), Cenozoic (Berggren et al., 1995), and European Neogene (Steininger et al., 1996) (Fig. 4). This temporal range is admittedly extensive and the validity of the genus might be questioned on these grounds. Based on the phylogenetic framework proposed here, *Albanerpeton* could be partitioned and the generic name restricted to any of the four less inclusive monophyletic units that includes the type species—*A. inexpectatum* alone or the Tertiary, robust-snouted, or post-middle Albian clades. Compared to *Albanerpeton*, each of

these four less inclusive groups is better supported (Fig. 2) and the stratigraphical ranges of the first two are also considerably shorter (Fig. 4), at about 40 and eight million years, respectively. Depending on which less inclusive group is chosen to bear the name *Albanerpeton*, however, one to as many as four new genera would need to be erected to accommodate the excluded former congeners. The gracile-snouted clade and *A. nexuosus* may be distinctive enough to warrant separate generic rank, but this is more difficult to justify for *A. arthridion* and the Paskapoo species. Partitioning *Albanerpeton* into two or more less inclusive genera also does not better reflect the inferred phylogeny of taxa. In short, I see no compelling reason at present not to accept *Albanerpeton* as a long-lived Euramerican genus.

Evolution of *Albanerpeton*

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

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

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

The next series of modifications affects the suprapalatal pit in the premaxilla. These changes occur at two successively less inclusive nodes: the suprapalatal pit first increases in size and shifts ventrally at the node for the post-middle Albian clade, then changes in outline from oval to triangular or slit-shaped at the less inclusive node for the gracile-snouted clade. Assuming

that the suprapalatal pit housed a gland involved in feeding, olfaction, or both (Fox and Naylor, 1982; Gardner, 2000a), modifications to the pit presumably were reflected, in life, by changes to the form and function of the gland.

An incomplete pair of *Albanerpeton nexuosus*-like premaxillae from the upper part of the Cedar Mountain Formation in Utah (Gardner, 1999c) provides a minimum age of latest Albian/earliest Cenomanian both for the establishment of the post-middle Albian clade and for the divergence of the gracile- and robust-snouted clades (Fig. 4). The appearance of this indeterminate, *A. nexuosus*-like species coincides with the establishment of the Bering Land Bridge that linked Asia with the North American western subcontinent through the Late Cretaceous (Russell, 1993; Smith et al., 1994; Sereno, 1997). The timing of these occurrences raises the possibility that the *A. nexuosus*-like taxon may be an Asian immigrant; if correct, this implies that the post-middle Albian clade and, perhaps, *Albanerpeton*, did not originate in North America. Further consideration of these alternative ideas is hampered by the sparse record for albanerpetontids in Asia. The only albanerpetontid specimens known from the continent are five indeterminate dentaries from the Cenomanian and Coniacian of Uzbekistan (Gardner and Averianov, 1998) that only primitively resemble dentaries of North American taxa.

The unique outline (triangular to slit-shaped) of the suprapalatal pit is the sole innovation identified for the gracile-snouted clade. Relationships within the gracile-snouted clade are unresolved and will probably continue to be so until additional elements are available for the most poorly known member, *Albanerpeton cifellii*. The middle Campanian species *A. gracilis* is a good structural ancestor for the gracile-snouted clade, although the species is too young to be ancestral to either *A. cifellii* (late Turonian) or *A. galaktion* (early Campanian to late Maastrichtian). The gracile-snouted clade is reliably known only from the Late Cretaceous of the Western Interior and, thus, appears to be endemic to the region. Although the gracile- and robust-snouted clades presumably diverged around the Albian–Cenomanian boundary (see above), the earliest direct evidence for the gracile-snouted clade occurs some 10 million years later, in the form of the holotype premaxilla of *A. cifellii* from the late Turonian part of the Straight Cliffs Formation in Utah (Gardner, 1999c). The last appearance of the clade is recorded by a referred premaxilla of *A. galaktion* from the late Maastrichtian Lance Formation in Wyoming (Gardner, 2000b).

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

CONCLUSIONS

Cladistic analysis of 16 characters scored for the seven recognized species of *Albanerpeton* and three other albanerpetontid taxa yields the following results and interpretations:

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

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

(3) Fossil occurrences and hypothesized relationships within the genus suggest that the history of *Albanerpeton* was centered in North America. *Albanerpeton* may have originated on the continent, but the earliest reported occurrence in the latest Aptian/earliest Albian of Oklahoma undoubtedly underestimates the time of origin for the genus. All four of the less inclusive clades appear to have originated in North America. The final and only occurrence from elsewhere, that of the type species *A. inexpectatum* in the Miocene of Western Europe, is probably due to the immigration of an unknown ancestral species from North America.

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

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APPENDIX 1

Stratigraphical and geographical information used to construct Figure 4.

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