

Revised taxonomy of albanerpetontid amphibians

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Characters of the jaws and frontals are often used to differentiate albanerpetontid genera and species, yet the reliability of these characters has rarely been examined. Frontals are diagnostic for the genera *Albanerpeton* and *Celtdens* and for species in the latter genus. The value of frontals at the specific level in *Celtdens* may be inflated by lack of information about variation in jaw structure. Characters of the frontals, jaws, and body size differentiate species of *Albanerpeton*. Differential diagnoses are presented for the Albanerpetontidae based on cranial and vertebral characters and for the two named genera based on frontal characters. Each genus is characterized by one autapomorphy: fused frontals triangular in *Albanerpeton* and internasal process bulbous in *Celtdens*. An enigmatic albanerpetontid from the Middle Jurassic (upper Bathonian) of England has a unique mixture of frontal and premaxillary character states that precludes it from being included in either *Celtdens* or *Albanerpeton*. This leaves the oldest occurrences of the two genera in, respectively, the Late Jurassic (Kimmeridgian) and Early Cretaceous (latest Aptian/earliest Albian).

Key words: *Albanerpeton*, Albanerpetontidae, Allocaudata, Amphibia, *Celtdens*, Lissamphibia, taxonomy.

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Introduction

The Albanerpetontidae Fox & Naylor, 1982 are salamander-like, Middle Jurassic to Miocene amphibians that are of general interest because they constitute a clade of lissamphibians distinct from caudates, salientians, and gymnophionans. Two genera, containing at least nine species, are currently recognized: the type genus *Albanerpeton* Estes & Hoffstetter, 1976, from the Lower Cretaceous–Paleocene of the North American Western Interior and Miocene of France (Estes & Hoffstetter 1976; Estes 1981; Fox & Naylor 1982; Gardner 1999a, b, c) and *Celtdens* McGowan & Evans, 1995 from the

Lower Cretaceous, Upper Jurassic, and, purportedly, Middle Jurassic of Europe (McGowan & Evans 1995; McGowan 1996, 1998; McGowan & Ensom 1997).

Jaws and frontals are the most commonly recovered albanerpetontid elements at most sites, and characters of these elements are widely used to diagnose genera and species (Estes 1981; Nessov 1981; Fox & Naylor 1982; McGowan & Evans 1995; McGowan 1998; Gardner 1999a, b, c; Rage & Hossini in press). In many cases, the reliability of such characters has not been adequately established. This is the result of a combination of factors: scarcity of well preserved specimens; a reluctance on the part of some workers to examine appropriate comparative collections; and misinterpretations of structure. To cite a recent example, McGowan (1998) used only frontal characters to diagnose *Albanerpeton*, *Celtdens*, and their respective species. McGowan's (1998) claims about the diagnostic utility of frontals for *Albanerpeton* and its species are suspect because he considered just two of the four named species then included in the genus (I recognize seven species), examined only material of the type species *A. inexpectatum* Estes & Hoffstetter, 1976, and misinterpreted the structure of the frontal in *A. galaktion* Fox & Naylor, 1982 based on photographs (Fox & Naylor 1982: fig. 1d, e) of an incomplete specimen. McGowan's (1998) reliance on frontal characters alone to diagnose species of *Albanerpeton* is also at odds with observations that characters of the jaws are also useful for this purpose (Estes 1981; Fox & Naylor 1982; Gardner 1999a, b, c; Rage & Hossini in press).

Here I assess the taxonomic value of characters for albanerpetontids, with emphasis on frontals and jaws. Isolated examples of these are available for all species of *Albanerpeton* (Estes & Hoffstetter 1976; Fox & Naylor 1982; Gardner 1999a, b, unpublished data), except for a new Turonian species known only by its distinctive holotype premaxilla (Gardner 1999c). Frontals are also reasonably well known for *Celtdens*, both as disassociated elements from indeterminate species and articulated in the respective holotype skeletons of both named species, *C. megacephalus* (Costa, 1864) and *C. ibericus* McGowan & Evans, 1995 (McGowan & Evans 1995; McGowan 1996, 1998; McGowan & Ensom 1997). Jaws in these skeletons are difficult to study because they are preserved in articulation and, in the case of the holotype of *C. megacephalus*, also poorly preserved. The only isolated, reasonably well preserved jaws available for *Celtdens* are incomplete premaxillae and dentaries of an indeterminate species from the Lower Cretaceous of Purbeck, England (McGowan & Ensom 1997). In the second part of this paper, I provide revised diagnoses and select comments for the Albanerpetontidae and its genera, then examine the identity of a purported *Celtdens*-like taxon (McGowan 1996, 1998) from the Middle Jurassic of England.

Osteological terms and measurements follow Gardner (1999a), with one exception. For the premaxilla, I propose the replacement term 'lacrimial notch' for the indentation along the laterodorsal edge of the pars dorsalis – this notch received the large lacrimial, not the reduced prefrontal (Gardner in press). I follow McGowan & Evans (1995) in placing albanerpetontids within the Lissamphibia Haeckel, 1866 and Milner (1988) in regarding lissamphibians as crown-clade temnospondyls.

Institutional abbreviations: BMNH, Natural History Museum, London, England; 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; MNP, Museo di Paleontologia dell'Università di Napoli, Naples, Italy; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Canada; UCK, University College London, London, England; and UCMP, University of California Museum of Paleontology, Berkeley, USA.

Taxonomic characters for albanerpetontids

Frontals (Figs 1, 2; Table 1). — Albanerpetontid frontals are solidly fused medially and have a prominent internasal process, two pairs of slots anterior to the orbital margin for mortise and tenon style articulation with posterior ends of the paired nasals and prefrontals, prominent ventrolateral crests adjacent to the orbital margin, and dorsal ornament comprised of polygonal pits enclosed by ridges. Comparisons with other temnospondyls indicate that the first three of these character states are synapomorphic for the family (Gardner unpublished data).

Table 1. Frontal characters for albanerpetontid genera and species. References are: ¹McGowan & Evans 1995; ²McGowan 1998; ³Gardner 1999a; ⁴Rage & Hossini in press; ⁵S.E. Evans personal communication 1999.

1. Dorsal or ventral outline of frontals^{1,2,3}.
2. Midline length of frontals relative to width across posterior edge between lateral edges of ventrolateral crests^{2,3,4}.
3. Dorsal or ventral outline of internasal process^{1,2,3}.
4. Length of internasal process relative to width across base².
5. Pattern of contact between internasal process and paired nasals³.
6. Form of anterolateral process⁵.
7. Medial emargination of posterior slot for receipt of prefrontal².
8. Width of frontals between slots for receipt of prefrontal relative to width across posterior edge of bone².
9. Angle at which lateral wall of frontal diverges posterolaterally from midline².
10. Position of anterior limit of orbital margin relative to midline length of frontals².
11. Dorsal or ventral outline of orbital margin^{1,2}.
12. Form of ventrolateral crest³.
13. Pattern of dorsal ornament².

Table 1 lists the 13 frontal characters that have been used to differentiate *Albanerpeton*, *Celtedens*, and their respective species. Seven characters (1–3, 6, 7, 10, and 11) differ between *Albanerpeton* and *Celtedens*, as follows (Figs 1, 2): 1, outline of frontals triangular in *Albanerpeton*, versus more nearly hourglass- or bell-shaped in *Celtedens*; 2, midline length of frontals relative to width across posterior edge between lateral edges of ventrolateral crests less than about 1.2 in *Albanerpeton*, versus more than about 1.2 in *Celtedens*; 3, outline of internasal process triangular in *Albanerpeton*, versus bulbous in *Celtedens*; 6, anterolateral process distinct from main body of frontal, extending anterolaterally, and pointed distally in *Albanerpeton*, versus a poorly differentiated, broadly rounded shoulder in *Celtedens*; 7, dorsal and ventral edges of slot for receipt of prefrontal excavated medially in *Albanerpeton*, versus unexcavated in *Celtedens*;

10, anterior end of orbital margin, as marked by posterior edge of slot for receipt of prefrontal, lies approximately in line with, or posterior to, anteroposterior midpoint of frontals in *Albanerpeton*, versus anterior end of orbital margin lies anterior to midpoint of frontals in *Celtedens*; and 11, outline of orbital margin uniformly shallowly curved to nearly straight in *Albanerpeton*, versus margin more concave medially and, occasionally, deflected posterolaterally near posterior end in *Celtedens*. Where known, the pattern of frontal-nasal contact (character 5) also differs between the two genera. Ventral facets on the internasal process of an incomplete frontal (Fig. 2A) of *Celtedens* sp. from Purbeck indicate that the lateral edges of the process dorsally overlapped the medial edges of the paired nasals. This differs from the condition in *Albanerpeton*, where a groove extending along the lateral face of the internasal process (Fig. 1G) held the medial edge of the nasal in a tongue-in-groove joint. Outgroup comparisons with other temnospondyls argue for the triangular-shaped frontals of *Albanerpeton* and the bulbous-shaped internasal process in *Celtedens* being the derived states for characters 1 and 3, respectively. Polarities for states of the other frontal characters are uncertain.

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

A final three frontal characters (3, 4, and 12) differ significantly within *Albanerpeton*. Characters 3 and 4 describe, respectively, the outline and proportions of the internasal process. Among species of *Albanerpeton*, these two characters are essentially identical:

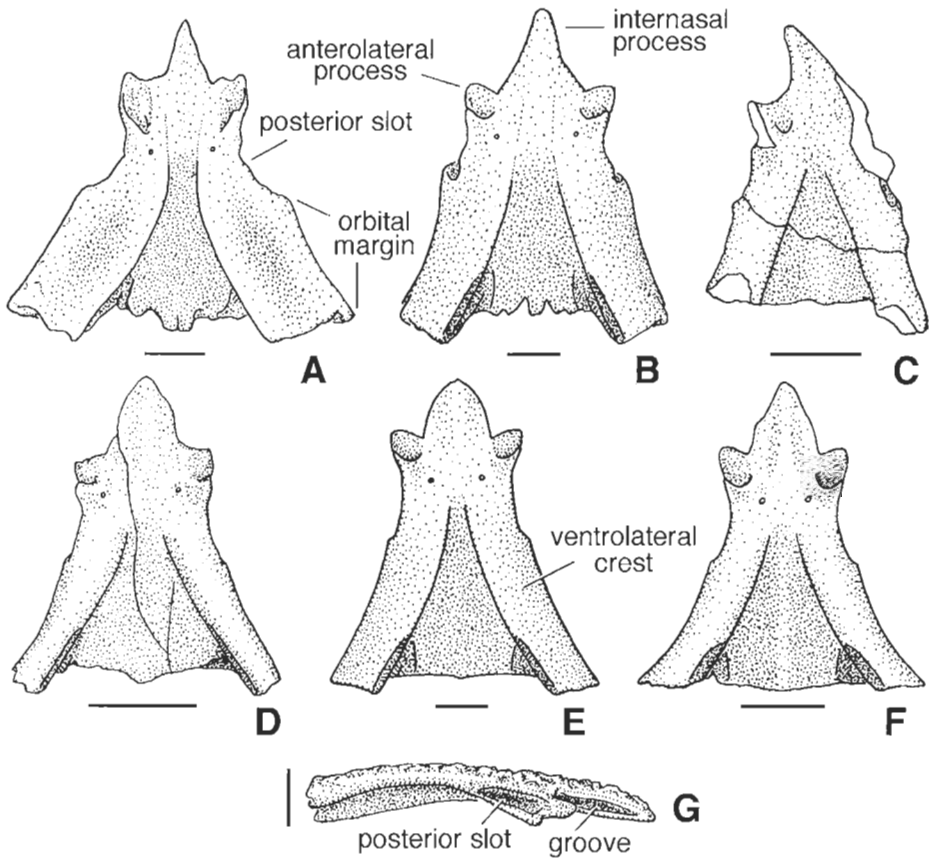


Fig. 1. Azygous frontals of *Albanerpeton*. **A.** *Albanerpeton inexpectatum*, MNHN.LGA 1222, complete frontals, ventral view; middle or ?lower Miocene fissure fill, La Grive-St. Alban, France. **B.** *Albanerpeton nexuosus*, reconstructed frontals based on UALVP 39983, 39986, 39989, and 39996, ventral view; Milk River Formation (lower Campanian), Alberta, Canada. **C.** Unnamed late Paleocene species, UALVP unnumbered, incomplete frontals with internasal process warped to the right (left side in figure) and missing much of anterolateral process on right side, all of anterolateral process on left side, and posterior end of bone, ventral view; Paskapoo Formation (upper Paleocene), Alberta, Canada. **D.** *Albanerpeton arthridion*, FMNH PR2026, nearly complete frontals missing distal end of both anterolateral processes, ventral view; Antlers Formation (uppermost Aptian–middle Albian), Texas and Oklahoma, USA. **E.** *Albanerpeton galaktion*, reconstructed frontals based on UALVP 16216, 39946, 39949, and 39951, ventral view; Milk River Formation (lower Campanian), Alberta, Canada. **F.** Unnamed middle Campanian species, reconstructed frontals based on RTMP 86.194.8, 95.181.67, 96.1.57, and 96.78.135, ventral view; Dinosaur Park and Oldman formations (middle Campanian), Alberta, Canada. **G.** *Albanerpeton inexpectatum*, MNHN.LGA 1220, complete frontals, right lateral view, showing more posterior slot for receipt of prefrontal and groove for contact with medial edge of nasal. Broken surfaces are white. Scale bars = 1 mm.

the process is either acuminate and relatively narrow or acute and relatively broad (cf. Fig. 1A–C versus D–F). As an aside, I should point out that McGowan & Evans' (1995: fig. 3b) and McGowan's (1998: fig. 1b) figures of fused frontals of *A. galaktion* incorrectly depict the internasal process as broad, short, and wedge-shaped. These authors' drawings were based on published photographs (Fox & Naylor 1982: fig. 1d, e) of

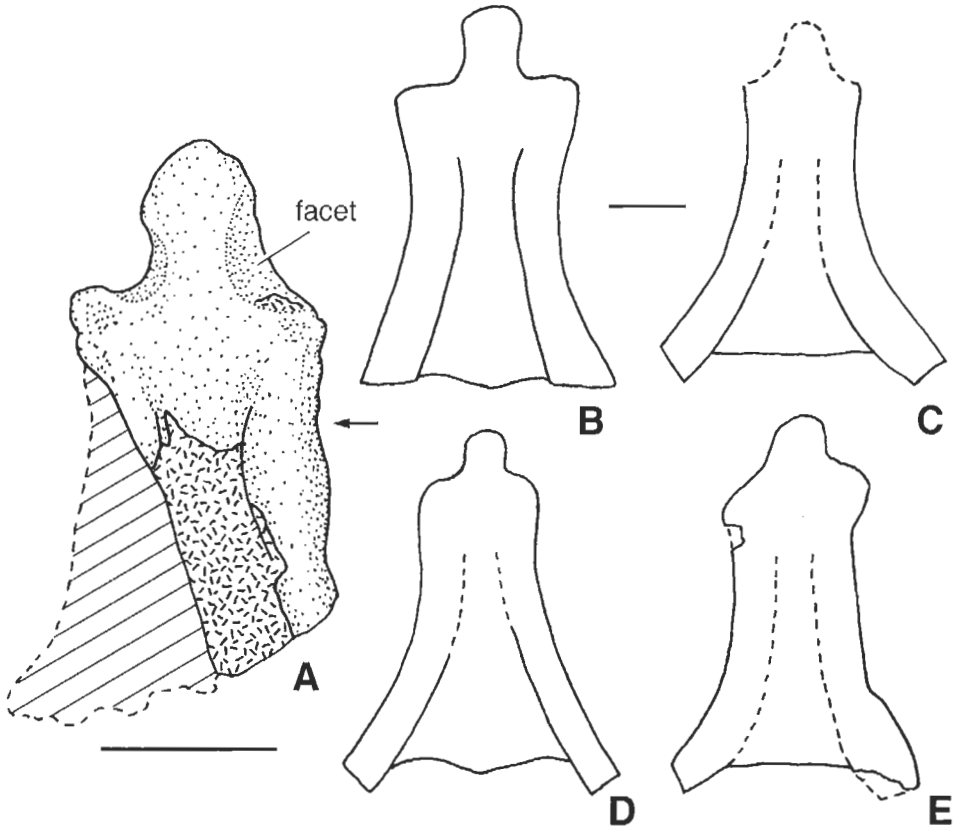


Fig. 2. Azygous frontals of *Celledens*, all in ventral view. **A.** *Celledens* sp. indet., DORCM GS35, incomplete frontals, with arrow indicating anterior end of orbital margin, cross-hatching showing area once present but now missing (see McGowan & Ensom 1997: fig. 2a), and hash marks indicating matrix; Purbeck (Berriasian), England. **B.** *Celledens ibericus*, outline drawing of frontals articulated in holotype skull LH 6020; Las Hoyas (upper Barremian), Spain. **C.** *Celledens megagephalus*, outline drawing of frontals articulated in holotype skull MNP 542; Pietraroia (lower Albian), Italy. **D.** *Celledens* sp. indet., catalogue number unreported, outline drawing of frontals; Uña (Barremian), Spain. **E.** *Celledens* sp. indet., catalogue number unreported, outline drawing of frontals; Guimarota (Kimmeridgian), Portugal. Frontals in figures **B–E** redrawn from McGowan (1998: fig. 1). Scale bars = 1 mm: left scale bar is for figure **A**, right scale bar is for figures **B** and **C**; scales for specimens in figures **D** and **E** were not reported by McGowan (1998).

a referred frontal (UALVP 16216) that is broken anteriorly and lacks the internasal process entirely. The surface that McGowan & Evans (1995) and McGowan (1998) interpreted as the outline of the internasal process is actually the broken anterior end of the specimen. Other referred frontals in the collection of the UALVP show the proper form of the process for *A. galaktion*; this information is incorporated into my reconstruction in Fig. 2E. Character 12 describes the transverse profile and relative width of the ventrolateral crest. In transverse profile, the crest is either convex ventrally or resembles a right-angled triangle, with the medial edge deep and the lateral edge shallow. The width of the crest immediately behind the slot for receipt of the prefrontal, in large specimens, is either less than about 0.40 or greater than about 0.45 the width across the poste-

rior edge of the frontals between the medial edges of the crest. Frontals from large individuals of *A. inexpectatum* and *A. arthridion* Fox & Naylor, 1982 exhibit the most extreme differences in the form of the ventrolateral crest (cf. Fig. 2A versus D).

Emargination of the slot for receipt of the prefrontal, relative length of the orbital margin, and pattern of dorsal ornament (characters 7, 10, and 13, respectively) are less variable among species of *Albanerpeton* than McGowan (1998) suspected. McGowan's (1998) belief that relative orbital lengths are diagnostic for species is, again, based on his misinterpretation of a figured frontal (UALVP 16216) of *A. galaktion*. The specimen is broken anteriorly, creating the impression that the anterior limit of the orbit lies more anterior. Emargination of the slot for receipt of the prefrontal and dorsal ornament both become more pronounced with growth in species of *Albanerpeton*; this is especially evident in *A. inexpectatum* (Gardner 1999a). Albanerpetontid frontals are typically ornamented dorsally with a system of polygonal pits enclosed by ridges. Occasional frontals are encountered in which the pits are so shallow and the ridges so low that the dorsal surface is virtually smooth. As this condition occurs in different-sized and, sometimes, well preserved frontals of species in both genera, it appears to be neither ontogenetic or diagenetic in origin nor taxonomically significant.

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

Jaws (Fig. 3). — Albanerpetontid jaws are distinctive, but superficially resemble and have been confused with jaws of other lissamphibians and lizards. For this reason and because albanerpetontid jaws are not uncommon in nonmarine Jurassic and Cretaceous microvertebrate assemblages, a brief review of their characteristic features is appropriate. For attachment of the highly pleurodont teeth, the premaxilla and maxilla each have a deep pars dentalis and the dentary has a tall dental parapet. Upper jaws are additionally characterized by having tiny, scattered external nutritive foramina labially, the tooth row extending along virtually the entire ventral margin of the pars dentalis, and a prominent, shelf-like pars palatinum lingually. The pars palatinum on the premaxilla is pierced by a palatal foramen and on the maxilla bears a trough dorsolingually for contact with one or more palatal bones. The premaxilla is further distinctive in having a facet on the labial face for contact with a complementary process from the maxilla. The pars dorsalis on the premaxilla is prominent, often with a dorsal boss labially and a lacrimal notch laterodorsally. The lingual face of the premaxillary pars dorsalis is excavated by the suprapalatal pit, a cavity that typically is bounded on either or both sides by a vertical strut. The maxilla is further characterized by having a low, posteriorly tapered pars facialis that dorsally bears a triangular-shaped internasal process. Anteriorly the maxilla bears an elongate premaxillary lateral process and a lingually broad, shelf-like premaxillary dorsal process, both of which articulate with the premaxilla. Additional diagnostic features of the dentary include a row of external nutritive foramina labially along about the anterior one-half to two-thirds of the bone, an elongate scar ventrally for attachment of the intermandibularis muscle, and a foramen in the base of a pit on the underside of the symphysis. Lingually, the Meckelian canal is closed anteriorly, the subdental shelf is low, narrow, and gutter-like anteriorly, becoming deeper and narrower posteriorly, and there is

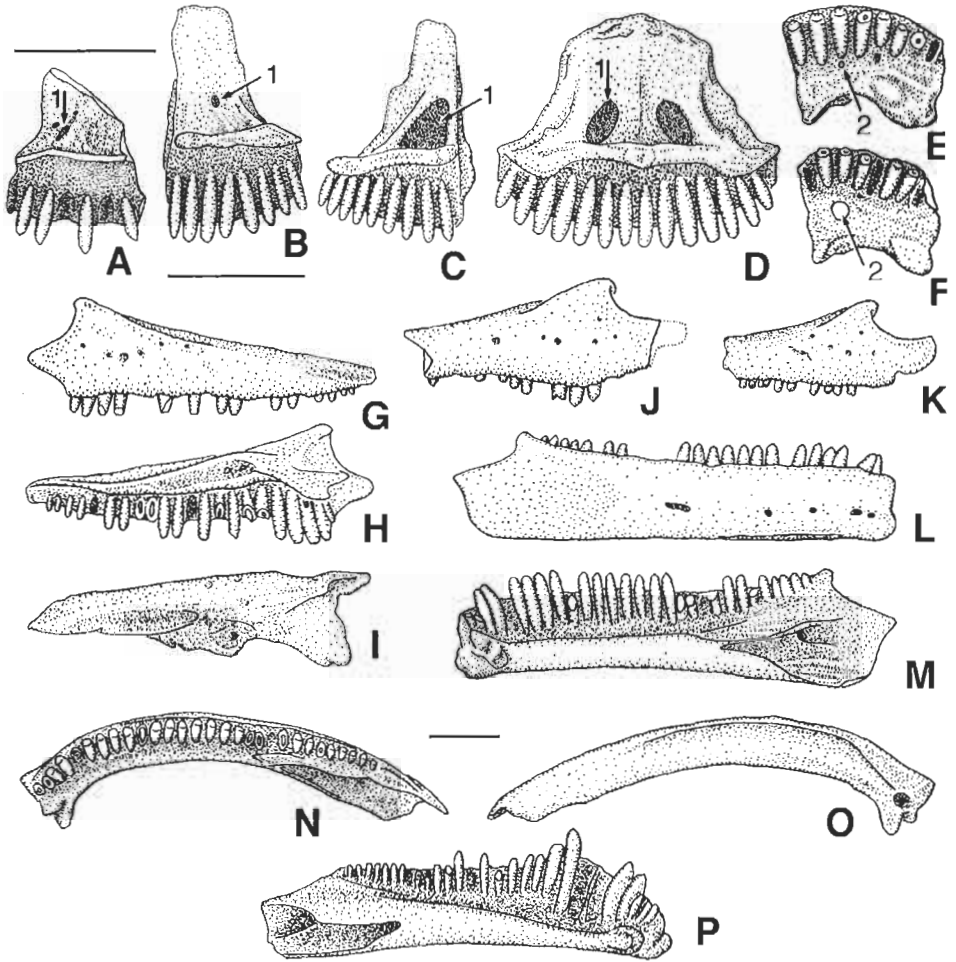


Fig. 3. Jaws of albanerpetontids. **A.** *Celtedens* sp. indet., DORCM GS34, incomplete left premaxilla lacking most of pars palatinum and dorsal part of pars dorsalis, lingual view. **B.** *Albanerpeton arthridion*, reconstructed right premaxilla based on FMNH PR805 (holotype) and FMNH PR2023, lingual view. **C.** *Albanerpeton galaktion*, reconstructed left premaxilla based on UALVP 16203 (holotype), 16204, and 16212, lingual view. **D, E.** *Albanerpeton nexuosus*, premaxillae: **D**, reconstructed fused premaxillae based on UALVP 16206 and 39955, lingual view; **E**, UALVP 39960, left premaxilla, occlusal view. **F.** *Albanerpeton galaktion*, UALVP 16212, left premaxilla, occlusal view. **G–I.** *Albanerpeton inexpectatum*, MNHN.LGA 1232, left maxilla, labial, lingual, and dorsal views. **J.** *Albanerpeton nexuosus*, UALVP 16242, incomplete right maxilla missing about posterior one-third of bone and crowns of anteriormost teeth, with outline of anterolateral premaxillary process (dotted line) from UALVP 16239, labial view. **K.** *Albanerpeton galaktion*, UALVP 16240, incomplete right maxilla missing about posterior one-third of bone and crowns of anteriormost teeth, labial view. **L–O.** *Albanerpeton inexpectatum*, MNHN.LGA 1249, nearly complete right dentary missing posteriormost end, labial, lingual, occlusal, and ventral views. **P.** *Albanerpeton nexuosus*, UCMP 49547 (holotype), nearly complete left dentary missing posterior end. Provenances for listed specimens: *Celtedens* sp. (**A**), Purbeck (Berriasian), England; *A. arthridion* (**B**), Antlers Formation (lower–middle Albian), Texas, USA; *A. galaktion* (**C, F, and K**) and UALVP specimens (**D, E, and J**) of *A. nexuosus*, Milk River Formation (lower Campanian), Alberta, Canada; holotype (**P**) of *A. nexuosus*, Lance Formation (upper Maastrichtian), Wyoming, USA; and *A. inexpectatum* (**G–I** and **L–O**) →

a broad area of attachment posteriorly for postdentary bones. One or two prominent symphyseal prongs project medially from the more posterior part of the symphysis. These articulate in a mortise and tenon fashion with complementary prongs from the opposite dentary to form a unique interlocking intermandibular joint (see Fox & Naylor 1982: fig. 4b–d). Symphyseal prongs are unique among gnathostomes to albanerpetontids and are unquestionably autapomorphic for the family (Milner 1988; Gardner unpublished data). The arrangement, attachment, and structure of the marginal teeth are also characteristic. Teeth are highly pleurodont in attachment – i.e., they are attached along most of the height of the pedicle to the inner wall of the jaw. Each tooth is relatively elongate, straight, and non-pedicellate. The base of each tooth is rarely perforated by a foramen and the pedicle is slightly compressed mesiodistally. The crown is chisel-like, labiolingually compressed, and bears three faint, mesio-distally aligned cusps. Such crowns are autapomorphic for the family, at least among other temnospondyls, whereas non-pedicely is convergent with various other lissamphibian taxa (Gardner unpublished data).

Jaws are too poorly known for *Celtedens* to determine if these elements differ at the generic level for albanerpetontids or among species of *Celtedens*. I suspect that better jaw material would demonstrate at least species level differences, comparable to those documented below for *Albanerpeton*. Where known, jaws of *Celtedens* have a generalized albanerpetontid construction. Premaxillae of the indeterminate species from Purbeck primitively resemble those of *A. arthridion* in having a tiny suprapalatal pit located high on the lingual face of the pars dorsalis, well above the pars palatinum (Gardner 1999b; here: cf. Fig. 3A versus B).

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

L–O), middle and ?lower Miocene fissure fills, La Grive-St. Alban, France. Specimens in **B–D** redrawn from Gardner (1999c: fig. 2), **L–O** redrawn from Gardner & Averianov (1998: fig. 2), and **P** redrawn from Estes (1964: fig. 44c). Arrow 1 (**A–D**) points to suprapalatal pit and arrow 2 (**F, G**) points to palatal foramen, both in premaxilla. Broken surfaces are white. Scale bars = 1 mm: specimens in **A** and **B** have separate scale bars; bottom center scale bar is for other specimens.

I attach considerable importance to the suprapalatal pit (Fig. 3A–D: arrow 1). Fox & Naylor's (1982) suggestion that the suprapalatal pit held a gland is reasonable, considering the position of the pit in the lingual face of the premaxillary pars dorsalis and its associated foramina. Although the identity of such a gland is unknown, it presumably functioned in olfaction, feeding, or both. The suprapalatal pit is intimately associated with the palatal foramen (Fig. 3E, F: arrow 2), a typically small foramen that extends dorsally through the pars palatinum to open beneath, or in the floor of, the suprapalatal pit, regardless of the position of the pit mediolaterally across the pars dorsalis. Assuming that the suprapalatal pit held a gland, the palatal foramen likely carried a duct between the gland and the roof of the mouth. Differences in the size, shape, and position of the suprapalatal pit are pronounced among species of *Albanerpeton*, and it is tempting to speculate that these modifications were reflected in life by variation in the form and function of the presumed gland.

Neither the maxilla nor dentary, where adequately known, are diagnostic for *Albanerpeton* or *Celtdens*. None of the dentary characters that Nessov (1981) believed were taxonomically useful at the generic level for albanerpetontids seem appropriate for this purpose (Gardner & Averianov 1998). Taxonomically useful variation is, however, evident at the specific level in *Albanerpeton* in the following (Fig. 3G–P): proportions and outline of the premaxillary lateral process on the maxilla; presence of a dorsal process immediately behind the tooth row on the dentary; presence of labial ornament on both jaws in large individuals; and labial outline of the ventral edge of the pars dentalis on the maxilla and of the dorsal edge of the dental parapet on the dentary. The last character is linked with size heterodonty of the teeth (see below).

Two tooth characters differ among species of *Albanerpeton*. Teeth located about one-third of the distance posteriorly along the tooth row on the maxilla and dentary are usually only slightly longer than the more anterior and posterior teeth, but in *A. nexuosus* Estes, 1981 (Fig. 3J, P) teeth about one-third of the distance along the row are relatively longer and, occasionally, more robust than adjacent teeth. Although not evident in Fig. 3, the position of the anterior end of maxillary tooth row also varies: the anterior end of the tooth row is approximately in line with the leading edge of the nasal process in *A. inexpectatum* and two new North American species (middle Campanian and Paleocene), but extends several loci more anteriorward in other congeners. Spacing of teeth and crown structure do not vary reliably among species of *Albanerpeton*, but undescribed jaws from Europe and North Africa suggest that this may not be true for some other albanerpetontid taxa.

Other characters and elements. — The only other character that I have identified as being taxonomically important within the Albanerpetontidae is maximum head–body length (i.e., length of head plus body). This straightline value can be measured or estimated directly from skeletons or calculated from the midline length of frontals (Gardner 1999b). Head–body length is informative at the species level in *Albanerpeton*, where estimated maximum values range from about 30 to over 60 mm, depending on the species (Gardner 1999b). This value does not appear to vary significantly among species of *Celtdens*. The anteriormost three vertebrae in albanerpetontids are highly modified in a unique manner (see familial diagnosis, below). Too few examples of these and more posterior vertebrae are available to determine if vertebral structure varies significantly among genera and species.

Systematic paleontology

Subclass Lissamphibia Haeckel, 1866

Order Allocaudata Fox & Naylor, 1982

Family Albanerpetontidae Fox & Naylor, 1982

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

Remarks. — The above diagnosis is derived from my unpublished phylogenetic analysis of the relationships of albanerpetontids. This is the first diagnosis for the clade that is differential and explicitly identifies polarities of character states (cf. Fox & Naylor 1982; McGowan 1998).

Two other albanerpetontid genera have been named. The two species of *Nukusurus* Nesson, 1981 (Cenomanian and Coniacian, Uzbekistan) are each named on a dentary, neither of which is diagnostic below the familial level. Hence, the names *Nukusurus*, *N. insuetus* Nesson, 1981, and *N. sodalis* Nesson, 1997 are *nomina dubia* within the Albanerpetontidae (Gardner & Averianov 1998). The name *Bishara* Nesson, 1997 (Santonian or Campanian, Kazakhstan) denotes an indeterminate caudate taxon, not an albanerpetontid, because the holotype of the type and only species, *B. backa* Nesson, 1997, is an atlantal centrum from an indeterminate salamander (Gardner & Averianov 1998). The first Gondwanan albanerpetontids were recently reported by Sigogneau-Russell *et al.* (1998) from the basal Cretaceous (Berriasian) of Morocco.

Albanerpeton Estes & Hoffstetter, 1976

Figs 1, 3B–P.

Type species: *Albanerpeton inexpectatum* Estes & Hoffstetter, 1976, middle and ?lower Miocene, France.

Other species: *A. arthridion* Fox & Naylor, 1982, uppermost Aptian/lowermost Albian–middle Albian, Texas and Oklahoma, USA; *A. galaktion* Fox & Naylor, 1982 and *A. nexuosus* Estes, 1981, both Campanian and Maastrichtian, North American Western Interior; and three unnamed species, one each from the upper Turonian of Utah, USA, middle Campanian of the North American Western Interior, and upper Paleocene of Alberta, Canada.

Distribution. — Uppermost Aptian/lowermost Albian–upper Paleocene, North American Western Interior; and middle and ?lower Miocene, France.

Diagnosis (revised from McGowan 1998; Gardner 1999a). — Genus of albanerpetontid differing from *Celtedens* in having fused frontals more derived in being triangular-shaped in outline and more primitive in retaining anteriorly pointed internasal process. Differs further from *Celtedens* in another six frontal character states of uncertain polarities: ratio of midline length to width across posterior edge between lateral edges of ventrolateral crests about 1.2 or less; lateral face of internasal process indented by anteroposteriorly elongate groove for tongue-in-groove contact with medial edge of nasal; anterolateral process prominent and pointed distally; dorsal and ventral edges of slot for receipt of prefrontal excavated medially; anterior end of orbital margin located approximately in line with, or posterior to, anteroposterior midpoint of frontals; and orbital margin uniformly shallowly concave to nearly straight along entire length in dorsal or ventral outline.

Remarks. — I recently presented revised diagnoses and redescrptions for *Albanerpeton inexpectatum* (Gardner 1999a) and *A. arthridion* (Gardner 1999b). The new late Turonian species is named in a forthcoming paper (Gardner 1999c). Descriptions of the unnamed middle Campanian and late Paleocene species and redescrptions of *A. nexuosus* and *A. galaktion* are in preparation. I (Gardner 1999c: fig. 2) also presented a simplified version of my hypothesis of relationships within the genus. *A. arthridion* is the basalmost species and the sister to a less inclusive clade comprised of two sister-clades: the so-called gracile-snouted clade of *A. galaktion* and the late Turonian and middle Campanian species and the so-called robust-snouted clade of *A. nexuosus*, *A. inexpectatum*, and the late Paleocene species. Details of this phylogeny will be published elsewhere.

***Celtedens* McGowan & Evans, 1995**

Figs 2, 3A.

Type species: *Celtedens megacephalus* (Costa, 1864), lower Albian, Italy.

Other species: *C. ibericus* McGowan & Evans, 1995, upper Barremian, Spain.

Distribution. — Kimmeridgian (see Remarks below)—lower Albian, Europe.

Diagnosis (revised from McGowan 1998). — Genus of albanerpetontid differing from *Albanerpeton* in having fused frontals more derived in bearing bulbous-shaped internasal process and more primitive in retaining hourglass- or bell-shaped outline. Differs further from *Albanerpeton* in another six frontal character states of uncertain polarities: ratio of midline length to width across posterior edge between lateral edges of ventrolateral crests greater than about 1.2; internasal process ventrolaterally has facet for dorsally overlapping medial edge of nasal; anterolateral process a poorly differentiated, broadly rounded shoulder; dorsal and ventral edges of slot for receipt of prefrontal not excavated medially; anterior end of orbital margin located anterior to

anteroposterior midpoint of frontals; and orbital margin deeply concave in dorsal or ventral outline, occasionally deflected posterolaterally near posterior end.

Remarks. — Neither of the named species of *Celtedens* is well documented. *C. megacephalus* is known by the holotype skeleton from near Pietraroia (lower Albian), Italy. This skeleton is poorly preserved and, consequently, difficult to interpret (Estes 1981; Gardner in press). McGowan & Evans (1995) briefly reported on two articulated skeletons of *C. ibericus*, one of which preserves details of the soft tissue, both from Las Hoyas (upper Barremian), Spain. McGowan's (1994) more detailed interpretations of all three skeletons remain unpublished, although he (McGowan 1998) presented revised diagnoses for both species and a controversial cranial reconstruction (see Gardner in press) for *C. ibericus*. *Celtedens* is reliably known by frontals from another three localities: Uña (Barremian, Spain), Purbeck (Berriasian, England), and Guimarota (Kimmeridgian, Portugal) (McGowan & Ensom 1997; McGowan 1998). McGowan (1998) implied that frontals from Uña and Guimarota may pertain to previously unrecognized species. McGowan (1998: p. 192) also reported *Celtedens* at Galve (Barremian), Spain, but did not figure examples of the frontals. Reports of *Celtedens* from the Middle Jurassic (upper Bathonian) of England (McGowan 1996, 1998) are incorrect (see account below); this raises the earliest occurrence of the genus to the Kimmeridgian.

Genus and species indeterminate

Fig. 4.

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

Celtedens cf. *megacephalus* (Costa); McGowan & Ensom 1997: p. 117; McGowan 1998: fig. 1G.

Celtedens ibericus McGowan & Evans; McGowan 1998: fig. 4.

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

Horizon and locality: Middle Jurassic (upper Bathonian) Forest Marble Formation, Kirtlington Cement Quarry, Oxfordshire, southcentral England.

Remarks. — The Kirtlington Cement Quarry is one of four localities in the Forest Marble Formation to have produced albanerpetontid elements (Evans 1992; Evans & Milner 1994). Fossils from the formation are the second oldest record (late Bathonian) for the family, after an atlantal centrum reported by Seiffert (1969) from Gardies (early Bathonian in age; Kriwet *et al.* 1997), France. McGowan (1996) described a modest collection of albanerpetontid skull and postcranial elements from Kirtlington and referred the specimens to *Celtedens* on the strength of an incomplete frontal (UCK 26; Fig. 4A). While this specimen more closely resembled frontals of *Celtedens* than *Albanerpeton* in the apparent hourglass shape of the bone (the inferred primitive albanerpetontid state) and the outline of the orbital margin, it is important to emphasize that none of the frontals from Kirtlington available to McGowan at the time of his study preserved the diagnostic internasal process. Such a specimen is now available: BMNH R.14158 (Fig. 4B, C) consists of about the anterior one-third of a pair of fused frontals, broken posteriorly between the slots for receipt of the prefrontals. As there is no evidence from other specimens that more than one albanerpetontid taxon is represented at Kirtlington, BMNH R.14158 and UCK 26 evidently pertain to the same species. Whereas the poorly differentiated anterolateral processes on BMNH R.14158

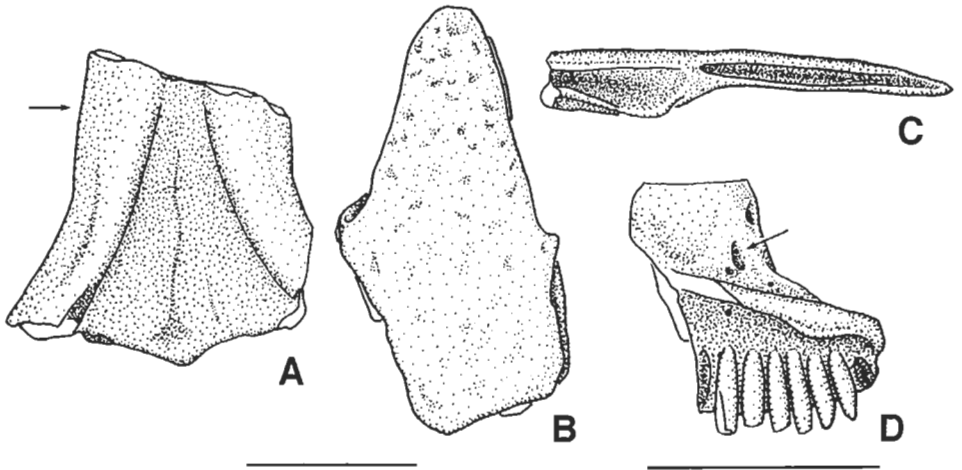


Fig. 4. Frontals and jaws of *Albanerpetontidae* gen. et sp. indet.; Middle Jurassic (upper Bathonian) Forest Marble Formation, Kirtlington Cement Quarry, England. **A**, UCK 26, posterior two-thirds of fused frontals missing posterior end of both ventrolateral crests, ventral view, with arrow indicating anterior limit of orbital margin. **B**, **C**, BMNH R.14158, anterior one-third of fused frontals, dorsal and right lateral views. **D**, UCK 15, incomplete right premaxilla, lacking dorsal end of pars dorsalis and medial parts of pars palatinum and pars dentalis, lingual view, with arrow indicating suprapalatal pit. Broken surfaces are white. Scale bars = 1 mm: left scale bar is for frontals (**A–C**) and right scale bar is for premaxilla (**D**).

also recall the condition in *Celtedens*, the internasal process instead resembles that of *Albanerpeton* in being triangular in outline (the inferred primitive albanerpetontid state) and in having an elongate groove along the lateral face for articulation with the nasal. Premaxillae from Kirtlington (Fig. 4D) are also distinctive in having the suprapalatal pit located more laterally within the external narial margin and facing laterolingually. By contrast, the suprapalatal pit lies more medially in the lingual face of the pars dorsalis and opens lingually in *Celtedens* and *Albanerpeton*. This mixture of frontal and premaxillary character states precludes the Kirtlington albanerpetontid from membership in either of the two currently recognized genera.

Conclusions

- Frontals are diagnostic for *Albanerpeton*, *Celtedens*, and species of *Celtedens*, as previous authors have suggested. The relative diagnostic value of frontals in these cases may be inflated, because no other elements are as well known for *Celtedens*. In particular, I suspect that better jaw specimens would also show specific level differences within *Celtedens*. This is the case in *Albanerpeton*, where the premaxilla is the most taxonomically informative element for species. Characters of the maxilla, dentary, and frontals and inferred head–body size are also useful for diagnosing species of *Albanerpeton*.
- I provide revised, differential diagnoses for the *Albanerpetontidae*, *Albanerpeton*, and *Celtedens*. These are the first diagnoses for the taxa in which the inferred polarities of character states are explicitly stated. One frontal autapomorphy is identified

for each genus: the fused frontals are triangular in *Albanerpeton* and the internasal process is bulbous in *Celteledens*.

- A Middle Jurassic albanerpetontid from Kirtlington cannot be assigned to *Celteledens* or *Albanerpeton*, because the taxon in question has frontal character states of both genera and premaxillary character states not seen in either genus. This combination of character states, especially the lack of obvious generic level apomorphies, is not surprising considering that the Kirtlington albanerpetontid predates by some 15 and 50 million years (Gradstein *et al.* 1995) the oldest unequivocal occurrences of, respectively, *Celteledens* in the Kimmeridgian of Portugal and *Albanerpeton* in the uppermost Aptian/lowermost Albian of Oklahoma, USA.

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Rewizja taksonomiczna płazów z rodziny Albanerpetodontidae

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Streszczenie

Rodzaje albanerpetodontów klasyfikowano na podstawie cech morfologicznych szczęk i kości czołowych, ale rzadko zastanawiano się nad przydatnością taksonomiczną tych cech. Budowa kości czołowych jest diagnostyczna dla rodzajów *Albanerpeton* i *Celtedens* oraz gatunków w obrębie tego ostatniego (zwłaszcza, że brak jest danych na temat zróżnicowania morfologii szczęk w obrębie tego rodzaju). W obrębie rodzaju *Albanerpeton* gatunki wyróżniają się cechami kości czołowych i szczęk oraz rozmiarami ciała. Podano diagnozy różnicujące dla obu rodzajów opisanych na podstawie powyższych cech, obejmujące także morfologię kręgow. Każdy z rodzajów odznacza się jedną autapomorfią: *Albanerpeton* – trójkątnymi zrosniętymi kośćmi czołowymi, a *Celtedens* – pękatym wyrostkiem międzynosowym tych kości. Zagadkowy albanerpetodont ze środkowej jury (baton) Anglii ma mieszane cechy, nie pozwalające zaliczyć go do wyżej wymienionych. Oznacza to, że *Celtedens* znany jest od późnej jury (kimeryd) a *Albanerpeton* – od wczesnej kredy (apt/alb).