New albanerpetontid amphibians from the Early Cretaceous of Morocco and Middle Jurassic of England

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A third albanerpetontid genus, *Anoualerpeton* gen. nov., is erected for two new species: *An. unicus* sp. nov. (type species) from the Early Cretaceous (Berriasian) of Morocco and *An. priscus* sp. nov. from the Middle Jurassic (late Bathonian) of England. *Anoualerpeton* differs from the exclusively Laurasian albanerpetontid genera *Albanerpeton* (Early Cretaceous–Paleocene, North America; Miocene, Europe) and *Celtedens* (?Late Jurassic and Early Cretaceous, Europe) in a unique combination of primitive and derived character states of the jaws and azygous frontals. Monophyly of *Anoualerpeton* is supported by two synapomorphies of the maxilla and dentary (occlusal margin convex in labial outline and teeth strongly heterodont in size anteriorly) that are convergent with an unrelated, relatively derived Late Cretaceous species of *Albanerpeton* from North America. The two species of *Anoualerpeton* differ in character states of the premaxilla and azygous frontals. Cladistic analysis of 20 characters scored for ten albanerpetontid taxa postulates *Anoualerpeton* as the sister-taxon of *Albanerpeton* + *Celtedens*. The sister-pair of *Albanerpeton* + *Celtedens* is founded on one or, perhaps, two premaxillary synapomorphies. *Anoualerpeton unicus* documents the only known Gondwanan occurrence for the Albanerpetontidae and provides a minimum age of basal Cretaceous for the establishment of the clade in Africa. Characters of the mandible, vertebrae, and limbs support the interpretation that *Ramonellus* (Aptian; Israel) is a caudate, not an albanerpetontid.

Key words: Albanerpetontidae, Cretaceous, England, Jurassic, Lissamphibia, Morocco, *Ramonellus*.

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Introduction

The Albanerpetontidae Fox and Naylor, 1982 are a clade of salamander-like, Middle Jurassic–Miocene lissamphibians that are characterized by such features as non-pedicellate and chisel-like teeth, a mortise-and-tenon style intermandibular joint, azygous frontals, and specialized first three vertebrae that convergently resemble the atlas-axis complex of mammals (Fox and Naylor 1982; McGowan and Evans 1995; Gardner 2001). Two genera containing nine species are currently recognized (Gardner 2000a, 2002). The type genus *Albanerpeton* Estes and Hoffstetter, 1976 includes one species from the Miocene of Western Europe and six species from the Early Cretaceous–Paleocene of the North American Western Interior (Estes and Hoffstetter 1976; Estes 1981; Fox and Naylor 1982; Sanchíz 1998; Böhme 1999; Gardner 1999a–d, 2000a, b, 2002; Wiechmann 2001). *Celtedens* McGowan and Evans, 1995 is an exclusively European genus that contains two named Early Cretaceous species and may extend back to the Late Jurassic (McGowan and Evans 1995; McGowan and Ensom 1997; McGowan 1998a, 2002; Gardner 2000a; Evans and McGowan 2002). Additional

genera and species may be represented in collections of albanerpetontid material from the Upper Jurassic of Portugal and Lower Cretaceous of Spain that are being studied by M.F. Wiechmann (see Wiechmann 2000). Two genera and three species of albanerpetontids also have been reported from the Late Cretaceous of Asia (Nessov 1981, 1988, 1997); however, Gardner and Averianov (1998) argued that the generic name *Nukusurus* Nessov, 1981 and the names of its two species, both of which are from Uzbekistan, are *nomina dubia* within the Albanerpetontidae and that the generic name *Bishara* Nessov, 1997 (one species, Kazakhstan) pertains to an indeterminate caudate, not an albanerpetontid.

Here we report on elements and new taxa of albanerpetontids from the Lower Cretaceous (Berriasian) Anoual locality in Morocco and the Middle Jurassic (late Bathonian) Kirtlington Cement Quarry in England. Both localities are non-marine microvertebrate deposits that have produced significant collections of vertebrate fossils (see reviews by Evans and Milner 1994; Sigogneau-Russell et al. 1998), including isolated and rare articulated skull and postcranial bones of albanerpetontids. Anoual has yielded a modest-sized collection of albanerpetontid bones that represents the only

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Gondwanan occurrence for the clade. The first mention of albanerpetontid material at Anoual was by Broschinski and Sigogneau-Russell (1996: 149) in a descriptive paper devoted to lizards from the locality. In a subsequent review paper on the Anoual assemblage, Sigogneau-Russell et al. (1998) noted the occurrence of albanerpetontids and commented that the material seemed more similar to *Celtedens* than *Albanerpeton*. Compared to Anoual, Kirtlington has produced over three times as many albanerpetontid bones. These specimens are one of the oldest records for the clade and constitute the largest series of albanerpetontid fossils from any Middle Jurassic locality. Albanerpetontid fossils from Kirtlington initially were attributed to *Albanerpeton* (Evans and Milner 1991, 1994: 306; Evans 1992). McGowan (1996) briefly described a small number of albanerpetontid specimens from Kirtlington, and in a series of papers (McGowan 1996, 1998a, b, 2002; McGowan and Ensom 1997) attributed this material to *Celtedens*. McGowan's (1996) generic identification for the Kirtlington material relied on an incomplete frontal that lacked the diagnostically critical anterior end. More recently, one of us (Gardner 2000a) proposed that the Kirtlington albanerpetontid material could not be assigned to either *Albanerpeton* or *Celtedens*, because premaxillae and frontals from the locality exhibit a suite of features not seen in either genus.

Below we formally name two new albanerpetontid species—one each for specimens from Anoual and from Kirtlington—and erect a new Eurafrican genus to accommodate these species. Both species were informally recognized and included as terminal taxa in a recent cladistic analysis of *Albanerpeton* (Gardner 2002). In the second part of our paper we consider the phylogenetic and biogeographic implications of these new taxa.

Material and comparative specimens.—Our report focuses on jaws and frontals, because these are the most taxonomically and phylogenetically informative elements for albanerpetontids (Gardner 2000a). For comparison we examined the following albanerpetontid specimens and taxa: jaws and frontals listed by Gardner (1999a–c, 2000a, b) for the seven currently recognized species of *Albanerpeton*; all available skeletons for the two named species of *Celtedens* (see Estes 1981; McGowan and Evans 1995; McGowan 2002) and disarticulated jaws and frontals of *Celtedens* sp. from the Lower Cretaceous of England (McGowan and Ensom 1997; Evans and McGowan 2002); indeterminate jaws and frontals from various localities in the Cretaceous of North America (Gardner 1999b, c, 2000b), the Upper Cretaceous of Asia (Gardner and Averianov 1998), and the Middle Jurassic (Evans and Milner 1994) and Lower Cretaceous of Europe (Rees and Evans 2002; Evans et al., unpublished observation); and some of the undescribed frontals currently being studied by M.F. Wiechmann (see Wiechmann 2000) from the Upper Jurassic (Kimmeridgian) of Guimarota, Portugal, and the Lower Cretaceous (Barremian) of Uńa, Spain.

Anatomical conventions and abbreviations.—Tooth counts for jaws include all positions (i.e., *in situ* teeth + empty tooth slots). Osteological measurements and terms follow Gardner and Averianov (1998) and Gardner (1999a, 2000a).

Institutional abbreviations.—BMNH, Natural History Museum, London, England; MNHN.MCM, collection from Anoual in the Muséum National d'Histoire Naturelle, Paris, France; and UCK, University College London, England.

Systematic palaeontology

Subclass Lissamphibia Haeckel, 1866
Order Allocaudata Fox and Naylor, 1982
Family Albanerpetontidae Fox and Naylor, 1982
Anoualerpeton gen. nov.

Type species: *Anoualerpeton unicus* sp. nov.

Other species: *Anoualerpeton priscus* sp. nov.

Etymology: *Anoual*, the type locality near the city of Anoual in Morocco + *erpeton*, Greek noun meaning "creeping [creature]", now used for amphibians and reptiles.

Distribution.—Middle Jurassic (late Bathonian), England, and Early Cretaceous (Berriasian), Morocco.

Diagnosis.—Genus of albanerpetontid having no recognized autapomorphies. Differs from *Celtedens* and most species of *Albanerpeton*, but convergently resembles *A. nexuosus* Estes 1964, in two maxillary and dentary synapomorphies: occlusal edge of bone convex occlusally in labial or lingual outline and teeth about one-third of distance from anterior end of tooth row markedly longer than nearby teeth. In addition to generic characters listed below, primitively differs from *A. nexuosus* in having premaxillae unfused, relatively more gracile in build, and more weakly sutured dorsally with nasals, with boss covering less than about one-third of premaxillary pars dorsalis and ornamented with irregular pits and ridges, with suprapalatal pit relatively smaller and opening higher on pars dorsalis, and with dorsal ridge on lingual edge of maxillary process lower and in having maxilla with premaxillary lateral process relatively longer. Primitively differs from *Celtedens* and *Albanerpeton* in having premaxilla with suprapalatal pit in pars dorsalis facing more laterally; from *Celtedens* and resembles *Albanerpeton* in having frontals with internasal process tapered anteriorly and lateral edge of process indented by anteroposteriorly elongate groove for tongue-in-groove contact with medial edge of nasal; from *Albanerpeton* and resembles *Celtedens* in having frontals relatively longer (midline length no less than about 1.2 times posterior width) and more nearly bell-shaped or rectangular in dorsal or ventral outline; and from *Albanerpeton* (condition not reliably known for *Celtedens*) in having premaxilla with canal between dorsal and ventral openings of palatal foramen extending dorsolaterally–ventromedially through pars palatinum.

Remarks.—*Anoualerpeton* differs from *Albanerpeton* and *Celtedens* in a unique combination of eight character states. Chief among these are two linked characters that describe size

heterodonty of teeth and the profile of the occlusal margin on the maxilla and dentary. Marginal teeth in albanerpetontids are highly pleurodont—i.e., teeth are attached along about the basal one-half or more of their labial surface to the inner wall of the jaw. As tooth lengths vary along the jaw, so must the depth of the pars dentalis on the maxilla and the height of the dental parapet on the dentary to ensure that the teeth remain adequately braced labially (Gardner 2002). Teeth in most albanerpetontids are moderately heterodont in size along the maxillary and dentary row. The longest teeth occur about one-third of the distance from the anterior end of the tooth row, but are not substantially longer than nearby teeth in the same row. Concomitantly, the occlusal edge of the jaw is essentially straight in labial outline (see Gardner and Averianov 1998: fig. 2A, B). These two character states appear to be primitive for albanerpetontids, based on outgroup comparisons with other temnospondyls (Gardner 2002). Enlargement of teeth about one-third of the distance posteriorly (i.e., from anterior end) along the maxillary and dentary tooth rows and a more strongly convex occlusal margin, with the apex adjacent to the longest teeth, are derived character states within the Albanerpetontidae (Gardner 2002). These apomorphies occur in the two species of *Anoualerpeton*, in the North American Campanian and Maastrichtian *Albanerpeton nexuosus* (Estes 1964: figs. 43e, 44c; Gardner 2000b: figs. 2D, 3A), and in an indeterminate dentary from the Albian–Cenomanian boundary in Utah, USA (Gardner 1999c: fig. 3D, E). The nested sets of synapomorphies that place *A. nexuosus* crownward within *Albanerpeton* (Gardner 2000b, 2002; this study) argue against a close relationship with *Anoualerpeton* and, instead, imply that strongly heterodont teeth and a convex occlusal margin on the maxilla and dentary developed convergently in *A. nexuosus* and *Anoualerpeton*. In this context it is worth noting that both conditions tend to be more pronounced in *A. nexuosus*, although we have not been able to quantify these differences. In some dentaries and maxillae of *A. nexuosus* the enlarged teeth appear relatively larger or more massive and the occlusal edge of the bone is more strongly convex in labial or lingual outline; in extreme cases the occlusal edge of the dentary assumes a more nearly angular profile, with an obtuse-angled apex.

Stratigraphical distributions of character states among albanerpetontids and, where informative, outgroup comparisons with other temnospondyls imply that the remaining character states that are diagnostic at the generic level for *Anoualerpeton* are primitive for albanerpetontids, as follows: (1) suprapalatal pit in premaxilla opens laterolingually (*versus* opens lingually in *Celtedens* and *Albanerpeton*); (2) canal between dorsal and ventral openings of palatal foramen in premaxilla extends dorsolaterally–ventromedially (*versus* vertically in *Albanerpeton*; condition unknown in *Celtedens*); (3) internasal process on frontals tapered anteriorly (shared with *Albanerpeton*; *versus* bulbous in outline in *Celtedens*); (4) internasal process has lateral groove for tongue-in-groove contact with nasal (shared with *Albanerpeton*; *versus* groove absent and, instead, lateral margin of

process dorsally overlaps medial edge of nasal in *Celtedens*); (5) fused frontals relatively elongate, with midline length no less than about 1.2 times posterior width (shared with *Celtedens*; *versus* midline length no more than about 1.2 times posterior width in *Albanerpeton*); and (6) fused frontals more nearly bell-shaped or rectangular in dorsal or ventral outline (shared with *Celtedens*; *versus* triangular in *Albanerpeton*).

Albanerpetontid specimens at Anoual consistently differ from those at Kirtlington in two premaxillary and three frontal characters. This suite of differences, along with the considerable temporal and geographical gaps between the Anoual and Kirtlington localities, support our interpretation that specimens from each locality pertain to a different species of *Anoualerpeton*. For the species from Anoual, outgroup comparisons suggest the taxon exhibits the derived state for one character describing the form of the paired anterolateral processes on the frontals, while stratigraphical distributions of character states within the Albanerpetontidae suggest the species also exhibits the derived states for two premaxillary characters describing the positions of the suprapalatal pit and the dorsal opening of the palatal foramen. For the species from Kirtlington, outgroup comparisons suggest the taxon exhibits the derived state for one character describing the form of the internasal process on the frontals, while both outgroup comparisons and stratigraphical distributions of character states within the Albanerpetontidae suggest the taxon exhibits the derived state for one character describing the form of the ventrolateral crests.

Anoualerpeton unicus sp. nov.
Figs. 1, 2.

Anoual species; Gardner 2002: 12.
Anoual albanerpetontid; Gardner 2002: 14.

Etymology: *Unicus*, Latin "alone" or "solitary", referring to this being the only known albanerpetontid species from Gondwana.

Holotype: MNHN.MCM 187, right premaxilla missing most of pars palatinum and lateralmost part of pars dentalis, with preserved tooth row containing three broken teeth and five tooth slots (Figs. 1A, 2A).

Holotype locality, horizon, and age: Anoual microvertebrate locality, about 100 km east of the city of Anoual and near a fort called Ksar Met Lili, Talsinnt Province, eastern High Atlas Mountains, east-central Morocco (Sigogneau-Russell et al. 1998: fig. 1); unnamed non-marine limestone lens, Couches Rouges ("red beds") sandstone. The fossiliferous lens occurs within marine beds in the upper part of the Couches Rouges sandstone (Sigogneau-Russell et al. 1990) and is interpreted as having been deposited in a deltaic setting (Sigogneau-Russell et al. 1998). Nanofossils support an Early Cretaceous age, probably Berriasian, for the lens (Sigogneau-Russell et al. 1990; Duffin and Sigogneau-Russell 1993). See Sigogneau-Russell et al. (1998) and Evans and Sigogneau-Russell (2001) for additional information.

Referred specimens.—Premaxillae (n = 4): MNHN.MCM 188, 198–200; maxillae (n = 5): MNHN.MCM 13, 189, 201–203; dentaries (n = 34): MNHN.MCM 4, 5, 19–34, 41–48, 192–197, 204, 205; frontals (n = 3): MNHN.MCM 11, 190, 191; parietal (n = 1): MNHN.MCM 12; articular (n = 1): MNHN.MCM 6; humerus (n = 4): MNHN.MCM 7, 14–16;

trunk vertebrae (n = 15): MNHN.MCM 8, 9, 35–40, 49–55; and caudal vertebrae (n = 3): MNHN.MCM 10, 17, 18.

Distribution.—Known only from the holotype locality.

Diagnosis.—Species of *Anoualerpeton* differing from Middle Jurassic congener described below as follows: suprapalatal pit located more medially in pars dorsalis of premaxilla, just medial to margin for external narial opening and in line with fourth or fifth locus from medial end of tooth row; dorsal opening of palatal foramen in premaxilla below or within base of suprapalatal pit; internasal process on frontals relatively shorter (midline length subequal to width across base) and pointed distally; anterolateral processes on frontals pointed distally and distinct from main body of bone; and ventrolateral crests on frontals convex ventrally to bevelled in transverse view.

Description.—None of the 71 catalogued specimens at hand is complete, but the available jaws and frontals document most of the structure of these elements. Because the specimens are small and fragile, in some cases we have left cemented matrix attached to the bone rather than risk irreparable damage by attempting to remove it.

Premaxilla (Figs. 1A, B, 2A, B).—The two most nearly complete premaxillae are MNHN.MCM 187 (holotype) and 188. The holotype (Figs. 1A, 2A) is from the right side, is about 1.9 mm high, and retains an intact pars dorsalis, but lacks the more lingual part of the pars palatinum and the lateral end of the pars dentalis. MNHN.MCM 188 (Figs. 1B, 2B) is from the left side, is about 1.7 mm high, and lacks the lateral end of the pars dentalis, dorsolateral part of the pars dorsalis, and the lateral and medial parts of the pars palatinum. The former specimen is more robust than the latter and is from a slightly larger individual. The remaining premaxillae are from comparable-sized individuals, but preserve only the base of the pars dorsalis and varying amounts of the pars palatinum and pars dentalis.

The medial edge of each specimen bears elongate grooves and a flange, indicating that the premaxillae were sutured (i.e., paired) in life with their opposite. MNHN.MCM 187 and 188 show that the pars dorsalis is relatively short and broad, with the ratio of height:width across the suprapalatal pit about 1.4. On MNHN.MCM 187 the dorsal edge of the pars dorsalis bears weak suture marks for contact with the nasal and the process is indented laterally above the external narial margin by a narrow, shallow notch for receipt of the lacrimal. In labial aspect about the dorsal one-third of the pars dorsalis on MNHN.MCM 187 bears a low, indistinct boss that is ornamented with low, relatively broad ridges enclosing shallow, irregular pits. MNHN.MCM 188 preserves the medial edge of an evidently less prominent boss. All specimens show that the remainder of the labial face of the bone is relatively smooth and perforated by small, scattered external nutritive foramina. The lateral corner of the pars dentalis is indented by a smooth facet that, in life, was overlapped labially by a complementary process from the maxilla.

MNHN.MCM 187 and 188 are the most informative specimens for documenting the lingual structure of the pars

dorsalis. The suprapalatal pit (Fig. 1A$_2$, B$_2$) lies in the lateral half of the process, medial to the external narial margin and in line with the fourth or fifth tooth position from the medial end of the tooth row, and well dorsal to the pars palatinum. The pit is oval in outline, relatively small (i.e., occupies about two percent of lingual surface area of pars dorsalis), and opens laterolingually. To either side, the suprapalatal pit is bracketed by an indistinct internal strut. A few tiny, sediment-infilled lateral foramina perforate the pars dorsalis laterally, in the wall for the external narial opening. The remainder of the lingual surface of the pars dorsalis is smooth.

None of the five specimens retains an intact pars palatinum, but judging by preserved sections and broken surfaces the process was a lingually broad, horizontal shelf as in other albanerpetontids. MNHN.MCM 188 medially preserves the base of the lingually projecting vomerine process. MNHN.MCM 187, 188, and 198 are useful for documenting and interpreting the openings associated with the pars palatinum. The first two specimens have two tiny foramina that open dorsally in the junction between the pars palatinum and pars dorsalis, in the vicinity of the suprapalatal pit. The larger and more dorsolabial of these two foramina opens just below the suprapalatal pit in MNHN.MCM 187 (Fig. 1A$_2$), but more dorsally within the ventral margin of the pit in MNHN.MCM 188 (Fig. 1B$_2$). We interpret this foramen as the dorsal opening of the palatal foramen, because in other albanerpetontid taxa, including the Jurassic species described below, the dorsal opening of the palatal foramen is consistently present and closely associated with the ventral margin of the suprapalatal pit (Gardner 2000a). In life the suprapalatal pit probably housed a gland (Fox and Naylor 1982) and the palatal foramen may have carried a duct from the gland into the roof of the mouth (Gardner 2000a). The inferred ventral opening of the palatal foramen lies in the junction between the pars palatinum and pars dentalis in MNHN.MCM 187 (Fig. 1A$_2$) and, although not visible in figures published here, slightly more lingually in the ventral face of the pars palatinum in MNHN.MCM 188; these positions are consistent with the pattern in other albanerpetontids. In both specimens the ventral opening of the palatal foramen is displaced medially relative to the dorsal opening of the foramen. Although the palatal foramen is plugged with matrix in both specimens, the relative positions of the dorsal and ventral openings imply that the canal connecting the two openings extends dorsolaterally–ventromedially through the pars palatinum. This canal is exposed in the broken surface of the pars palatinum on MNHN.MCM 198 (unfigured) and confirms that the canal extended obliquely through the shelf. As for the smaller and more lingual foramen (= "unknown foramen" in Fig. 1A$_2$, B$_2$) that opens in the dorsal surface of the pars palatinum, judging by the condition in other albanerpetontids this foramen likely communicates, via a canal extending obliquely through the pars palatinum, with a similarly small foramen that opens in the lingual face of the pars dentalis, medial to and slightly below the ventral opening of the palatal foramen. The function of this smaller foramen is
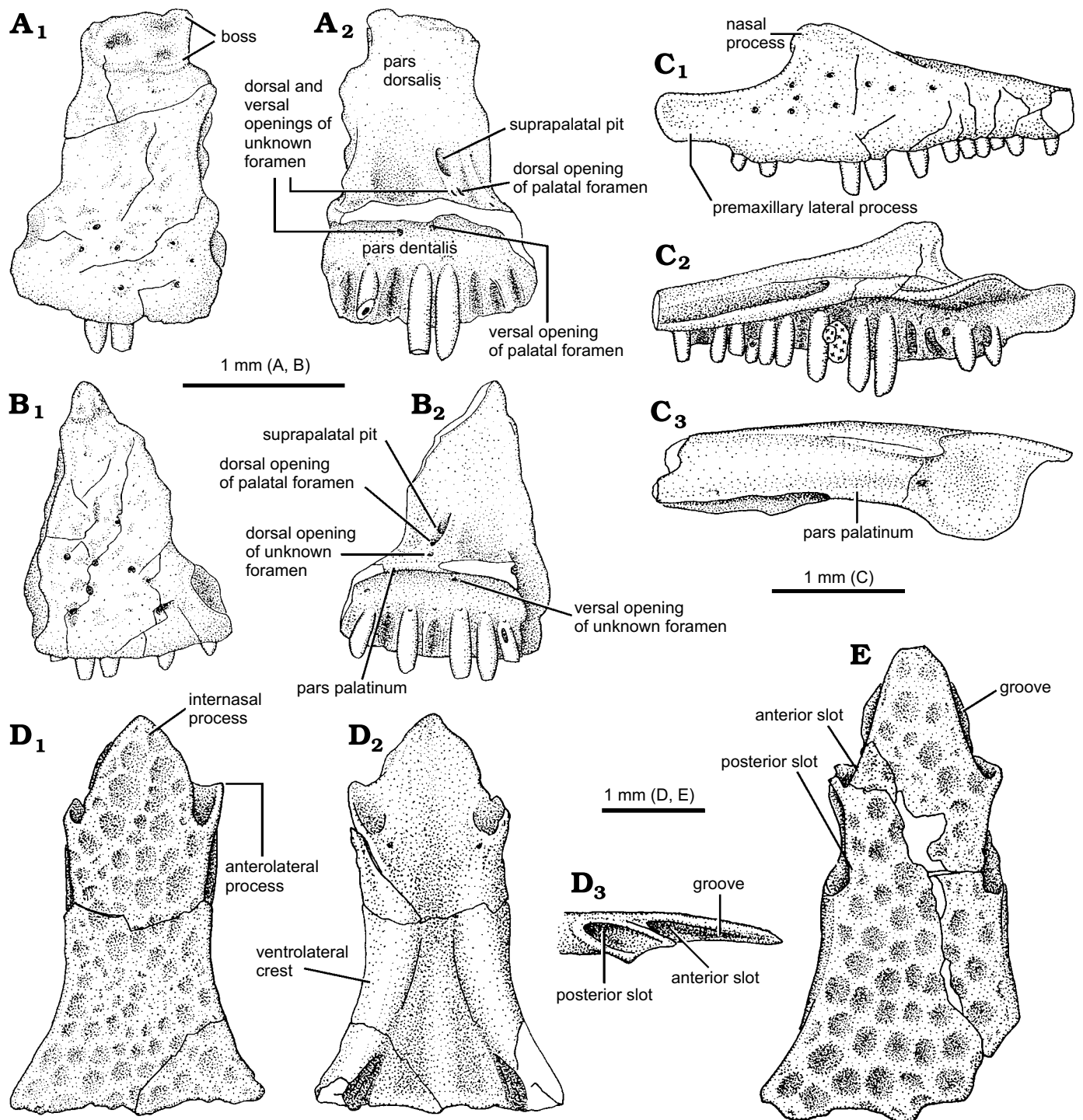
Fig. 1. Upper jaws and frontals of *Anoualerpeton unicus* sp. nov., type species; Lower Cretaceous (Berriasian), Anoual, Morocco. **A**, **B**. Premaxillae. **A**. MNHN.MCM 187, holotype, right premaxilla, lacking pars palatinum, in labial (A$_1$) and lingual (A$_2$) views. **B**. MNHN.MCM 188, left premaxilla, lacking dorsolateral part of pars dorsalis and vomerine and maxillary processes on pars palatinum, in labial (B$_1$) and lingual (B$_2$) views. **C**. MNHN.MCM 189, left maxilla, lacking about posterior one-fifth of bone, in labial (C$_1$), lingual (C$_2$), and dorsal (C$_3$) views. **D**, **E**. Fused frontals. **D**. MNHN.MCM 190, nearly complete frontals, lacking distal end of left anterolateral process and posterior end of ventrolateral crests on both sides, entire specimen in dorsal (D$_1$) and ventral (D$_2$) views and closeup of anterior part in right lateral view (D$_3$). **E**. MNHN.MCM 191, less nearly complete frontals, missing distal tip of internasal process, posterior end of left ventrolateral crest, and right posterolateral corner of bone and showing damage to median portion sustained during photography (cf., Fig. 2K), in dorsal view. White areas are broken surfaces and cross hatches are sand grains. Specimens at different scales.

unknown. The pars dentalis is deep. Tiny foramina pierce the lingual face of the pars dentalis above some tooth positions.

Maxilla (Figs. 1C, 2C).—The two best preserved maxillae collectively document all but the posteriormost end of the

bone. MNHN.MCM 189 (Figs. 1C, 2C) and 201 (unfigured) are broken well behind the internal narial margin and preserve about the anterior two-thirds to four-fifths of the bone. The former specimen is from the left side and has the first 17 loci, whereas the latter is from the right side and retains the first 14 loci. MNHN.MCM 189 is about 3.1 mm long and was probably about 4.5 mm long when the bone was intact; MNHN.MCM 201 is from a slightly smaller individual. Available specimens resemble other albanerpetontid maxillae as follows: pars facialis elongate and low, becoming shallower posteriorly; nasal process projects dorsally, triangular in outline, and bevelled posteriorly for articulation with lacrimal; premaxillary dorsal and lateral processes prominent, the former a lingually expanded shelf and the latter an anteriorly projecting flange; pars palatinum a lingually broad shelf, narrowing posteriorly, with lingual edge indented anteriorly by concave internal narial margin, and, more posteriorly, bearing shallow trough dorsolingually for articulation with unknown palatal bone(s); and pars dentalis deep, becoming shallower posteriorly. The labial face of the bone is smooth, except for tiny external nutritive foramina scattered across the more anterior part of the pars facialis. The premaxillary lateral process is relatively long (i.e., length greater than height at base) and blunt distally. Unlike many other albanerpetontid maxillae, including the Jurassic material described below, the dorsal surface of the pars palatinum adjacent to the nasal process lacks a saddle-shaped bony patch for contact with the base of the lacrimal. Also, the ventral surface of the premaxillary dorsal process lacks the transverse ridge that, in life, abutted against the lateral edge of the maxillary process on the premaxilla when the two bones were articulated. The occlusal edge of the pars dentalis is convex ventrally in labial or lingual outline. In MNHN.MCM 189 the pars dentalis is deepest adjacent to about the sixth locus. Tiny foramina are variably present in the lingual face of the pars dentalis above the teeth. The anterior end of the tooth row lies several loci anterior to the level of the leading edge of the nasal process.

Dentary (Fig. 2D–G).—A catalogued size series of 34 broken dentaries is available. The most nearly complete specimen, MNHN.MCM 204 (Fig. 2D), is a left dentary that is intact from the symphysis back to the level of the anterior margin of the opening for the Meckelian canal and bears 30 tooth positions with 25 teeth and five tooth slots. The specimen is about 3.6 mm long and would have been about one-third again as long when the bone was complete. In dentaries from Anoual the occlusal edge of the dental parapet is strongly convex dorsally in labial or lingual outline, with the apex labial to the eighth–tenth loci. This condition is most pronounced in larger specimens, such as MNHN.MCM 204 and MNHN.MCM 195 (Fig. 2D₁, E, respectively), but it also occurs in smaller specimens (e.g., MNHN.MCM 4 and 5; unfigured). In other respects, the structure of the dentary is typical for albanerpetontids. In dorsal aspect the bone is broadly curved. The labial face is smooth and a row of up to five or six external nutritive foramina extends along the anterior half of the bone. Below these foramina a low ridge is variably developed; this ridge marks the upper boundary of a shallow scar that extends anteroposteriorly along the lateroventral and ventral surfaces of the bone, for attachment of the intermandibularis musculature. A foramen opens in the underside of the symphysis. The symphyseal face is vertical anteriorly and posteriorly bears one or two symphyseal prongs that, in life, interlocked in a mortise-and-tenon fashion with one or two complementary prongs on the opposite dentary. In lingual aspect the dental parapet is moderately deep. The subdental shelf is moderately broad lingually, shallow, and gutter shaped anteriorly, and becomes deeper and narrower posteriorly. No dentary has the area for attachment of the postdentary bones intact, but several specimens, including MNHN.MCM 192 and 193 (Fig. 2F, G, respectively), preserve enough of this region to show that the opening for the Meckelian canal extends forward below about the posterior one-quarter to one-third of the tooth row and that the dorsal edge of the bone behind the tooth row was smooth and lacked a dorsal process.

Teeth (Figs. 1A–C₂; 2A–I).—Marginal teeth are characteristic for albanerpetontids in being highly pleurodont, nonpedicellate, straight, closely packed, and in having crowns that are labiolingually compressed and bear three mesiodistally-aligned cuspules. The structure of the tooth crowns is more variable than in species of *Albanerpeton*. Crowns on some teeth in *Anoualerpeton unicus* are decidedly chisel-like, with the central cuspule relatively low and the occlusal surface of the crown essentially convex in lingual outline; this pattern is typical for *Albanerpeton*. Some tooth crowns in *An. unicus* are more wedge-shaped in lingual or labial outline, with the central cuspule considerably longer than the mesial and distal cuspules (Fig. 2H, I). Similar variation in tooth crown structure also occurs in the Jurassic congener described below and in an indeterminate Early Cretaceous (Berriasian) *Celtedens* sp. from Purbeck, England (Evans and McGowan 2002: pl. 1: 9); in these European taxa the central cuspule on some teeth is even more elongate, result-

Fig. 2. Jaws and frontals of *Anoualerpeton unicus* sp. nov., type species; Lower Cretaceous (Berriasian), Anoual, Morocco. **A**, **B**. Premaxillae. **A**. MNHN.MCM 187, holotype, right premaxilla, lacking pars palatinum, in lingual (A₁) and laterolingual (A₂) views. **B**. MNHN.MCM 188, left premaxilla, lacking dorsolateral part of pars dorsalis and vomerine and maxillary processes on pars palatinum, in lingual (B₁) and laterolingual (B₂) and slightly dorsal views. **C**. MNHN.MCM 189, left maxilla, lacking about posterior one-fifth of bone, in lingual and slightly ventral view. **D–G**, dentaries. **D**. MNHN.MCM 204, left dentary, posteriorly incomplete ramus, broken at level of opening for Meckelian canal and preserving about anterior three-quarters of bone, in labial (D₁), lingual (D₂), and occlusal (D₃) views. **E**. MNHN.MCM 195, right dentary, posteriorly incomplete ramus preserving about anterior two-fifths of bone, in lingual view. **F**. MNHN.MCM 192, right dentary, anteriorly and posteriorly incomplete ramus preserving posterior part of tooth row and anterior part of area for attachment of postdentary bones, in lingual view. **G**. MNHN.MCM 193, left dentary, anteriorly and posteriorly
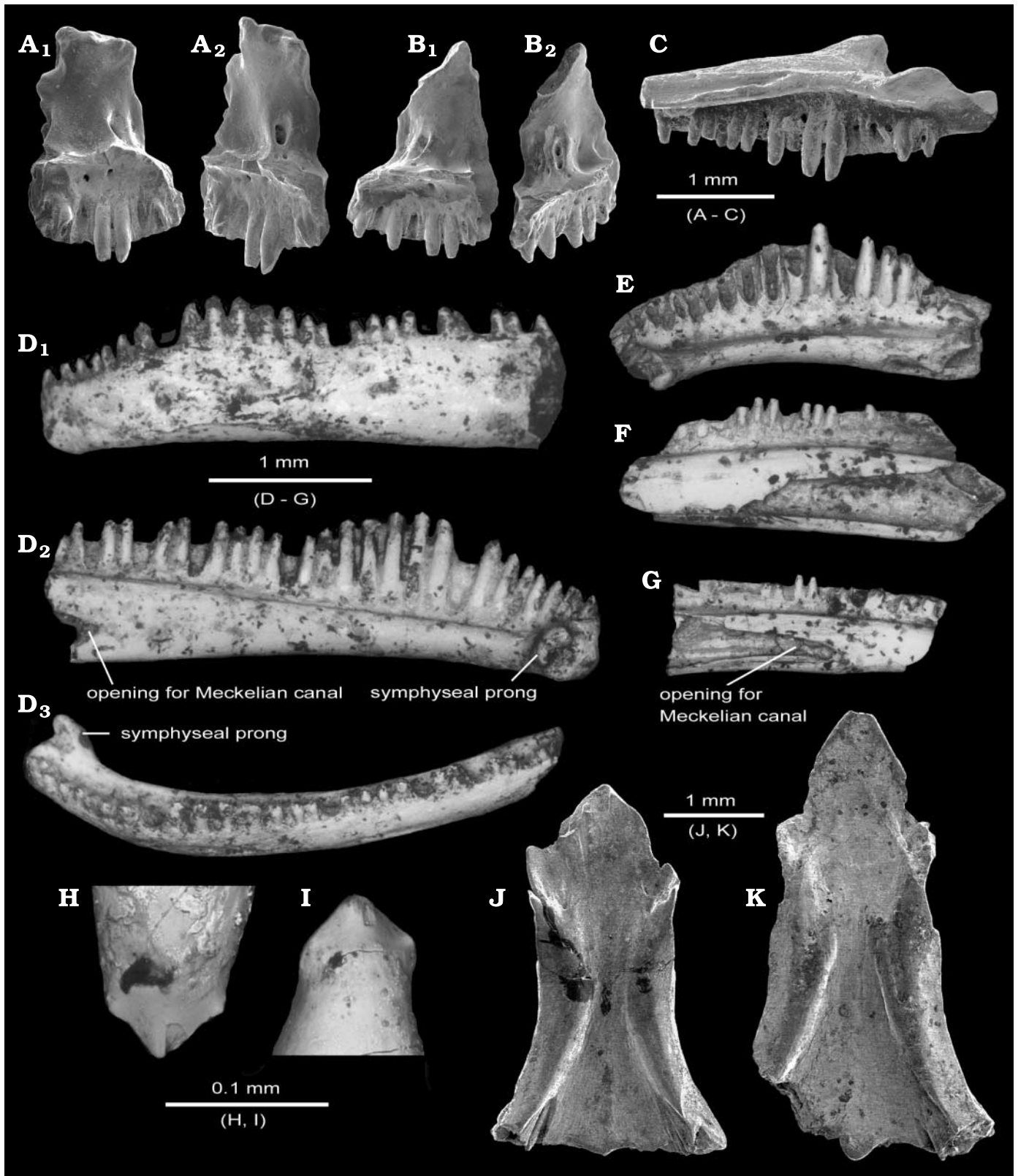
incomplete ramus preserving posterior part of tooth row and anterior part of area for attachment of postdentary bones, in lingual view. **H, I**. Close ups of tooth crowns, both in lingual view. **H**. MNHN.MCM 199, right premaxilla, crown of tooth at sixth locus from medial end of tooth row. **I**. MNHN.MCM 5, right dentary, crown of tooth at eighth locus from anterior end of tooth row. **J, K**. Fused frontals, both in ventral view. **J**. MNHN.MCM 190, nearly complete frontals, lacking distal end of left anterolateral process and posterior end of ventrolateral crests on both sides. **K**. MNHN.MCM 191, less nearly complete frontals, missing distal tip of internasal process, posterior end of left ventrolateral crest, and right posterolateral corner of bone, photographed before damage (cf., Fig 1E). Specimens at different scales.

ing in a more pointed crown. In jaws from Anoual the premaxillary teeth and the more anterior teeth on the maxilla and dentary tend to have wedge-shaped crowns, whereas teeth farther back tend to have more chisel-shaped crowns. Tooth counts are typical for albanerpetontids. MNHN.MCM 198 is the only premaxilla with an intact tooth row and preserves ten tooth positions. No maxilla or dentary preserves a complete tooth row, but specimens with anatomically overlapping sections of the row yield estimated, maximum counts of, respectively, 25 and 35 tooth positions. Most specimens preserve evidence of tooth replacement in the form of empty replacement slots and several, such as the maxilla MNHN. MCM 189 (Figs. 1C_2, 2C: anteriormost tooth), also have a lingual resorption pit in the base of one or more teeth. The dentary MNHN.MCM 34 (unfigured) preserves a non-functional, replacement tooth at the second locus. Teeth on the maxilla and dentary are strongly heterodont in size, with teeth about one-third of the distance along the tooth row from the anterior end being longer than nearby teeth (Figs. 1C_2, 2D_2).

Frontals (Figs. 1D, E, 2J, K).—The two most nearly complete specimens are figured here: MNHN.MCM 190 (Figs. 1D, 2J) and MNHN.MCM 191 (Figs. 1E, 2K). The more nearly complete specimen, MNHN.MCM 190, lacks only the distal end of the left anterolateral process and the posterior end of the ventrolateral crests on both sides. The two halves are solidly fused medially. The specimen is 3.7 mm in midline length and 2.4 mm wide across the posterior edge, which yields a relative length (ratio of midline length:posterior width) of about 1.5. The internasal process is acuminate in dorsal or ventral outline and relatively broad, with the midline length subequal to the width across the base. The lateral face of the internasal process bears an elongate groove (Fig. 1D_3) for articulation with the medial edge of the nasal. The anterolateral process is distinct from the main body of the bone and is pointed distally. The more anterior slot between the internasal and anterolateral processes for receipt of the posterior end of the nasal and the more posterior slot between the anterolateral process and the orbital margin for receipt of the posterior end of the prefrontal are both deep. The dorsal margin of the latter slot is shallowly excavated medially. The anterior end of the orbital margin, as demarcated by the posterior end of the slot for receipt of the prefrontal, is approximately in line with the anteroposterior midpoint of the bone. MNHN.MCM 190 is vaguely bell-shaped in outline, with the posterior edge nearly two times wider than the distance between the slots for receipt of the prefrontals. Behind the base of the anterolateral process, the lateral edge of the bone first extends posteriorly in a straight line, then curves outwards in a shallow arc at about 25° from the midline. The posterior edge of the bone is transverse and shallowly concave to either side of the midline. Dorsally, the bone is ornamented with shallow, broad polygonal pits enclosed by a network of narrower, low ridges. In ventral view, the ventrolateral crest is relatively narrow—i.e., crest at the anterior limit of the orbital margin is about 0.4 times as wide as the

width across the posterior edge of the frontals, between the medial edges of the crest. The ventrolateral crest is somewhat convex ventrally in transverse profile, with the more lateral part along the orbital margin shallowly bevelled and facing ventrolaterally. Posteriorly the medial face of the ventrolateral crest is indented by a facet for receipt of a complementary process from the parietal. Although the ventrolateral crest is broken more posteriorly, this structure probably extended farther back to underlap the parietal, as in other albanerpetontids (e.g., Estes and Hoffstetter 1976: pl. 8: 2).

MNHN.MCM 191 (Figs. 1E, 2K) is a larger, but less nearly complete fused pair of frontals. Originally the specimen lacked only the distal ends of the internasal and left anterolateral processes, the posterior end of the left ventrolateral crest, and the right posterolateral corner (Fig. 2K). The specimen was broken during photography and some bone was lost from the median area (Fig. 1E). The specimen is 4.6 mm long in midline length and was probably 4.8 mm long or slightly longer when complete; the posterior width is estimated at about 3.0 mm. The estimated ratio of midline length:posterior width is 1.6, which compares favorably with MNHN.MCM 190. Based on the assumption that snout–pelvic length in albanerpetontids is about ten times the midline length of the frontals (Gardner 1999b), MNHN.MCM 191 suggests a snout–pelvic length of about 50 mm. In addition to being larger, MNHN.MCM 191 differs from MNHN.MCM 190 as follows: bone somewhat more triangular in dorsal or ventral outline; laterodorsal margins of internasal process straighter in dorsal or ventral outline (but with midline length of process remaining subequal to width across the base); lateral edge of bone more nearly concave along its entire length and extending laterally at a lesser angle of about 20° in dorsal or ventral outline; and ventral face of ventrolateral crest more bevelled. In other respects, MNHN.MCM 190 and 191 resemble one another.

Other elements.—An articular, 15 trunk vertebrae, three caudal vertebrae, and four humeri complete the inventory of albanerpetontid material from Anoual. These are typical for albanerpetontids and do not differ appreciably from homologous specimens reported from the Middle Jurassic (McGowan 1996), Lower Cretaceous (Estes and Sanchíz 1982; McGowan and Ensom 1997), and Miocene (Estes and Hoffstetter 1976) of Europe and from the Lower Cretaceous of North America (Gardner and Averianov 1998; Gardner 1999b).

Remarks.—Association of albanerpetontid specimens from Anoual within one species is supported by three lines of evidence. First, the provenance of the specimens is unique—no other albanerpetontids are known from Gondwana. Second, the specimens were collected from a single horizon at one locality. The fossiliferous lens at Anoual is restricted, with a depth of only about 20 cm and an areal extent of some 200 m^2 (Sigogneau-Russell et al. 1998). Third, there is no compelling morphological evidence that more than one taxon of albanerpetontid is represented. The maxillae and dentaries have two complementary attributes that justify their associa-

tion: occlusal margin of jaw convex and teeth strongly heterodont in size anteriorly. Comparisons with other albanerpetontids known by more extensive series of frontals and premaxillae, particularly species of *Albanerpeton* (see Gardner 2000a, b), suggest that differences among the Anoual premaxillae in relative build and proportions and among frontals in overall shape and in details of the internasal process, lateral edge of the bone, and transverse crest are within the expected limits of intraspecific variation for albanerpetontids.

Anoualerpeton priscus sp. nov.
Figs. 3, 4.

Albanerpeton Estes and Hoffstetter; Evans and Milner 1994: 306.
Celtedens megacephalus (Costa); McGowan 1996: 233, figs. 1–9, 11–13; McGowan 1998b: 116; McGowan 2002: 3.
Celtedens cf. *C. megacephalus* (Costa); McGowan and Ensom 1997: 117.
Celtedens cf. *megacephalus* (Costa); McGowan 1998a: fig. 1G.
Celtedens ibericus McGowan and Evans; McGowan 1998a: fig. 4.
Genus and species indeterminate; Gardner 2000a: 67, fig. 4.
Kirtlington albanerpetontid; Gardner 2000a: 68; Gardner 2002: 14.
Kirtlington species; Gardner 2002: 12.

Etymology: *Priscus*, Latin "ancient", referring to this being the oldest known, diagnosable albanerpetontid species.

Holotype: BMNH R.16336 (original number UCK 14), incomplete left premaxilla lacking dorsal end of pars dorsalis, lateral end of pars dentalis, and most of pars palatinum, with preserved tooth row containing nine broken tooth bases and empty tooth slots, one of which preserves an *in situ* replacement crown (Fig. 3A).

Holotype locality, horizon, and age: Kirtlington Cement Quarry, Oxfordshire, south-central England (Evans and Milner 1994: fig. 18.1); "Kirtlington Mammal Bed" *sensu* Freeman (1979), basal part of Forest Marble Formation. The lower part of the Forest Marble Formation is dated as Middle Jurassic (middle late Bathonian) based on correlation with the *Oppelia aspidoides* ammonite zone (see Metcalf et al. 1992: fig. 2). The Kirtlington Mammal Bed is interpreted as having been deposited under non-marine conditions in a swampy coastal region (Evans and Milner 1994). See Freeman (1979) and Evans and Milner (1994) for additional information.

Referred specimens.—All catalogued and uncatalogued specimens are in the collection of the BMNH. Specimens previously listed by McGowan (1996) each bore informal UCK catalogue numbers, which are indicated below in brackets following the permanent BMNH catalogue number. Premaxillae (n = 24) BMNH R.14157, R.16337 (UCK 15), R.16353 (UCK 17), and 21 uncatalogued; maxillae (n = 33): BMNH R.16338 (UCK 10), R.16339, R.16357 (UCK 05), R.16364, R.16365, and 28 uncatalogued; dentaries (n = 97): BMNH R.16340, R.16343 (UCK 01), R.16344 (UCK 03), R.16354 (UCK 06), R.16355 (UCK 02), R.16356 (UCK 08), R.16477, and 90 uncatalogued; frontals (n = 19): BMNH R.14158–14160, R.16342 (UCK 26), R.16345 (UCK 27), R.16351 (UCK 25), R.16352 (UCK 24), and 12 uncatalogued; parietals (n = 5): BMNH R.16346 (UCK 23) and four uncatalogued; quadrates (n = 17): BMNH R.16358 (UCK 33), R.16359 (UCK 34), and 15 uncatalogued; atlantes (n = 6): BMNH R.16341, R.16348 (UCK 18), R.16349 (UCK 21), R.16350 (UCK 20), and two uncatalogued; axes (n = 2) BMNH R.16347 (UCK 22) and one uncatalogued; trunk vertebrae (n = 14): BMNH R.16360 (UCK 28), R.16361 (UCK 29), R.16362 (UCK 31), and 11 uncatalogued; caudal vertebra (n = 1): BMNH R.16363 (UCK 32); and indeterminate pieces of dentition and unsorted material.

Distribution.—Known only from the holotype locality.

Diagnosis.—Species of *Anoualerpeton* differing from Early Cretaceous congener described above as follows: suprapalatal pit located more laterally in pars dorsalis of premaxilla, essentially within margin for external narial opening and in line with sixth or seventh tooth position from medial end of tooth row; dorsal opening of palatal foramen in premaxilla medial to base of suprapalatal pit; internasal process on frontals relatively more elongate (midline length about 1.2 times width across base) and blunt distally; anterolateral processes on frontals an indistinct shoulder, with distal end blunt; and ventrolateral crests on large frontals triangular in transverse view, with ventral face flat to shallowly concave.

Description.—The collection from Kirtlington contains substantial numbers of isolated jaws, frontals, parietals, quadrates, and vertebrae, none of which is complete. Examples of these elements previously were reported and figured by McGowan (1996) and, where known, generally resemble those of *Anoualerpeton unicus*. For these reasons, our descriptions below focus on taxonomically significant and otherwise notable features of the jaws, frontals, and atlas.

Premaxilla (McGowan 1996: fig. 1; Gardner 2000a: fig. 4d; here: Fig. 3A–C).—The most nearly complete specimens are the holotype BMNH R.16366 (Fig. 3A), BMNH R.16337 (Fig. 3B), and BMNH R.14157 (Fig. 3C); collectively these three specimens document much of the structure of the premaxilla. All premaxillae are isolated and none shows evidence of medial fusion. As no specimen at hand preserves the dorsal part of the pars dorsalis, nothing can be said about the relative proportions of the pars dorsalis, the pattern of contact dorsally with the nasal, or the nature of the dorsal boss. The pars dorsalis on the holotype preserves the base of the lateral notch for contact with the lacrimal. The suprapalatal pit resembles that in *Anoualerpeton unicus* in being similarly small and oval in outline, in lying above the level of the pars palatinum, and in opening laterolingually, but differs in being positioned farther laterally across the pars dorsalis, virtually within the external narial margin and in line with the sixth or seventh tooth position from the medial end of the row. The palatal foramen is relatively small, but in contrast to *An. unicus* the dorsal opening of this foramen lies medial to the base of the suprapalatal pit. The palatal foramen is free of sediment in BMNH R.14157 and a thread pushed into the dorsal opening (Fig. 3C$_2$) demonstrates that the canal descends ventromedially through the pars palatinum (Fig. 3C$_1$). The pars palatinum is lingually broad as in other albanerpetontids, with a prominent vomerine process medially and broad maxillary process laterally. The lingual face of both processes is indented by a shallow facet for contact with a
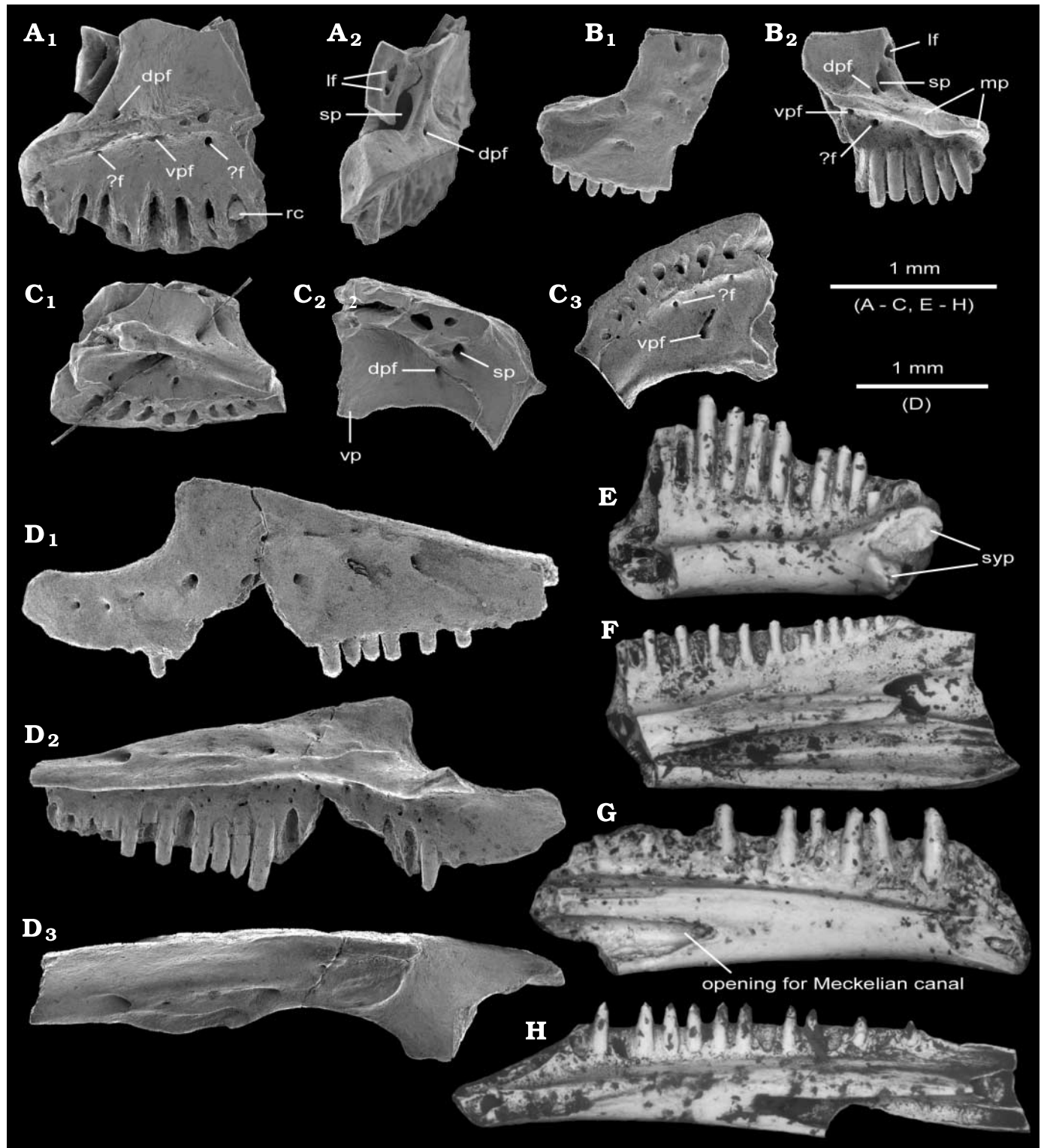
Fig. 3. Jaws of *Anoualerpeton priscus* sp. nov.; Middle Jurassic (late Bathonian), Kirtlington, England. **A–C**. Premaxillae. **A**. BMNH R.16336, holotype, left premaxilla, lacking dorsal part of pars dorsalis, lateral part of pars dentalis, and most of pars palatinum and preserving no intact teeth, in lingual (A_1) and laterolingual (A_2) views. **B**. BMNH R.16337, right premaxilla, lacking dorsal part of pars dorsalis and medial pars of pars palatinum and pars dentalis, in labial (B_1) and lingual (B_2) views. **C**. BMNH R.14157, right premaxilla, lacking dorsal part of pars dorsalis, ventral part of pars dentalis, and lateral end of maxillary process and preserving no intact teeth, in lingual (C_1) and dorsal (C_2) views, both with hair extending obliquely through palatal foramen, and in occlusal (C_3) view. **D**. BMNH R.16338, left maxilla, missing part of pars dentalis below nasal process and about posterior one-fifth of bone, in labial (D_1), lingual (D_2), and dorsal (D_3) views. **E–H**. Dentaries, all in lingual view. **E**. BMNH R.16344, left dentary, posteriorly incomplete ramus preserving about anterior one-quarter of bone. **F**. BMNH R.16354, right dentary, anteriorly and posteriorly incomplete ramus preserving posterior part of tooth row and anterior part of area for attachment of postdentary bones; **G**, BMNH R.16356, left dentary, anteriorly and posteriorly incomplete ramus preserving about (posterior

palatal bone, presumably the vomer. The lingual edge of the maxillary process dorsally bears a low ridge that, in life, held the lingual edge of the premaxillary dorsal process on the maxilla when the two jaws were articulated.

Maxilla (McGowan 1996: fig. 2; here: Fig. 3D).—The two most nearly complete specimens, BMNH R.16338 and R.16339, are from the left side and anatomically overlap for about a dozen tooth positions behind the posterior edge of the internal narial margin. The more nearly complete specimen, BMNH R.16338 (Fig. 3D), preserves most of about the anterior four-fifths of the bone, but lacks the leading edge of the premaxillary dorsal process and a large triangular piece from the pars dentalis below the nasal process. This specimen has been broken in two; the more posterior part was figured by McGowan (1996: fig. 2). Judging by the profile of the ventral edge of the bone immediately in front of and behind the missing section of the pars dentalis, the occlusal edge was ventrally convex in the missing region. This interpretation is supported by the convex dorsal edge on the referred dentaries (see below). BMNH R.16339 (unfigured) is broken anteriorly across the posterior limit of the internal narial margin and preserves about the posterior half of the bone with the last 16 tooth positions. Maxillae from Kirtlington resemble those of *Anoualerpeton unicus* as follows: labial ornament absent; similarly elongate premaxillary lateral process; anterior end of tooth row lies anterior to level of leading edge of nasal process; and, evidently, occlusal edge of pars dentalis ventrally convex in outline.

Dentary (McGowan 1996: figs. 7, 8; here: Fig. 3E–H).—The available dentaries are fragmentary and no specimen preserves more than about one-half of the bone. One of the most informative specimens is BMNH R.16344, which is the anterior end of a left dentary that preserves the first 11 tooth positions. Figured in labial view by McGowan (1996: fig. 8d) and here in lingual view (Fig. 3E), BMNH R.16344 shows that dentaries of *Anoualerpeton priscus* resemble those of *An. unicus* in having the occlusal edge of the anterior part of the bone strongly convex in labial or lingual outline. The other specimens figured here preserve more posterior areas of the dentary (Fig. 3F–H). As in most other albanerpetontids, including *An. unicus*, the labial face of the bone is unornamented and there is no dorsal process immediately behind the tooth row. In other respects, dentaries of *An. priscus* are typical for albanerpetontids.

Teeth (Figs. $3A_1$, B, D_1, D_2, E–H, 4A–E).—Intact teeth resemble those of other albanerpetontids and, particularly, *Anoualerpeton unicus* in arrangement, attachment, and structure. Although no jaw preserves an intact tooth row, tooth counts on the upper and lower jaws are probably similar to those in other albanerpetontids. Teeth on the dentary and, evidently, the

maxilla are heterodont in size anteriorly, to about the same extent as in *An. unicus*. On the dentary BMNH R.16344 (Fig. 3E) the teeth adjacent to the apex of the dental parapet are larger than the more anterior teeth and, presumably, the more posterior ones as well. Although the maxilla BMNH R.16338 is missing the critical region of the pars dentalis below the nasal process, judging by adjacent teeth and tooth slots, the teeth along the missing part of the tooth row were also enlarged. The form of the tooth crowns varies to an even greater extent than in *An. unicus*. Crowns range in labial or lingual outline from chisel-shaped (Fig. 4A), to wedge-shaped (Fig. 4B, C), to pointed (Fig. 4D). Differences in crown form are due to variation in the following attributes: length of central cuspule relative to mesial and distal cuspules (e.g., central cuspule moderately longer than mesial and distal cuspules on chisel-shaped crowns *versus* central cuspule markedly longer on pointed crowns); relative expression of distal and mesial cuspules (e.g., mesial and distal cuspules typically more strongly developed on chisel- and wedge-shaped crowns *versus* comparatively less well developed on pointed crowns); and mesio-distal width of crown relative to pedicel width (e.g., crown typically broader than pedicel in teeth with chisel- and wedge-shaped crowns *versus* crown typically narrower than pedicel in teeth with pointed crowns). As in *An. unicus*, tooth crowns tend to be more pointed or wedge-shaped along the anterior part of the maxilla and dentary, and more chisel-shaped posteriorly (Fig. 4E).

Frontals (McGowan 1996: figs. 3, 4; Gardner 2000a: fig. 4A–C; here: Fig. 4F–I).—Frontals are solidly fused medially, with occasional specimens retaining a faint median line of fusion ventrally. The two most nearly complete and informative specimens anatomically overlap one another in the area of the posterior slots for receipt of the prefrontals: BMNH R.14158 (Fig. 4F) is about the anterior one-third of a pair of large frontals, whereas BMNH R.16342 (Fig. 4G) is about the posterior two-thirds of a slightly smaller pair of frontals. Frontals of *Anoualerpeton priscus* resemble those of *An. unicus* in overall structure and proportions, but differ in the form of the internasal and anterolateral processes and the ventrolateral crest. BMNH R.14158 shows that the internasal process is relatively more elongate (midline length about 1.2 times width across base) and rounded distally and that the anterolateral processes are less pronounced and more rounded distally. BMNH R.14159 (Fig. 4H) and R.14160 (Fig. 4I) are less nearly complete examples of small and large frontals, respectively; these specimens show that with growth the ventrolateral crest changed from convex to more nearly triangular in transverse profile and the ventral face of the crest became shallowly concave dorsally. Some specimens at hand for *An. priscus* come from individuals slightly

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two-thirds of tooth row. **H**. BMNH R.16340, right dentary, anteriorly and posteriorly incomplete ramus preserving about posterior two-thirds of tooth row and anterior part of area for attachment of postdentary bones. Osteological abbreviations: dpf, dorsal opening of palatal foramen; lf, lateral foramen; mp, maxillary process on pars palatinum; rc, *in situ* replacement crown; sp, suprapalatal pit; syp, symphyseal process; vp, vomerine process on pars palatinum; vpf, ventral opening of palatal foramen; ?f, unknown foramen. Specimens at different scales.
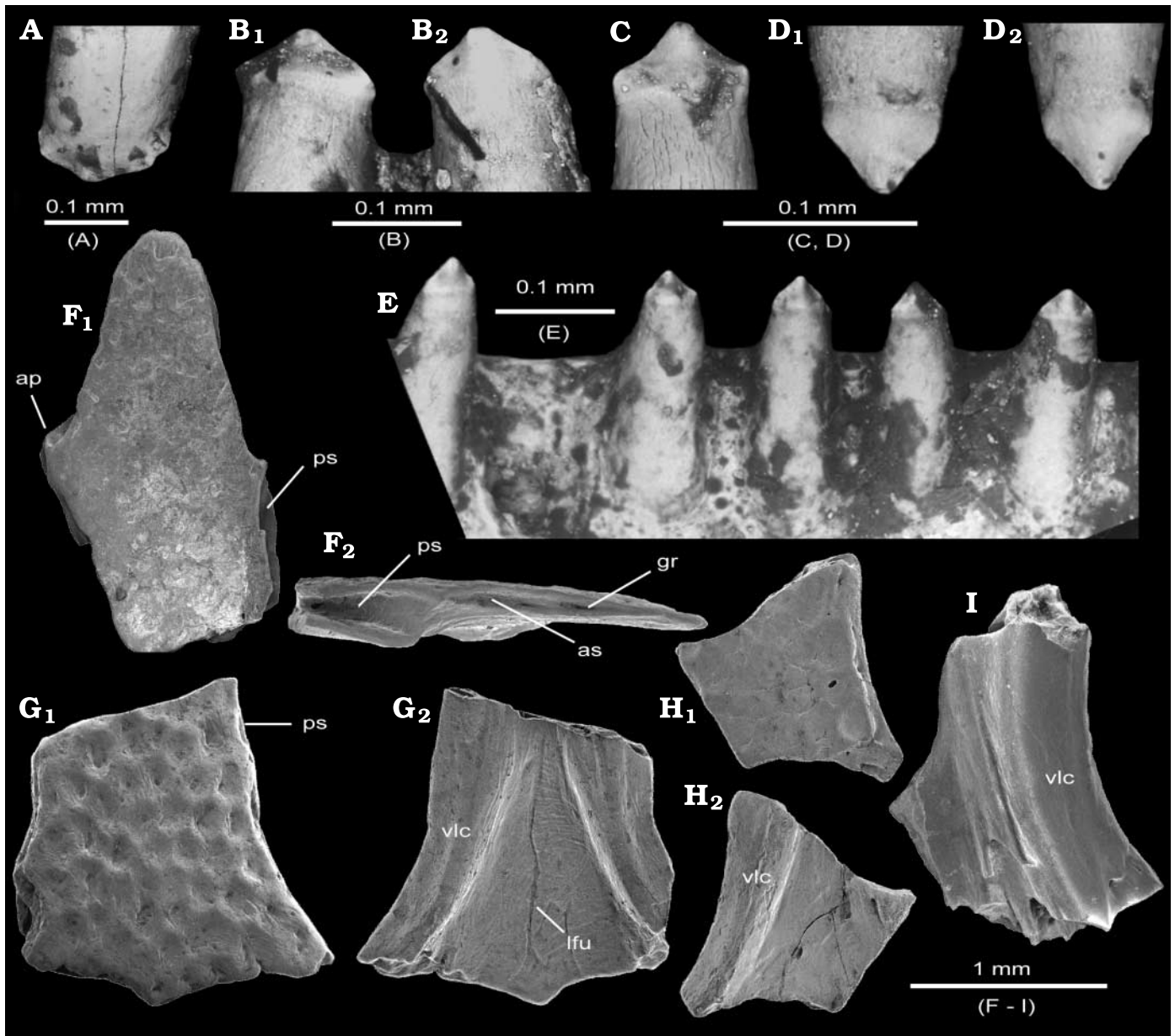
Fig. 4. Teeth and frontals of *Anoualerpeton priscus* sp. nov.; Middle Jurassic (late Bathonian), Kirtlington, England. **A–E**. Close ups of teeth, all in lingual view. **A**. BMNH R.16365, right maxilla, crown of tooth at second locus from broken anterior end of bone or, when tooth row was complete, about one-fifth of distance posteriorly along row. **B**. BMNH R.16356, left dentary, crowns of adjacent teeth at fourth (B_1) and fifth (B_2) loci from broken anterior end of bone or, when tooth row was complete, about three-fifths of distance posteriorly along row. **C**. BMNH R.16477, right dentary, crown of tooth at eighth locus from broken anterior end of bone or, when tooth row was complete, about one-half of distance posteriorly along row. **D**. BMNH R.16357, right maxilla, crowns of teeth at seventh (D_1) and ninth (D_2) loci from broken anterior end of bone or, when tooth row was complete, about one-third of distance posteriorly along row. **E**. BMNH R.16340, right dentary, row of five teeth and one empty tooth slot, extending from second to seventh loci from broken anterior end of bone or, when tooth row was complete, about three-fifths of distance posteriorly along row. **F–I**. Frontals. **F**. BMNH R.14158, anterior one-third of fused frontals, broken posteriorly between slots for receipt of prefrontals, in dorsal (F_1) and right lateral (F_2) views. **G**. BMNH R.16342, posterior two-thirds of fused frontals, broken anteriorly between slots for receipt of prefrontals and missing posterior end of ventrolateral crests on both sides, in dorsal (G_1) and ventral (G_2) views. **H**. BMNH R.14159, posterior part of small, fused frontals, broken anteriorly between slot for receipt of prefrontals on right side and midway along orbital margin on left side and missing left posterior corner, in dorsal (H_1) and ventral (H_2) views. **I**. BMNH R.14160, fragment of large, left frontal, preserving orbital margin, in ventral view. Osteological abbreviations: ap, anterolateral process; as, anterior slot; gr, groove; lfu, line of fusion; ps, posterior slot; vlc, ventrolateral crest. Specimens at different scales.

larger than those represented for *An. unicus* and give an estimated snout–pelvic length of about 50 mm for the former species.

Other elements (McGowan 1996: figs. 5, 6, 9, 11–13).— Other albanerpetontid elements from Kirtlington include parietals, quadrates, and vertebrae. In general these elements

are similar to those described elsewhere for albanerpetontids, with one notable exception. Each of the six atlantal centra from Kirtlington bears a transverse groove on either side of the centrum, above and behind the anterior cotyle; in life, this groove carried the first spinal nerve. Although the walls of the arch are broken behind the groove in all specimens, the smooth dorsal surface along the anterior rim of the groove indicates that the groove was open dorsally and that no bony bridge extended dorsoposteriorly over the groove to create an enclosed foramen. Atlantes are not known for *Anoualerpeton unicus*, but an open groove for the first spinal nerve also has been noted in undescribed, basal Cretaceous atlantes of *Celtedens* sp. from Purbeck, England (S.E. Evans, unpublished observation). In all other albanerpetontid atlantes for which the path of the spinal nerve has been documented, the spinal foramen is completely enclosed within the base of the wall of the neural arch. These latter specimens are from the Cretaceous of North America and Miocene of France, and most can be attributed with confidence to *Albanerpeton* (Estes and Hoffstetter 1976; Fox and Naylor 1982; Gardner 1999a–c, 2000b). The above observations suggest that the form of the spinal foramen in the atlas may vary at the generic level among albanerpetontids.

Remarks.—Association of albanerpetontid skull and postcranial elements from Kirtlington within one species is justified because there are no significant morphological differences among homologous elements recovered from the site (McGowan 1996; Gardner 2000a). The only exception involves the degree of dorsal ornament on the frontals. Most frontals exhibit the usual albanerpetontid pattern of polygonal pits enclosed by low ridges. BMNH R.14158 is notable because the dorsal surface is virtually smooth (cf., Fig. 4F$_1$ versus G$_1$); this condition does not appear to be due to postmortem abrasion or erosion. Similar variation has been documented in some other albanerpetontid species for which adequate series of frontals are available (e.g., *Albanerpeton nexuosus*; Gardner 2000b: fig. 6A, C). Although the source of variation in frontal ornament is uncertain, it does not appear to be taxonomically significant (Gardner 2000b). Specimens from Kirtlington show considerable size variation, with the largest two or three times the size of the smallest, but morphological differences among homologous specimens (e.g., form of ventrolateral crest on frontals; cf., Fig. 4G$_2$, H$_2$, I) are within the expected range of individual and ontogenetic variation within a single species.

Three localities in the Forest Marble Formation collectively have yielded the second oldest occurrences of albanerpetontids from anywhere in the world. Besides the Kirtlington Cement Quarry, fragmentary albanerpetontid elements have been reported from the formation at Tarlton Clay Pit in Gloucestershire and at Watton in Dorset, both in England (Evans and Milner 1994: table 18.2). Specimens from the last two localities are too incomplete to be identified to species or genus. Evans and Milner (1994: table 18.2) questionably listed albanerpetontids at the slightly older (early Bathonian) Hornsleasow Quarry, in the Chipping Norton Limestone For-

mation of Gloucestershire, but no mention of albanerpetontids appeared in subsequent, more detailed accounts of the locality and its assemblage (Metcalf et al. 1992; Metcalf and Walker 1994). An undescribed axis has since been identified that confirms the presence of albanerpetontids at Hornsleasow Quarry (S.E. Evans, unpublished observation). The only reliable record of similar antiquity for the Albanerpetontidae is an atlantal centrum (Seiffert 1969; Estes and Hoffstetter 1976) from the Gardies locality, southern France. Gardies originally was considered to be late Bajocian in age (Seiffert 1969), but more recent work has revised the age estimate upwards to early Bathonian (Kriwet et al. 1997 and references therein). Nessov (1988) reported an albanerpetontid frontal from the upper Middle Jurassic (Callovian) of Kirghizia, but this record is unproven (Gardner and Averianov 1998). Elsewhere in the Jurassic, albanerpetontids are known by isolated and largely undescribed elements, including frontals that have been referred to *Celtedens* (McGowan 1998a, 2002; however, see Wiechmann 2000), from two Upper Jurassic (Kimmeridgian) localities in Portugal—Guimarota (Estes 1981; McGowan 1998a; Wiechmann 2000) and Porto Pinheiro (Estes 1981).

Discussion

One of us (Gardner 2002) recently examined monophyly and intrageneric relationships of *Albanerpeton*, using 16 informative characters scored for the seven recognized species of *Albanerpeton* and with *Celtedens*, *Anoualerpeton unicus* (= "Anoual species"), and *Anoualerpeton priscus* (= "Kirtlington species") as separate outgroups. In that analysis, relationships within *Albanerpeton* were almost completely resolved, with the only lack of resolution being a trichotomy among the three gracile-snouted species. Relationships among *Albanerpeton* and the three outgroups were left as an unresolved polychotomy.

Our expanded and slightly modified analysis (see Appendix for details) yields three equally parsimonious trees that corroborate the sister-pair relationship between the two species of *Anoualerpeton* and resolve relationships among the three albanerpetontid genera. Fig. 5 depicts the strict consensus of the three shortest trees, in which *Anoualerpeton* is identified as the most basal genus and the sister-taxon of the less inclusive clade of *Celtedens* + *Albanerpeton*. Indices of support for allying the two species of *Anoualerpeton* and for allying *Celtedens* + *Albanerpeton* are moderately strong (Table 1), with both sister-pairs having bootstrap values over 80% and decay values of two steps, despite the fact that both sister-pair relationships rely on few apomorphies. Monophyly of *Anoualerpeton* is founded on two apomorphies that converge with *Albanerpeton nexuosus*—18(1), occlusal edge of maxilla and dentary convex in occlusal view, and 19(1), maxillary and dentary teeth heterodont in size anteriorly. The hypothesized sister-pair relationship between *Celtedens* and *Albanerpeton* relies on one or, perhaps, two premaxillary synapomorphies. The ACCTRAN and DELTRAN character state optimizations

Table 1. Bootstrap and decay values for less inclusive clades within the Albanerpetontidae in branch-and-bound searches for trees up to four steps longer than the minimum of 32 steps. Strict consensus of the three shortest trees is shown in Fig. 5.

Clade	Bootstrap value (percent for 2000 runs)	Percentage of trees recovering clade				
		min 32 steps (3 trees)	min +1 33 steps (15 trees)	min +2 34 steps (36 trees)	min + 3 35 steps (142 trees)	min + 4 36 steps (292 trees)
Anoualerpeton	82	100	100	83	77	68
Celtedens + Albanerpeton	85	100	100	92	85	76
Albanerpeton	81	100	100	83	80	74
post-middle Albian clade	80	100	100	83	68	55
gracile-snouted clade	62	100	20	67	32	41
robust-snouted clade	94	100	100	100	100	99
Tertiary clade	96	100	100	100	89	90

both identify a lingually opening suprapalatal pit [26(1)] as synapomorphic for the clade. ACCTRAN regards a vertical canal connecting the dorsal and ventral openings of the palatal foramen [27(1)] as an additional synapomorphy for *Celtedens + Albanerpeton*, but this arrangement is uncertain because the condition cannot be scored in premaxillae available to us for *Celtedens*. The more conservative DELTRAN arrangement restricts this apomorphy to the next less inclusive node for *Albanerpeton*. Inferred relationships within *Albanerpeton* remain unchanged from Gardner's (2002) analysis. Relationships within *Celtedens* cannot be assessed until the diversity and osteology of the constituent species are better understood. At present only two species of *Celtedens* are recognized (McGowan and Evans 1995; McGowan 2002) and our knowledge of their osteology remains incomplete.

Any attempt to assess the evolutionary history of the Albanerpetontidae in a temporal or geographical context is complicated by the group's sparse fossil record and the suspicion that a substantial gap of at least 80 million years, according to the time scale of Gradstein et al. (1995), separates the clade's inferred origin at, or before, the Permo–Triassic boundary (Milner 1994; Gardner and Averianov 1998) and the oldest fossil records in the early Bathonian of France (Seiffert 1969) and England (Evans and Milner 1994). The oldest confirmed occurrences of albanerpetontids on other continents are younger still: Berriasian of Africa (this study), Aptian/Albian of North America (Gardner 1999b), and Cenomanian of Asia (Gardner and Averianov 1998). Our phylogenetic analysis provides minimum estimated ages of late Bathonian for the origin of *Anoualerpeton*, based on the age of *An. priscus*, and perhaps Kimmeridgian for the split between *Celtedens* and *Albanerpeton*. The latter age estimate is based on McGowan's (1998a) belief that frontals from Guimarota, Portugal, are diagnostic for *Celtedens*; this identification may change once M. F. Wiechmann has completed his study of the Guimarota albanerpetontid material (see Wiechmann 2000). The first unequivocal occurrence of *Celtedens* is some 10 million years younger, according to Gradstein et al.'s (1995) time scale, at the lowermost Cretaceous (Berriasian) Purbeck locality in England (Gardner

2002; Evans and McGowan 2002). Depending on which first occurrence for *Celtedens* is favored, the estimated split between *Celtedens* and *Albanerpeton* is about 15 or 25 million years after the inferred origin of *Anoualerpeton*. These estimates imply, in turn, that about the first 30 to 40 million years of the history of *Albanerpeton*—which is first known from the latest Aptian or earliest Albian of Oklahoma, USA (Gardner 1999b)—remains undocumented.

A relationship between albanerpetontids and the enigmatic long-bodied amphibian *Ramonellus longispinus* Nevo and Estes, 1969 from the Lower Cretaceous (late Aptian; Krassilov and Dobruskina 1995 and references therein) Hatira Formation of south-central Israel has been suggested by several authors. Estes (1981) allied *Ramonellus* with *Albanerpeton* and *Prosiren* Goin and Auffenberg, 1958 (early–middle Albian, Texas, USA) in the caudate family Prosirenidae Estes, 1969, and implied a close relationship between *Albanerpeton* and *Ramonellus* based on features of the humerus and post-atlantal vertebrae. In their pivotal contribution on the affinities of *Albanerpeton*, Fox and Naylor (1982) transferred *Albanerpeton* to a new family and new order distinct from caudates, and questionably retained *Ramonellus* with *Prosiren* in the Prosirenidae. Most recently, Milner (2000: 1440) remarked "it is possible that *Ramonellus* was a long-skulled, long-bodied albanerpetontid." *Ramonellus* is known from 16 articulated skeletons but, as is evident from Nevo and Estes's (1969) published description and figures, the material is not well preserved and is difficult to interpret. The resemblances that Estes (1981: 18) noted between *Ramonellus* and *Albanerpeton*—and by extension all other albanerpetontids—in the structure of the humerus are probably primitive for lissamphibians as a whole, if not at an even more inclusive level. Resemblances listed by Estes (1981: 25) in vertebral structure between the two genera may be more valid, as Milner (2000) noted, but need to be weighed against the fact that details of post-atlantal vertebral structure are not well documented in either *Ramonellus* or albanerpetontids.

Although the published skeletons of *Ramonellus* are too poorly preserved to evaluate whether the taxon possesses the full suite of diagnostic albanerpetontid features, informative
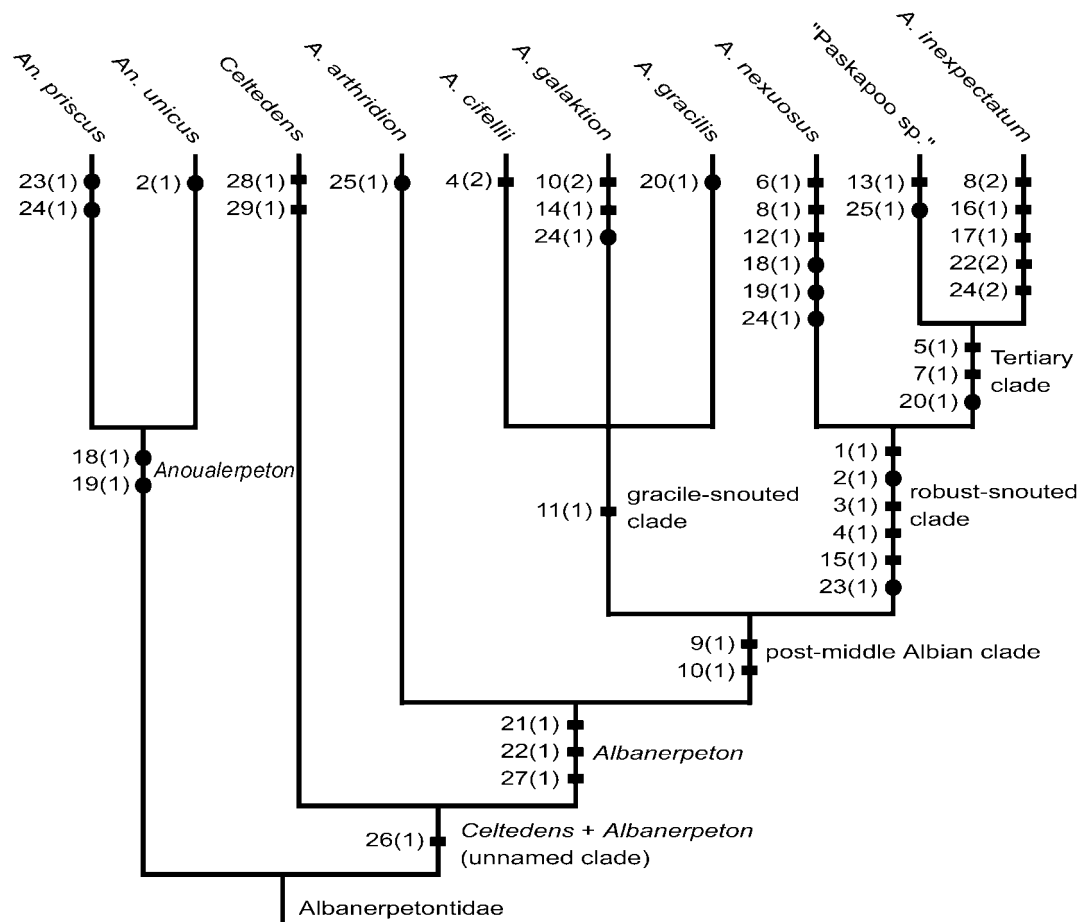
Fig. 5. Strict consensus of three shortest trees, based on branch-and-bound search of 20 informative characters scored for 10 albanerpetontid taxa and a hypothetical "all zero" ancestor (see Appendix). Indices of support for less inclusive clades are reported in Table 1. Distribution of apomorphies for all 29 characters are depicted according to the more conservative and preferred DELTRAN character state optimization. Distribution of apomorphies within the gracile-snouted clade is based on one of the three shortest trees that has the same topology for this clade as the strict consensus tree. The ACCTRAN optimization differs in shifting four derived character states one node down towards the stem, as follows: 2(1) to the node for *Anoualerpeton*; 6(1) to the node for the robust-snouted clade; 22(2) to the node for the unnamed Tertiary clade; and 27(1) to the node for *Celtedens + Albanerpeton*. Symbols for apomorphies are: horizontal bar, synapomorphic or autapomorphic; circle, convergent. Tree statistics (uninformative characters excluded): tree length = 32 steps; CI = 0.750; HI = 0.250; and RI = 0.826.

details of the skull–mandible joint, vertebrae, and limbs can be seen. Albanerpetontids are unique among temnospondyls in having a nearly vertical articular–quadrate joint (Fox and Naylor 1982; Milner 1988; Gardner 2001). The mandible of *Ramonellus* (Nevo and Estes 1969: figs. 2B, 3B, 4D) differs from albanerpetontids in primitively retaining a more nearly horizontal articular–quadrate joint. The mandible of *Ramonellus* differs further from albanerpetontids and resembles that of caudates in two derived character states—a posteriorly elongate retroarticular process (variably developed in caudates *versus* absent in albanerpetontids) and a convex articular that fits into a concave quadrate (synapomorphy of caudates and salientians [Gardner 2001] *versus* opposite arrangement in albanerpetontids). The latter derived character state and the presence of double-headed rib bearers on trunk vertebrae (single in albanerpetontids) are evidence that *Ramonellus* is a caudate. *Ramonellus* differs further from albanerpetontids in another two character states that are de-

rived among temnospondyls: forelimbs reduced and hindlimbs perhaps absent (*versus* fore- and hindlimbs unreduced and of approximately equal size in albanerpetontids) and an elongate trunk having at least 35 presacral vertebrae (*versus* shorter trunk with 22 presacrals in albanerpetontids). In short, *Ramonellus* differs from unequivocal albanerpetontids in a combination of primitive and derived character states of the jaws, limbs, and vertebrae. The only resemblances between *Ramonellus* and albanerpetontids are generalized, primitive character states such as the structure of the humerus, presence of a tail, and amphicoelous vertebrae. Retention of *Ramonellus* within the Caudata leaves *Anoualerpeton unicus* as the only confirmed Gondwanan albanerpetontid.

The identification of congeneric albanerpetontids in the Middle Jurassic of England and in the basal Cretaceous of northern Africa raises interesting biogeographic questions. The age estimate of Berriasian for the fossiliferous lens at

Anoual indicates that albanerpetontids were established in Africa at least by that time. Considering the sparse pre-Cretaceous record for small, non-marine vertebrates in Africa (see review by Sigogneau-Russell et al. 1998), the Anoual record probably underestimates the first appearance of albanerpetontids on the continent. How albanerpetontids became established in Africa is unknown. They may already have been in place on the proto-African continent before the opening of the Tethys Seaway in the Late Jurassic (Rage 1995) separated Africa from Eurasia. Alternatively, or in addition, albanerpetontids may have immigrated from Europe, perhaps more than once, across land bridges that intermittently connected the two continents (Rage 1988, 1995). *Anoualerpeton unicus* is most closely related to the European species *An. priscus* and, aside from subtle morphological differences, the former species is not substantially different from Laurasian albanerpetontids. As such, *An. unicus* provides no evidence for a distinctive Gondwanan radiation of albanerpetontids, as has been suggested for Cretaceous caudates (Rage 1997; however, see Evans et al. 1996).

Conclusions

- Fossil specimens reported herein permit the recognition of a third albanerpetontid genus, *Anoualerpeton*, which differs from the other two accepted albanerpetontid genera, *Albanerpeton* and *Celtedens*, in a unique combination of primitive and derived character states of the jaws and frontals. *Anoualerpeton* contains two new species that are differentiated by primitive and derived character states of the premaxilla and frontals: the type species *An. unicus* is from the basal Cretaceous (Berriasian) of Morocco, whereas *An. priscus* is from the Middle Jurassic (late Bathonian) of England.

- A cladistic analysis based on 20 informative characters scored for ten albanerpetontid taxa places *Anoualerpeton unicus* and *An. priscus* as sister-taxa within a monophyletic *Anoualerpeton*. Inter-generic relationships are fully resolved in the analysis, with *Anoualerpeton* as the sister-taxon to a less inclusive clade comprised of *Celtedens + Albanerpeton*. This arrangement yields minimum estimated ages of late Bathonian for the origin of *Anoualerpeton* and either Kimmeridgian or Berriasian for the split between *Celtedens* and *Albanerpeton*. Work in progress on Kimmeridgian and Barremian albanerpetontids from the Iberian Peninsula promises to be important for testing the phylogeny and divergence times proposed in our study.

- *Anoualerpeton unicus* is the only unequivocal record for the Albanerpetontidae in Gondwana and provides a minimum age of earliest Cretaceous for the establishment of albanerpetontids in Africa. There are two scenarios, neither of which is mutually exclusive, for how and when albanerpetontids became established in northern Africa by the earliest Cretaceous: they were already on the proto-African continent before the opening of the Tethys Seaway in the Late Jurassic separated Africa from Eurasia or they immigrated from Europe, perhaps more than once, across land bridges that intermittently connected the two continents across the Tethys Seaway.

- Although *Ramonellus longispinus* from the Early Cretaceous (Aptian) of Israel has often been allied with albanerpetontids, the genus lacks the vertical articular–quadrate joint that is unique to albanerpetontids. Other character states of the mandible, vertebrae, and limbs indicate that *Ramonellus* is probably a caudate, but we can offer no further suggestions about its relationships with other salamanders.

Acknowledgements

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Appendix

Phylogenetic analysis, character descriptions, and data matrix

General information.—Analysis expanded from Gardner (2002). Analysis here relies on 20 informative characters (16 binary and four multistate) scored for ten albanerpetontid terminal taxa and a hypothetical "all zero" ancestor used to root the tree (see "Data Matrix", below). A further nine characters (6, 8, 12–14, 16, 17, 28, and 29; eight binary and one multistate) are uninformative for assessing relationships and were excluded from searches, but are mapped onto the strict consensus tree (Fig. 5). PAUP 3.1.1 (Swofford 1993) was used in all searches and to compute the strict consensus tree and tree statistics. Searches were run using the branch-and-bound algorithm. All characters were run unweighted and most were run unordered, except for characters 10 and 22; running these characters as unordered did not affect the topologies of the shortest trees. Monophyly of *Celtedens* is assumed based on derived character states of the frontals (Gardner 2000a); character scores for this genus are composites based on skeletons of *C. megacephalus* and *C. ibericus* and on isolated elements of an indeterminate congener from Purbeck, England (see Gardner 2002).

Character descriptions.—Characters 1–25 were described in more detail by Gardner (2002); characters 26 and 27 are new; and characters 28 and 29 were discussed by Gardner (2000a). Anatomical breakdown of characters is as follows: premaxilla (n = 16), characters 1–14, 26, and 27; maxilla and dentary (n = 6), characters 15–20; frontals (n = 6), characters 21–24, 28, 29; and body size (n = 1), character 25.

1. Build of premaxilla: 0, gracile; 1, robust.

2. Ratio of height of premaxillary pars dorsalis *versus* width of pars dorsalis across suprapalatal pit: 0, "high", ratio greater than about 1.55; 1, "low", ratio less than about 1.55.

3. Inter-premaxillary contact: 0, sutured medially (i.e., paired); 1, fused medially in some individuals.

4. 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 braced ventrolaterally by expanded dorsal end of lateral internal strut.

5. Boss on premaxilla: 0, present; 1, absent.

6. Relative size of premaxillary boss, if present: 0, covers about dorsal one-quarter to one-third of pars dorsalis; 1, covers about dorsal one-half of pars dorsalis.

7. Distribution of labial ornament on large premaxillae: 0, restricted to dorsal part of pars dorsalis; 1, covers entire face of pars dorsalis.

8. Pattern of premaxillary labial ornament: 0, discontinuous, anastomosing ridges and irregular pits; 1, continuous ridges defining polygonal pits; 2, pustulate.

9. Vertical position of suprapalatal pit on pars dorsalis: 0, "high", with ventral edge of pit well above dorsal face of pars palatinum; 1, "low", with ventral edge of pit just above or, more typically, continuous with dorsal face of pars palatinum.

10. Size of suprapalatal pit relative to lingual surface area of pars dorsalis: 0, "small", about 1%; 1, "moderate", about 4–15%; 2, "large", about 20–25%.

11. Outline of suprapalatal pit: 0, oval; 1, triangular or slit-like.

12. Form of dorsal process on lingual edge of maxillary process: 0, low, isolated ridge; 1, high flange, continuous labially with base of lateral internal strut.

13. Form of vomerine process on premaxilla: 0, prominent; 1, weak.

14. Diameter of palatal foramen in premaxilla relative to diameter of base of medial teeth on bone: 0, "small", foramen diameter tooth diameter; 1, "large", foramen diameter > about one and one-third tooth diameter.

15. Length of premaxillary lateral process on maxilla relative to height of process at base: 0, "long", length > height; 1, "short", length height.

16. Dorsal process behind dentary tooth row: 0, absent; 1, present.

17. Labial ornament on large maxilla and dentary: 0, absent; 1, present.

18. Labial or lingual profile of occlusal margin of maxilla and dentary: 0, essentially straight; 1, strongly convex or angular, with apex adjacent to tallest teeth.

19. Size heterodonty of teeth on maxilla and dentary: 0, weakly heterodont anteriorly; 1, strongly heterodont anteriorly.

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.

21. Dorsal or ventral outline of fused frontals: 0, approximately rectangular- or bell-shaped; 1, approximately triangular.

22. Ratio of midline length of fused frontals *versus* width across posterior edge of bone, between lateral edges of ventrolateral crests, in large specimens: 0, "long", ratio more than about 1.2; 1, "moderate", ratio between about 1.2 and 1.1; 2, "short", ratio equal to or less than about 1.0.

23. Proportions of internasal process on frontals: 0, "short", length approximately equal to width; 1, "long", length > width.

24. Form of ventrolateral crest on large frontals: 0, narrow and convex ventrally to bevelled ventrolaterally in transverse view; 1, narrow and triangular in transverse view, with ventral face flat to shallowly concave; 2, wide and triangular in transverse view, with ventral face deeply concave.
25. Estimated maximum snout–pelvic length: 0, "large", > about 50 mm; 1, "small", < about 45 mm.
26. Direction faced by suprapalatal pit in pars dorsalis of premaxilla: (0) laterolingually; (1) lingually.

27. Path followed by canal through pars palatinum in premaxilla, between dorsal and ventral openings of palatal foramen: (0) dorso-laterally–ventromedially; (1) vertically.
28. Frontal–nasal contact: (0) groove along lateral face of internasal process on frontals receives medial edge of nasal; (1) internasal process dorsally overlaps onto medial edge of nasal.
29. Dorsal or ventral outline of internasal process on frontals: (0) tapered anteriorly; (1) bulbous.

Data matrix.—Matrix expanded from Gardner (2002: table 1) by addition of characters 26–29. Symbols: ?, unknown; 9, inapplicable. The "Paskapoo species" is an undescribed species of *Albanerpeton* from the Paleocene of Alberta, Canada.

	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345	2222 6789	percent missing
Ancestor	00000	00000	00000	00000	00000	0000	0
Anoualerpeton priscus sp. nov.	0?0??	?0?00	00000	00110	00110	0000	17
Anoualerpeton unicus sp. nov.	01000	00000	00?00	??110	00000	0000	10
Celtedens	000??	?0?00	0????	0000?	00000	1?11	34
Albanerpeton arthridion	00000	00000	0000?	00000	11001	1100	03
Albanerpeton gracilis	00000	00011	10000	00001	11000	1100	0
Albanerpeton galaktion	00000	00012	10010	?0000	11010	1100	03
Albanerpeton cifellii	00020	00011	1000?	?????	?????	11??	45
Albanerpeton nexuosus	11110	10111	01001	00110	11110	1100	0
Albanerpeton inexpectatum	11111	91211	00001	11001	12120	1100	03
Paskapoo species	11111	91011	00101	00001	1?101	1100	07